A network model of cortical surround suppression

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Read the general instructions carefully before starting the mini-project.

Introduction

Cortical networks in the brain perform a diverse range of computations, from sensory perception and processing to working memory and attention. In which dynamical regimes do cortical networks operate during these computations? In this project, we will explore this question for a phenomenon called *surround suppression* [1]: a seemingly paradoxical reduction in both excitatory and inhibitory neural responses to a visual stimulus when a similar neighboring stimulus is present (Fig. 1). This effect is observed in most visual and other sensory processing brain areas. It makes visual perception more efficient by implementing a sparse and metabolically efficient representation of the stimulus and allows for advanced visual processing such as contour or motion detection and continuous object recognition despite changes in lighting, color, or size. For this reason, the surround suppression mechanism is also being used in several computer vision algorithms [2, 3]. In the process of building your surround suppression model, you will also learn how to model neural populations as networks of firing rate neurons (*rate networks*) and explore the dynamics that arise from different kinds of inhibition in rate networks with excitation-inhibition balance.

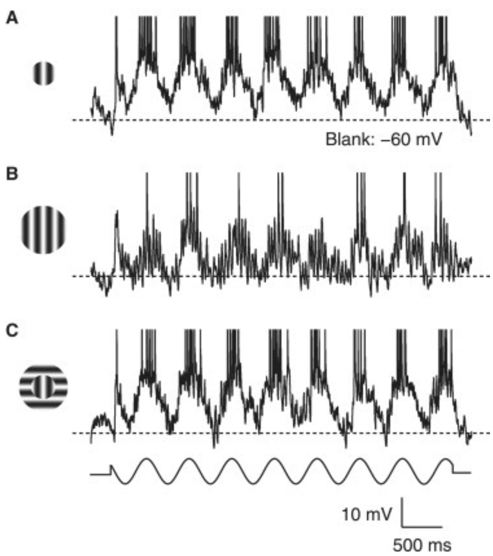

Figure 1: Surround suppression in the visual cortex. Image source: Ozeki et al. [1]

0 Rate models of neuronal populations

So far, you have mostly worked with (networks of) spiking neurons. Another way to model single neurons as well as neural populations is through so-called *rate models*. In rate models of neural populations (*population rate models*), the population activity or firing rate of a neural population is described by a single variable r. This firing rate r increases due to recurrent and external inputs to the population and decays exponentially in between:

$$\tau \frac{dr}{dt} = -r + f(I(t)), \tag{1}$$

where f is a (potentially nonlinear) gain function,τ is the time constant of the population activity and $I(t) = I_{rec}(t)+I_{ext}(t)$ is the sum of external and recurrent inputs. The rate model equations can be derived directly from spiking equations, based on the phenomenon that in a steady state, the population activity in homogeneous neural populations can be computed by the gain function and membrane potential of single neurons in that population. It is possible to extend this description to transient dynamics of the population activity outside of steady states (see Chapter 15 of the Neuronal Dynamics book for a detailed explanation of this argument). Despite being a minimalist model, rate models can be very useful in modeling the behaviours of neuronal populations in the brain, such as surround suppression in the visual cortex. But before we start modeling the dynamics of biological neuronal populations, let us first explore a few properties of our modeling framework.

1 Fixed vs. recurrent inhibition

1.1 Excitatory population with self-coupling

We can connect one or multiple population rate populations into networks (see Chapter 15.3.2 for details). As a first example, let us consider a network consisting of a single excitatory neural population with excitatory self-coupling, i.e. with excitatory recurrent connections to itself. The excitatory population also receives a constant external input.

1.1.1 Write down the equations that describe a single excitatory population with positive self-coupling as a rate network. Where exactly does the self-coupling appear?

1.1.2 Write code to simulate your rate neuron network equations numerically. Set the parameter for self-coupling $w_{EE} = 2$ and the population time constant $\tau_E = 0.60s$ and use a tanh nonlinearity for f. Simulate your recurrently connected E population with constant external input i_E. Vary i_E between -5 and 5 and plot the dynamics of the firing rate for each input current value. What do negative/positive/zero current inputs and firing rates of the E population correspond to, respectively? Give a biological interpretation.

