$$\rm M2\ Biology$$   $$\rm TD6\colon Rate\ Models$$   $$\rm \it Elie\ \it Oriol$ 

https://github.com/Elieoriol/2021\_UlmM2\_ThNeuro/tree/master/TD6

In this tutorial, we will consider a very standard example of rate model: the ring model.

## 1 Ring model

We consider a network of neurons responsive to a stimulus  $\theta$  which spans the range  $[0, 2\pi]$ . Each neuron has a preferred stimulus and the connection strength between two neurons respectively preferring  $\theta_1$  and  $\theta_2$  is proportional to  $J_0 + J_1 \cos(\theta_1 - \theta_2)$ . Additionally, each neuron receives en external input which depends on the neuron's preferred stimulus  $h(\theta)$ .

In the limit where the number of neurons is large and their preferred stimuli uniformly span the range  $[0, 2\pi]$ , we can write the neural activity as a continuous function  $m(\theta, t)$ . The input current to a neuron preferring  $\theta$  can then be written as:

$$I(\theta, t) = h(\theta) + \int_0^{2\pi} \frac{d\theta'}{2\pi} \left[ J_0 + J_1 \cos(\theta - \theta') \right] m(\theta', t)$$

The activity then evolves according to:

$$\frac{\mathrm{d}m(\theta,t)}{\mathrm{d}t} = -m(\theta,t) + f[I(\theta,t)] \tag{1}$$

$$f(x > 0) = x \tag{2}$$

$$f(x<0) = 0 (3)$$

1. Suppose that there is a constant, uniform and positive external current  $h(\theta) = h_0$ , which is sufficient for there to be positive, uniform network activity  $m(\theta, t) = m_0$ . What is the current received by each neuron? What is the network activity  $m_0$ ? How does it depend on  $J_0$ ?

Each neuron receives:

$$I(\theta) = h_0 + \int_0^{2\pi} \frac{d\theta'}{2\pi} \left( J_0 + J_1 \cos(\theta - \theta') \right) m_0 = h_0 + J_0 m_0$$

Therefore:

$$m_0 = f(h_0 + J_0 m_0) = h_0 + J_0 m_0 \quad \Rightarrow \quad m_0 = \frac{h_0}{1 - J_0}$$

The mean network activity is positive for  $J_0 < 1$ , goes to 0 for  $J_0 \to -\infty$  and diverges to  $+\infty$  for  $J_0 \to 1$ . It cannot exceed 1 here, otherwise  $m_0$  would be negative and we assumed it to be positive.

We wish to study whether this uniform state is stable, we therefore consider small perturbations around it:  $m(\theta,t) = m_0 + \delta m(\theta,t)$ . We wish to see how these evolve with time.

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To do so, we want to find a simple description of the dynamics. We introduce the order parameters:

$$M(t) = \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \delta m(\theta', t) \tag{4}$$

$$C(t) = \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \delta m(\theta', t) e^{i\theta'}$$
 (5)

2. What does M(t) correspond to?

M(t) is the average firing rate across neurons, to which  $m_0$  is subtracted. It is as such the deviation of the average firing rate from the uniform state.

3. Suppose that the perturbation is uniform:

$$\delta m(\theta, t) = \epsilon$$

What are the values of M and C?

One directly computes the integrals to find  $M = \epsilon$  and C = 0. The average deviation from the uniform state is logically equal to the uniform perturbation.

4. Suppose that the perturbation is a small bump centered around the angle  $\phi$ :

$$\delta m(\theta, t) = \epsilon \cos(\theta - \phi) = \epsilon \frac{e^{i(\theta - \phi)} + e^{-i(\theta - \phi)}}{2}$$

What are the values of M and C?

We directly find M = 0, the average deviation is null. We compute C:

$$\begin{split} C &= \epsilon \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \frac{e^{i(\theta'-\phi)} + e^{-i(\theta'-\phi)}}{2} e^{i\theta'} \\ &= \frac{\epsilon}{2} \left[ \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i(2\theta'-\phi)} + \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\phi} \right] \\ &= \frac{\epsilon}{2} e^{i\phi} \end{split}$$

5. What does C(t) correspond to?

C portrays how "bumpy"  $\delta m(\theta, t)$  is: it is a complex number whose phase corresponds to the center of the bump and whose amplitude corresponds to the amplitude of the activity modulation.

6. Now that we have understood what M(t) and C(t) characterize, we will try to obtain a description of the dynamics in terms of the evolution of these two order parameters. Linearize the dynamics of the activity around  $m_0$  and express it as a function of M(t) and C(t).

