

TD6 – Rate Models

1 Input current & Uniform state

① Total input current – General case

For a neuron preferring a stimulus value θ , the total input includes two terms :

- An external input $h(\theta)$.
- Recurrent inputs coming from all neurons at positions $\theta' \in [0, 2\pi]$. This term can be expressed as a sum over all neurons (integral, in the continuous case), each neuron at a position θ' contributing proportionally to its own activity $m(\theta', t)$ with weight $J_0 + J_1 \cos(\theta - \theta')$. The integral can be renormalized by 2π as a mean.

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

② Total input current – Particular case

- In the case of a constant input h_0 and uniform activity m_0 , each neuron receives the following input :

$$\begin{aligned} I(\theta) &= h_0 + \frac{1}{2\pi} \int_0^{2\pi} (J_0 + J_1 \cos(\theta - \theta')) m_0 d\theta' \\ &= h_0 + \frac{m_0}{2\pi} \left(J_0 \underbrace{\int_0^{2\pi} d\theta'}_{2\pi} + J_1 \underbrace{\int_0^{2\pi} \cos(\theta - \theta') d\theta'}_0 \right) \\ &= h_0 + J_0 m_0 \end{aligned}$$

- The network's activity at the equilibrium is obtained by cancelling the derivative and replacing by the input computed just above :

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

- The mean network activity is positive for $J_0 < 1$, so the parameter J_0 cannot exceed 1 (otherwise m_0 would be negative, which is forbidden by assumption). The mean activity goes to 0 for $J_0 \rightarrow -\infty$ and diverges to $+\infty$ for $J_0 \rightarrow 1$.

2 Description through order parameters

③ Interpretation of the order parameters

- $M(t)$ 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.
- $C(t)$ is a complex number, which portrays the "bumpyness" of the perturbation $\delta m(\theta, t)$. Its phase reflects the position of the center of the bump and its amplitude corresponds to the magnitude of the activity modulation at the bump.

④ Values of M and C

- The average deviation from the uniform state is equal to the uniform perturbation :

$$M(t) = \frac{1}{2\pi} \int_0^{2\pi} \epsilon d\theta' = \frac{\epsilon}{2\pi} 2\pi = \epsilon$$

- The perturbation does not feature any bump :

$$C(t) = \frac{1}{2\pi} \int_0^{2\pi} \epsilon e^{i\theta'} d\theta' = \frac{\epsilon}{2\pi} \int_0^{2\pi} (\cos(\theta') + i \sin(\theta')) d\theta' = 0$$

3 Bumpy perturbation

⑤ Values of M and C

- The average deviation is null with a cosine perturbation :

$$M(t) = \frac{1}{2\pi} \int_0^{2\pi} \epsilon \cos(\theta' - \phi) d\theta' = \frac{\epsilon}{2\pi} \times 0 = 0$$

- The perturbation features a bump centered on the angle ϕ :

$$\begin{aligned} C(t) &= \frac{1}{2\pi} \int_0^{2\pi} \epsilon \cos(\theta' - \phi) e^{i\theta'} d\theta' \\ &= \frac{\epsilon}{2\pi} \int_0^{2\pi} \frac{e^{i(\theta' - \phi)} + e^{-i(\theta' - \phi)}}{2} e^{i\theta'} d\theta' \quad \text{by Euler's formula} \\ &= \frac{\epsilon}{2} \frac{1}{2\pi} \int_0^{2\pi} (e^{i\theta'} e^{-i\phi} + e^{-i\theta'} e^{i\phi}) e^{i\theta'} d\theta' \\ &= \frac{\epsilon}{2} \frac{1}{2\pi} \left[e^{-i\phi} \underbrace{\int_0^{2\pi} e^{i2\theta'} d\theta'}_0 + e^{i\phi} \underbrace{\int_0^{2\pi} d\theta'}_{2\pi} \right] \\ &= \frac{\epsilon}{2} e^{i\phi} \end{aligned}$$

⑥ Linearization of the dynamics

When the network is initially perturbed around the uniform state m_0 , the evolution of the perturbation from this baseline can be obtained from the dynamical equation of the system :

$$\frac{d\delta_m(\theta, t)}{dt} = \frac{d(m(\theta, t) - m_0)}{dt} = \frac{dm(\theta, t)}{dt} = -m(\theta, t) + f[I(\theta, t)]$$

Since around m_0 , the activity leads to a positive current $I > 0$, then $f(I) = I$.

