THEORETICAL NEUROSCIENCE

TD5: RATE MODELS

All TD materials will be made available at `https://github.com/yfardella/Th_Neuro_TD_2025`.

This tutorial aims to study a very standard example of rate model: the Ring Model. This model was originally introduced for orientation coding in the visual cortex. More generally, this model could apply for any network encoding a circular one-dimensional variable. In order to understand the model's dynamics, we will use methods used in the previous tutorials to study nonlinear ODEs and introduce perturbation theory.

1 The 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 an 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

$$I(\theta, t) = h(\theta) + \int_0^{2\pi} \frac{1}{2\pi}(J_0 + J_1 \cos(\theta - \theta'))m(\theta', t)d\theta'. \tag{1}$$

The activity then evolves according to

$$\frac{dm(\theta, t)}{dt} = -m(\theta, t) + f(I(\theta, t)), \text{ with } f(x > 0) = x \text{ and } f(x < 0) = 0. \tag{2}$$

1.1 Uniform state

We 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 $m(\theta, t) = m_0$.

1. What is the current received by each neuron?

> Each neuron receives the following input
>
> $$I(\theta) = h_0 + \int_0^{2\pi} \frac{1}{2\pi}\left(J_0 + J_1 \cos(\theta - \theta')\right) m_0 d\theta'$$

$$
\begin{aligned}
&= h_0 + \left[\frac{1}{2\pi} m_0 \left(J_0 \theta' - J_1 \sin(\theta - \theta') \right) \right]_0^{2\pi} \\
&= h_0 + \frac{1}{2\pi} m_0 \left(J_0 2\pi - J_1 \sin(\theta - 2\pi) + J_1 \sin(\theta) \right) \\
&= h_0 + J_0 m_0.
\end{aligned}
$$

2. Deduce the equilibrium network activity m_0.

> The equilibrium is found by solving
>
> $$
> \begin{aligned}
> \frac{dm(\theta, t)}{dt} = 0 &\Leftrightarrow -m_0 + f(h_0 + J_0 m_0) = 0 \\
> &\Leftrightarrow -m_0 + h_0 + J_0 m_0 = 0 \\
> &\Leftrightarrow m_0 = \frac{h_0}{1 - J_0}.
> \end{aligned}
> $$

3. How does it depend on J_0 ?

> First, by hypothesis, we have that $m_0 > 0$ and therefore $J_0 < 1$. There are three scenarios for the network activity depending on the value of J_0:
>
> – $J_0 < 1$: the mean network activity is positive.
>
> – $J_0 \to -\infty$: the mean network activity goes to 0.
>
> – $J_0 \to 1$: the mean network activity diverges to $+\infty$.

1.2 Stability analysis through perturbations

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

$$
M(t) = \int_0^{2\pi} \frac{1}{2\pi} \delta m(\theta', t) d\theta', \tag{3}
$$
$$
C(t) = \int_0^{2\pi} \frac{1}{2\pi} \delta m(\theta', t) e^{i\theta'} d\theta'. \tag{4}
$$

4. Give an interpretation of $M(t)$.

> $M(t)$ is a scalar number, which represents the average perturbation across the network, i.e. the mean deviation of the network's firing rate from the uniform state.

1.2.1 Uniform perturbation

We suppose that the perturbation is uniform

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

5. Compute the values of $M(t)$ and $C(t)$.

> Computing the integrals, we find $M(t) = \epsilon$ and $C(t) = 0$. The average deviation from the uniform state is equal to the uniform perturbation.

1.2.2 Bumpy perturbation

We now suppose that the perturbation is a small bump centred around the angle ϕ

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

6. Compute the values of $M(t)$ and $C(t)$.

> We begin by computing $M(t)$
>
> $$M(t) = \int_0^{2\pi} \frac{1}{2\pi} \epsilon \cos(\theta' - \phi) d\theta' = 0.$$
>
> Therefore, the average deviation is null. We now compute C
>
> $$\begin{aligned} C(t) &= \int_0^{2\pi} \frac{1}{2\pi} \epsilon \frac{e^{i(\theta-\phi)} + e^{-i(\theta-\phi)}}{2} e^{i\theta'} d\theta' \\ &= \frac{\epsilon}{2} \frac{1}{2\pi} \left(\int_0^{2\pi} e^{i(2\theta'-\phi)} d\theta' + \int_0^{2\pi} e^{i\phi} d\theta' \right) \\ &= \frac{\epsilon}{2} \frac{1}{2\pi} \left(e^{-\phi} \int_0^{2\pi} e^{i2\theta'} d\theta' + e^{i\phi} \int_0^{2\pi} 1 d\theta' \right) \\ &= \frac{\epsilon}{2} \frac{1}{2\pi} \left(0 + e^{i\phi} 2\pi \right) = \frac{\epsilon}{2} e^{i\phi}. \end{aligned}$$

