M2 Biology **21/10/21**

TD5: Rate Models

Elie Oriol

TD material is available at:

`https://github.com/Elieoriol/2122_UlmM2_ThNeuro/tree/master/TD5`

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 θ which spans the range $[0, 2\pi]$. Each neuron has a preferred stimulus and the connection strength between two neurons respectively preferring θ_1 and θ_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 θ can then be written as:

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

The activity then evolves according to:

$$\frac{\mathrm{d}m(\theta,t)}{\mathrm{d}t} = -m(\theta,t) + f[I(\theta,t)] \tag{1}$$
$$f(x > 0) = x \tag{2}$$
$$f(x < 0) = 0 \tag{3}$$

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:

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

   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.

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

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

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

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 ϕ:

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

   What are the values of M and C?

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

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

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:

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

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

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

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

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.*

9. Consider $J_0 < 1$, $J_1 < 2$. Consider an external input with weak modulation, $h(\theta) = h_0 + \epsilon\cos(\theta)$, where $\epsilon \ll 1$. What is the profile of activity of the network induced by such an external input?

   Using the same method:

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

   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: $\frac{m_1}{m_0} > \frac{\epsilon}{h_0}$?

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

   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 $J_1 > 2J_0$*.*

Trigonometry:

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

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

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

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

$$\cos(\theta) = \frac{e^{i\theta} + e^{-i\theta}}{2} \tag{10}$$

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