Linearizing the dynamics requires (1) replacing $m(\theta, t)$ by $m_0 + \delta_m(\theta, t)$, (2) grouping together all constant terms (which does not depend $\delta_m(\theta, t)$) corresponding to the equilibrium, (3) keeping only terms which depend on $\delta_m(\theta, t)$ at the first order $\triangleright [TD]$:

$$\begin{aligned} \frac{d\delta_m(\theta, t)}{dt} &= -(m_0 + \delta_m(\theta, t)) + h_0 + \frac{1}{2\pi} \int_0^{2\pi} (J_0 + J_1 \cos(\theta - \theta')) (m_0 + \delta_m(\theta', t)) d\theta' \\ &= \underbrace{-m_0 + h_0 + \frac{1}{2\pi} \int_0^{2\pi} (J_0 + J_1 \cos(\theta - \theta')) m_0 d\theta'}_0 \text{ (equilibrium)} - \delta_m(\theta, t) + \frac{1}{2\pi} \int_0^{2\pi} (J_0 + J_1 \cos(\theta - \theta')) \delta_m(\theta', t) d\theta' \end{aligned}$$

The next step is to rewrite this expression so as to make $M(t)$ and $C(t)$ appear :

$$\begin{aligned} \frac{d\delta_m(\theta, t)}{dt} &= -\delta_m(\theta, t) + J_0 \underbrace{\frac{1}{2\pi} \int_0^{2\pi} \delta_m(\theta', t) d\theta'}_{M(t)} + J_1 \frac{1}{2\pi} \int_0^{2\pi} \underbrace{\cos(\theta - \theta')}_{\frac{e^{i(\theta - \theta')} + e^{-i(\theta - \theta')}}{2}} \delta_m(\theta', t) d\theta' \quad \text{(to introduce exponentials)} \\ &= -\delta_m(\theta, t) + J_0 M(t) + \frac{J_1}{2} \left(\frac{1}{2\pi} \int_0^{2\pi} e^{i(\theta - \theta')} \delta_m(\theta', t) d\theta' + \frac{1}{2\pi} \int_0^{2\pi} e^{-i(\theta - \theta')} \delta_m(\theta', t) d\theta' \right) \\ &= -\delta_m(\theta, t) + J_0 M(t) + \frac{J_1}{2} \left(e^{i\theta} \frac{1}{2\pi} \int_0^{2\pi} e^{-i\theta'} \delta_m(\theta', t) d\theta' + e^{-i\theta} \frac{1}{2\pi} \int_0^{2\pi} e^{i\theta'} \delta_m(\theta', t) d\theta' \right) \\ &= -\delta_m(\theta, t) + J_0 M(t) + J_1 \frac{e^{i\theta} \overline{C(t)} + e^{-i\theta} C(t)}{2} \quad \text{with } \overline{C(t)} \text{ the complex conjugate of } C(t). \end{aligned}$$

⑦ Differential equations for the order parameters

The differential equations for the order parameters can be obtained by deriving the expressions of those variables

with respects to the time variable, and making the variables $M(t)$ and $C(t)$ appear :

• Variable M

$$\begin{aligned}
 \frac{dM}{dt} &= \frac{d}{dt} \left(\frac{1}{2\pi} \int_0^{2\pi} \delta_m(\theta', t) d\theta' \right) \\
 &= \frac{1}{2\pi} \int_0^{2\pi} \frac{d\delta_m(\theta', t)}{dt} d\theta' \\
 &= \frac{1}{2\pi} \int_0^{2\pi} \left[-\delta_m(\theta', t) + J_0 M(t) + J_1 \frac{e^{i\theta'} \overline{C(t)} + e^{-i\theta'} C(t)}{2} \right] d\theta' \\
 &= \underbrace{-\frac{1}{2\pi} \int_0^{2\pi} \delta_m(\theta', t) d\theta'}_{M(t)} + J_0 M(t) \underbrace{\frac{1}{2\pi} \int_0^{2\pi} d\theta'}_{2\pi} + \frac{J_1}{2} \left(\overline{C} \underbrace{\frac{1}{2\pi} \int_0^{2\pi} e^{i\theta'} d\theta'}_0 + C \underbrace{\frac{1}{2\pi} \int_0^{2\pi} e^{-i\theta'} d\theta'}_0 \right) \\
 &= (J_0 - 1) M
 \end{aligned}$$