7. Give an interpretation of $C(t)$.

> $C(t)$ is a complex number, which portrays the "bumpiness" of the perturbation $\delta m(\theta, t)$. Its phase reflects the position of the centre of the bump and its amplitude corresponds to the magnitude of the activity modulation at the bump. From the previous question, the perturbation features a bump centred on the angle ϕ.

Now that we have understood what $M(t)$ and $C(t)$ characterise, we will try to obtain a description of the dynamics in terms of the evolution of these two order parameters.

8. Linearise the dynamics of the activity around the equilibrium 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 $f(I) = I$. The dynamics are therefore
>
> $$\frac{d\delta m(\theta, t)}{dt} = -\delta m(\theta, t) + \int_0^{2\pi} \frac{1}{2\pi} \left(J_0 + J_1 \cos(\theta - \theta') \right) \delta m(\theta', t) d\theta'$$

$$= -\delta m(\theta,t) + J_0 \int_0^{2\pi} \frac{1}{2\pi}\delta m(\theta',t)d\theta' + J_1 \int_0^{2\pi} \frac{1}{2\pi}\cos(\theta-\theta')\delta m(\theta',t)d\theta'$$

$$= -\delta m(\theta,t) + J_0 M(t) + J_1 \int_0^{2\pi} \frac{1}{2\pi}\frac{e^{i(\theta-\theta')}+e^{-i(\theta-\theta')}}{2}\delta m(\theta',t)d\theta'$$

$$= -\delta m(\theta,t) + J_0 M(t) + \frac{J_1}{2}\left(e^{i\theta}\int_0^{2\pi}\frac{1}{2\pi}e^{-i\theta'}\delta m(\theta',t)d\theta' + e^{-i\theta}\int_0^{2\pi}\frac{1}{2\pi}e^{i\theta'}\delta m(\theta',t)d\theta'\right)$$

$$= -\delta m(\theta,t) + J_0 M(t) + J_1\frac{e^{i\theta}\bar{C}(t)+e^{-i\theta}C(t)}{2}.$$

9. Determine the differential equations governing the evolution of the order parameters.

We now determine the equation governing the evolution of $M(t)$

$$\frac{dM(t)}{dt} = \frac{d}{dt}\int_0^{2\pi}\frac{1}{2\pi}\delta m(\theta',t)d\theta' = \int_0^{2\pi}\frac{1}{2\pi}\frac{d\delta m(\theta',t)}{dt}d\theta'$$

$$= \int_0^{2\pi}\frac{1}{2\pi}\left(-\delta m(\phi',t) + J_0 M(t) + J_1\frac{e^{i\theta'}\bar{C}(t)+e^{-i\theta'}C(t)}{2}\right)d\theta'$$

$$= -M(t) + \frac{1}{2\pi}J_0 M(t)\int_0^{2\pi}1d\phi' + \frac{J_1}{2}\left(\frac{\bar{C}(t)}{2\pi}\int_0^{2\pi}e^{i\phi'}d\phi' + \frac{C(t)}{2\pi}\int_0^{2\pi}e^{-i\phi'}d\phi'\right)$$

$$= -M(t) + \frac{1}{2\pi}J_0 M(t)\times 2\pi + \frac{J_1}{2}\left(\frac{\bar{C}(t)}{2\pi}\times 0 + \frac{C(t)}{2\pi}\times 0\right)$$

$$= (J_0 - 1)M(t),$$

and the equation governing the evolution of $C(t)$

$$\frac{dC(t)}{dt} = \frac{d}{dt}\int_0^{2\pi}\frac{1}{2\pi}\delta m(\theta',t)e^{i\theta'}d\theta' = \int_0^{2\pi}\frac{1}{2\pi}\frac{d\delta m(\theta',t)}{dt}e^{i\theta'}d\theta'$$