1.1.3 Which steady-state dynamics do you observe for the different input currents? How do the steady state firing rates change if you present short delta pulses with different total current after the system has settled into its steady state? Include one representative example for each regime in your report and give a biological and a mathematical explanation for what happens.

1.1.4 How does the range of input currents that generate each dynamics change if you increase/decrease the coupling strength?

Close to a fixed point, we can approximate the rate model equation Eq. (1) by a linear equation:

$$\tau \frac{dr}{dt} = -r + I(t), \tag{2}$$

where $I(t)$ is the sum of recurrent and external inputs into the population as above.

1.1.5 Implement a linear rate network and repeat your experiments from 1.1.1 - 1.1.4. What differences do you observe between the linear and the nonlinear rate network?

1.1.6 Plot the rate after 2 seconds simulation as a function of the input current for both of your networks. Describe the shapes that emerge for the different networks. How do they compare for the case of stable and unstable network dynamics, respectively?

1.2 Inhibition-stabilized network (ISN)

In the previous exercise, you have analyzed the stability of an excitatory population with self-coupling for different strengths of self-excitation and excitatory or inhibitory input. Let us now consider a network where inhibition to our self-coupled excitatory population is not provided as a fixed inhibitory input, but as the feedback from an inhibitory neuronal population. Like the excitatory population, the inhibitory population is coupled to itself (but its recurrent input is negative, since it emerges from an inhibitory population). The excitatory (E) and the inhibitory (I) population are connected to each other, i.e. the E sends inputs to I through weights w_{IE} and I sends inputs to E through weights w_{EI}. Both E and I receive a constant external input, i_E and i_I, respectively.

1.2.1 Write down the extended population equation for the linear E-I network, analogously to Eq. (1), and adapt your simulation code. Set $w_{EI} = 4$, $w_{II} = 7$, $\tau_E = 0.06$ and $\tau_I = 0.012$. Choose one value of w_{EE} that produces stable and and one that produces unstable dynamics in the linear E population (based on your results from Exercise 1.1). If you use each of these w_{EE} values in your E-I network, how do you need to choose w_{IE} so that your network is stable? Numerically determine at least one w_{IE} for each w_{EE} for which the network is stable and unstable (exploding). Can you formulate a condition for w_{EE} and w_{IE} that assures that the network is stable (for the given values of w_{EE}?

1.2.2 For the stable network regimes, plot the dynamics of the firing rates over time and the rate after 2 sec simulation as a function of the input current to the E population. How do the rate dynamics and the 'f-I' curve of the E-I network differ from the ones of the (linear) E population with self-coupling in Exercise 1.1 for strong and weak excitatory self-coupling?

1.2.3 Explain the role of the inhibitory population for the case of strong and weak excitatory self-coupling.

The networks with strong excitatory self-coupling and stable network dynamics you identified here are also called *inhibition-stabilized networks (ISN)*. In the next section, we will use them to simulate surround suppression.

2 Modeling surround suppression

2.1 Network mechanisms of surround suppression

Surround suppression is a phenomenon that appears in the visual cortex: When we show a visual stimulus in the center of a given neuron's receptive field (RF), this neuron will show its normal response (Fig. 1 A). But as soon as we add a visual stimulus in the surrounding area of the RF center, the neuron will decrease its firing (Fig. 1 B, C), i.e. suppress its response to the center stimulus. We can model this phenomenon using your ISN model from Exercise 1: For the first 500 ms of your simulation, we will give a constant input to both the E and the I population of your ISN, where the input to E is significantly larger than the input to I. This represents a center stimulus, i.e. a visual stimulus in the center of the RF that is represented by your E population. After 500 ms, we increase the input to the I population. This models the appearance of a so-called surround stimulus, i.e. a visual stimulus in the surrounding area of the RF center.