Since we linearize around  $m_0$  that corresponds to a positive current I > 0, we have f(I) = I. Then:

$$\frac{\mathrm{d}\delta_{m}(\theta,t)}{\mathrm{d}t} = -\delta_{m}(\theta,t) + J_{0} \int_{0}^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \delta_{m}(\theta',t) + J_{1} \int_{0}^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \cos(\theta - \theta') \, \delta_{m}(\theta',t)$$

$$= -\delta_{m}(\theta,t) + J_{0}M + \frac{J_{1}}{2} \left[ \int_{0}^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i(\theta - \theta')} \delta_{m}(\theta',t) + \int_{0}^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{-i(\theta - \theta')} \delta_{m}(\theta',t) \right]$$

$$= -\delta_{m}(\theta,t) + J_{0}M + J_{1} \frac{e^{i\theta}\overline{C} + e^{-i\theta}C}{2}$$

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7. Derive the differential equations governing the evolution of the order parameters.

$$\frac{\mathrm{d}M}{\mathrm{d}t} = \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \frac{\mathrm{d}\delta_m(\theta', t)}{\mathrm{d}t}$$

$$= -\int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \delta_m(\theta', t) + J_0 M \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} + \frac{J_1}{2} \left[ \overline{C} \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta'} + C \frac{\mathrm{d}\theta'}{2\pi} e^{-i\theta'} \right]$$

$$= (J_0 - 1) M$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta} \frac{\mathrm{d}\delta_m(\theta',t)}{\mathrm{d}t} 
= -\int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta} \delta_m(\theta',t) + J_0 M \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta} + J_1 \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta} \frac{e^{i\theta} \overline{C} + e^{-i\theta} C}{2} 
= -C + \frac{J_1}{2} \left[ \overline{C} \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{2i\theta} + C \int_0^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} \right] 
= \left( \frac{J_1}{2} - 1 \right) C$$

8. Under what conditions is the uniform activity stable? What happens when either of these conditions is not met?

There are two conditions for the network activity to be stable:

- $J_0 < 1$  otherwise any deviation of the mean activity below  $m_0$  leads to an activity of 0, and any deviation of the mean activity above  $m_0$  leads to exponentially growing activity.
- $J_1 < 2$  otherwise any non-uniform activity is expanded into a bump whose amplitude grows exponentially.
- Consider J<sub>0</sub> < 1, J<sub>1</sub> < 2. Consider an external input with weak modulation, h(θ) = h<sub>0</sub> + ε cos(θ), where ε ≪ 1. What is the profile of activity of the network induced by such an external input?
   Using the same method:

$$\frac{\mathrm{d}\delta_{m}(\theta,t)}{\mathrm{d}t} = -\delta_{m}(\theta,t) + \epsilon \cos(\theta) + J_{0}M + \frac{J_{1}}{2} \left[ e^{-i\theta}C + e^{i\theta}\overline{C} \right]$$

$$\frac{\mathrm{d}M}{\mathrm{d}t} = (J_{0} - 1) M$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = -C + \epsilon \int_{0}^{2\pi} \frac{\mathrm{d}\theta'}{2\pi} e^{i\theta'} \frac{e^{i\theta'} + e^{-i\theta'}}{2} + \frac{J_{1}}{2}C$$

$$= \frac{\epsilon}{2} + \left( \frac{J_{1}}{2} - 1 \right) C$$

Now C converges to  $\frac{\epsilon/2}{1-J_1/2}$ . The profile of activity converges to a bump centered on 0.

10. Suppose that the firing rate is given by  $m(\theta, t) = m_0 + m_1 \cos(\theta)$ , under what conditions does the network amplify the input, ie:  $\frac{m_1}{m_0} > \frac{\epsilon}{h_0}$ ?

$$C = \int_0^{2\pi} \frac{d\theta'}{2\pi} e^{i\theta'} m_1 \frac{e^{i\theta'} + e^{-i\theta'}}{2} = \frac{m_1}{2} = \frac{\epsilon/2}{1 - J_1/2}$$

Therefore:

$$\frac{m_1}{m_0} = \frac{\epsilon}{1 - J_1/2} \frac{1 - J_0}{h_0} = \frac{\epsilon}{h_0} \frac{1 - J_0}{1 - J_1/2}$$

The network amplifies the input if and only if  $J_1 > 2J_0$ .

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Trigonometry:

$$\cos(\theta + \phi) = \cos(\theta)\cos(\phi) - \sin(\theta)\sin(\phi) \tag{6}$$

$$\int_0^{2\pi} \frac{d\theta'}{2\pi} \cos(\theta') = \int_0^{2\pi} \frac{d\theta'}{2\pi} \sin(\theta') = 0 \tag{7}$$

$$\int_0^{2\pi} \frac{d\theta'}{2\pi} \cos(\theta') = \int_0^{2\pi} \frac{d\theta'}{2\pi} \sin(\theta') = 0$$

$$\int_0^{2\pi} \frac{d\theta'}{2\pi} \cos(\theta')^2 = \int_0^{2\pi} \frac{d\theta'}{2\pi} \sin(\theta')^2 = \frac{1}{2}$$
(8)

$$\int_0^{2\pi} \frac{d\theta'}{2\pi} \cos(\theta') \sin(\theta') = 0 \tag{9}$$

$$\cos(\theta) = \frac{e^{i\theta} + e^{-i\theta}}{2}$$

$$e^{i\theta} = \cos(\theta) + i\sin(\theta)$$
(10)

$$e^{i\theta} = \cos(\theta) + i\sin(\theta) \tag{11}$$