$$= \int_0^{2\pi}\frac{1}{2\pi}\left(-\delta m(\phi',t)e^{i\theta'} + J_0 M(t)e^{i\theta'} + J_1\frac{e^{i\theta'}\bar{C}(t)+e^{-i\theta'}C(t)}{2}e^{i\theta'}\right)d\theta'$$

$$= -C(t) + \frac{J_0 M(t)}{2\pi}\int_0^{2\pi}e^{i\theta'}d\theta' + \frac{J_1}{2}\frac{1}{2\pi}\left(\bar{C}(t)\int_0^{2\pi}e^{2i\theta'}d\theta' + C(t)\int_0^{2\pi}1\right)d\theta'$$

$$= -C(t) + \frac{J_0 M(t)}{2\pi}\times 0 + \frac{J_1}{2}\frac{1}{2\pi}\left(\bar{C}(t)\times 0 + C(t)\times 2\pi\right)$$

$$= \left(\frac{J_1}{2} - 1\right)C(t).$$

10. Determine the conditions under which the uniform activity is stable. What happens when either these conditions is not met?

Solving the two previous ODEs for $M(t)$ and $C(t)$, we obtain the following

– $M(t) = M_0 e^{(J_0-1)t} \to 0 \Leftrightarrow J_0 - 1 < 0 \Leftrightarrow J_0 < 1$.
  In this case, the perturbation vanishes. Otherwise, any perturbation leads to exponentially amplifying deviation from the equilibrium.

– $C(t) = C_0 e^{(J_1/2-1)t} \to 0 \Leftrightarrow J_1 < 2$.
  Otherwise, any non-uniform activity is expanded into a bump whose amplitude grows exponentially.

We consider $J_0 < 1$ and $J_1 < 2$. The network is submitted to an external input with weak modulation

$$h(\theta) = h_0 + \epsilon \cos(\theta), \text{ with } \epsilon \ll 1.$$

11. What is the profile of activity of the network induced by such an external input?

Using the same method, we obtain

$$\frac{d\delta m(\theta,t)}{dt} = -\delta m(\theta,t) + \epsilon\cos(\theta) + J_0 M(t) + \frac{J_1}{2}\left(e^{-i\theta}C(t) + e^{i\theta}\bar{C}(t)\right),$$

$$\frac{dM(t)}{dt} = (J_0 - 1)M(t),$$

$$\frac{dC(t)}{dt} = -C(t) + \epsilon\int_0^{2\pi}\frac{1}{2\pi}e^{i\theta'}\frac{e^{i\theta'} + e^{-i\theta'}}{2}d\theta' + \frac{J_1}{2}C(t) = \frac{\epsilon}{2} + \left(\frac{J_1}{2} - 1\right)C(t).$$

Now, $C(t)$ converges to $\dfrac{\epsilon/2}{1 - J_1/2}$.
The profile of activity converges to a bump centred on 0.

Suppose that the firing rate is given by

$$m(\theta,t) = m_0 + m_1\cos(\theta).$$

12. Determine the conditions such that the network amplifies the input, i.e.

$$\frac{m_1}{m_0} > \frac{\epsilon}{h_0}.$$

We have that

$$C(t) = \int_0^{2\pi}\frac{1}{2\pi}e^{i\theta'}m_1\frac{e^{i\theta'} + e^{-i\theta'}}{2} = \frac{m_1}{2} = \frac{\epsilon/2}{1 - J_1/2}.$$

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 $J_1 > 2J_0$.

2 Homogeneous Excitatory and Inhibitory Populations

We analyze a simple model in which all of the excitatory neurons are described by a single firing rate ν_E and all of the inhibitory neurons are described by a second firing rate ν_I. The equations describing the dynamics of the firing rates are

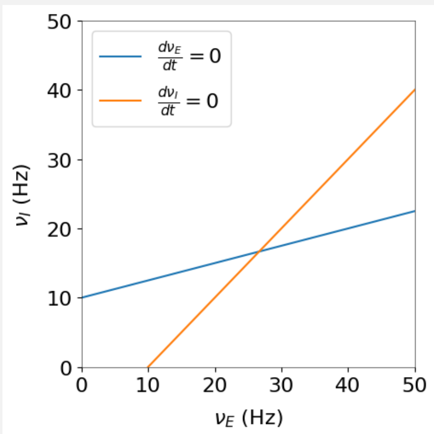
$$\tau_E \frac{d\nu_E}{dt}(t) = -\nu_E + [M_{EE}\nu_E + M_{IE}\nu_I - \gamma_E]_+ \,, \tag{5}$$

$$\tau_I \frac{d\nu_I}{dt}(t) = -\nu_I + [M_{EI}\nu_E + M_{II}\nu_I - \gamma_I]_+ \,, \tag{6}$$

where $[\cdots]_+$ represents the linear threshold function (or ReLU).