2.1.1 Why do we model the surround stimulus as an increased input to the I population? Give a biological interpretation.

Implement the stimulus protocol described above with $i_{E,c} = 4.0$, $i_{I,c} = 1.6$ and $i_{I,cs} = 3.8$ and simulate your ISN using this input protocol. Plot the rates of E and I population as well as the external and recurrent inputs to each population.

2.1.2 What can you observe? Explain the mechanism of surround suppression in your model based on your plots.

2.1.3 What happens if you use the same simulation protocol on a stable network with weak excitatory coupling? Answer this question based on the parameter regimes you found in the previous exercise.

2.2 Orientation tuning of surround suppression

In week 7, you have learned about orientation tuning in the visual cortex.

2.2.1 Explain orientation tuning in your own words. How are cortical columns with similar/different orientation tuning arranged inside the brain?

As electrophysiological recordings show, orientation tuning influences surround suppression: if center and surround stimulus have the same orientation, then surround suppression in the respective cortical column is stronger than if center and surround have different orientation (Fig. 1).

2.2.2 How can we encode the difference between center and surround orientation in our our model?

2.2.3 Use your idea to simulate surround suppression for iso-oriented and cross-oriented stimuli. Plot your results.

2.2.4 Quantify the impact of orientation tuning on surround suppression in your model by plotting (i) the maximal amplitude of the transient increase in inhibitory firing right after onset of the surround stimulus, (ii) the difference between the steady-state rates during center and center+surround stimulation for the E and I population, for iso-oriented and cross-oriented stimuli. Describe and interpret your figure.

2.3 Surround suppression in networks with bio-plausible connectivity

So far, we have considered population rate models, which are derived from spiking models under the assumption of full and homogeneous connectivity, i.e. every neuron connecting to every other neuron in the network with identical connection weights. In contrast, neural circuits in the brain are typically sparsely connected (around 5% connection probability) and have non-homogeneous connection weights. Often, the distribution of synaptic weights in a neural population follows a log-normal distribution. We will now include these weight constraints in our model and check whether this can give us additional insights into surround suppression.

2.3.1 Implement a rate network with 1000 individual neurons whose firing rate is described by Eq. (2). Include the equation (with the detailed formula of the input into every neuron) in your report. How do the weights need to be rescaled to obtain the same firing rates as in the population model?

2.3.2 Verify that your rate model with individual neurons and your weights scaling is correctly implemented by repeating the basic surround suppression experiment from 2.1 (plot your results).

2.3.3 To capture the sparsity of biological networks, now set the connection probability to 0.05. The non-zero connections are drawn randomly from all available connections between neurons in the network. Draw all non-zero weights from a lognormal distribution with mean equal to the rescaled connection weights from the homogeneous network and sigma equal to 2.75 times the mean. We want to keep the sum of all incoming weights to each neuron equal to the sum of incoming weights in the homogeneous network. Due to the sparsity, we therefore need to rescale the non-zero connection weights. What rescaling do we need to apply? Implement this weight matrix and plot the distribution of non-zero weights and its mean.

2.3.4 Simulate the heterogeneous network using the surround suppression protocol from Exercise 2.1. How do the population rates compare to the population rates in the homogeneous network?

2.3.5 Analyze the surround suppression amplitudes of the individual neurons. Do you observe differences between neurons? Explain your findings.

References

[1] Hirofumi Ozeki, Ian M. Finn, Evan S. Schaffer, Kenneth D. Miller, and David Ferster. Inhibitory stabilization of the cortical network underlies visual surround suppression. *Neuron*, 62, 2009.

[2] Damiano Melotti, Kevin Heimbach, Antonio Rodríguez-Sánchez, Nicola Strisciuglio, and George Azzopardi. A robust contour detection operator with combined push-pull inhibition and surround suppression. *Information Sciences*, 524:229–240, 2020.

[3] Qiling Tang, Nong Sang, and Haihua Liu. Contrast-dependent surround suppression models for contour detection. *Pattern Recognition*, 60:51–61, 2016.