In this exercise, we consider the case where $M_{EE} = 1.25$, $M_{IE} = 1$, $M_{II} = 0$, $M_{EI} = -1$, $\gamma_E = -10$ Hz and $\gamma_I = 10$ Hz with τ_I still varying.

13. Draw the nullclines for ν_E and ν_I. What is the (qualitative) condition for the existence of a fixed point?

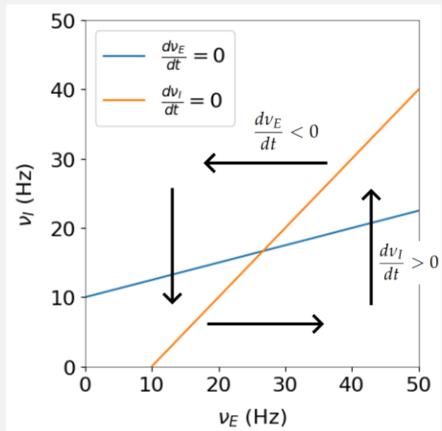
> We have, when the terms in the linear threshold functions are positive,
>
> $$\frac{d\nu_E}{dt} = 0 \Rightarrow \nu_I = \frac{(M_{EE}-1)\nu_E - \gamma_E}{M_{EI}},$$
> $$\frac{d\nu_I}{dt} = 0 \Rightarrow \nu_E = \frac{(M_{EE}-1)\nu_I - \gamma_I}{M_{IE}}.$$
>
> The resulting curve is,
>
> 
>
>
> The fixed point exists when the two nullclines intersect (and is located at the intersection).

14. Draw the flow field of ν_E and ν_I above and below the nullclines (draw only the vertical and horizontal arrows).

Using the previous question,

$$\nu_I > \nu_I^c \Rightarrow \frac{d\nu_E}{dt} < 0,$$
$$\nu_E > \nu_E^c \Rightarrow \frac{d\nu_I}{dt} > 0.$$

The resulting flows are given by the black arrows,



15. Study the stability of the fixed point. What happens if the fixed point is not stable to perturbations?
Hint: Use the values $\tau_I = 30$ ms, 40 ms and 50 ms.

We want to compute the eigenvalues of the matrix:

$$\begin{pmatrix} \partial_{\nu_E}\left(\frac{d\nu_E}{dt}\right) & \partial_{\nu_I}\left(\frac{d\nu_E}{dt}\right) \\ \partial_{\nu_E}\left(\frac{d\nu_I}{dt}\right) & \partial_{\nu_I}\left(\frac{d\nu_I}{dt}\right) \end{pmatrix} = \begin{pmatrix} \frac{M_{EE}-1}{\tau_E} & \frac{M_{EI}}{\tau_E} \\ \frac{M_{IE}}{\tau_I} & \frac{M_{II}-1}{\tau_I} \end{pmatrix}$$

Using the characteristic polynomial, the eigenvalues are given by:

$$\lambda_\pm = \frac{-b \pm i\sqrt{-\Delta}}{2}, \tag{7}$$

with

$$b = \frac{M_{EE}-1}{\tau_E} + \frac{M_{II}-1}{\tau_I}, \tag{8}$$

$$\Delta = \left(\frac{M_{EE}-1}{\tau_E} + \frac{M_{II}-1}{\tau_I}\right)^2 - 4\frac{(M_{EE}-1)(M_{II}-1) - M_{EI}M_{IE}}{\tau_E\tau_I}. \tag{9}$$

For the different values of τ_I:

(a) $\tau_I = 30$ ms: $b = -0.008$ and $\Delta = -0.01$,

(b) $\tau_I = 40$ ms: $b = 0$ and $\Delta = -0.0075$,

(c) $\tau_I = 50$ ms: $b = 0.005$ and $\Delta = -0.006$.

The fixed point is stable for $\tau_I < 40$ ms. When the fixed point is unstable to perturbations, the linear threshold function stops the rates from diverging and the systems go through a Hopf bifurcation (see notebook for more details).