• Variable C

$$\begin{aligned}
 \frac{dC}{dt} &= \frac{d}{dt} \left(\frac{1}{2\pi} \int_0^{2\pi} \delta_m(\theta', t) e^{i\theta'} d\theta' \right) \\
 &= \frac{1}{2\pi} \int_0^{2\pi} \frac{d\delta_m(\theta', t)}{dt} e^{i\theta'} d\theta' \\
 &= \frac{1}{2\pi} \int_0^{2\pi} \left[-\delta_m(\theta', t) + J_0 M(t) + J_1 \frac{e^{i\theta'} \overline{C(t)} + e^{-i\theta'} C(t)}{2} \right] e^{i\theta'} d\theta' \\
 &= \underbrace{-\frac{1}{2\pi} \int_0^{2\pi} \delta_m(\theta', t) e^{i\theta'} d\theta'}_{C(t)} + J_0 M(t) \underbrace{\frac{1}{2\pi} \int_0^{2\pi} e^{i\theta'} d\theta'}_0 + \frac{J_1}{2} \left(\overline{C(t)} \underbrace{\frac{1}{2\pi} \int_0^{2\pi} e^{2i\theta'} d\theta'}_0 + C(t) \underbrace{\frac{1}{2\pi} \int_0^{2\pi} d\theta'}_{2\pi} \right) \\
 &= \left(\frac{J_1}{2} - 1 \right) C(t)
 \end{aligned}$$

⑧ Conditions for stability

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

- From the variable $M(t)$: $J_0 < 1$, otherwise any deviation of the mean activity *below* m_0 leads to vanishing activity (0 is the only fixed point), and any deviation of the mean activity *above* m_0 leads to exponentially growing activity (this condition confirms the results from question ②).
- From the variable $C(t)$: $J_1 < 2$, otherwise any non-uniform activity is expanded into a bump whose amplitude grows exponentially.

⑨ Evolution of the profile of activity of the network

Following the same method, the evolution of the activity profile can be characterized through the order parameters. The only change compared to the previous case is the addition of a cosine term in the expression of $h(\theta)$:

$$h(\theta) = h_0 + \epsilon \cos(\theta) \quad \epsilon \ll 1$$

Therefore, the same results apply with an additional term in the expressions.

For the derivative of the perturbation $\frac{d\delta_m(\theta, t)}{dt}$:

$$\begin{aligned}
 \frac{d\delta_m(\theta, t)}{dt} &= -(m_0 + \delta_m(\theta, t)) + h_0 + \epsilon \cos(\theta) + \frac{1}{2\pi} \int_0^{2\pi} (J_0 + J_1 \cos(\theta - \theta')) (m_0 + \delta_m(\theta', t)) d\theta' \\
 &= -\delta_m(\theta, t) + \epsilon \cos(\theta) + J_0 M(t) + \frac{J_1}{2} (e^{-i\theta} C(t) + e^{i\theta} \overline{C(t)})
 \end{aligned}$$

For $\frac{dM}{dt}$, it induces an additional term $\frac{1}{2\pi} \int_0^{2\pi} \epsilon \cos(\theta') d\theta' = 0$, which does not change the expression.

For $\frac{dC}{dt}$, it induces an additional term $\frac{1}{2\pi} \int_0^{2\pi} \underbrace{\epsilon \cos(\theta')}_{\frac{e^{i\theta'} + e^{-i\theta'}}{2}} e^{i\theta'} d\theta' = \frac{\epsilon}{2} \frac{1}{2\pi} \int_0^{2\pi} (e^{2i\theta'} + 1) d\theta' = \frac{\epsilon}{2}$.

Thus the dynamics of the order parameters become :

$$\begin{aligned}\frac{dM}{dt} &= (J_0 - 1) M(t) \\ \frac{dC}{dt} &= \frac{\epsilon}{2} + \left(\frac{J_1}{2} - 1\right) C(t)\end{aligned}$$

(10) Activity profile at equilibrium

- Under the conditions $J_0 < 1$, $J_1 < 2$ (by assumption for these questions), the activity profile of the network admits a stable state (question (8)). It can be written relative to the uniform state : $m(\theta, t) = m_0 + g(\theta)$, with $g(\theta)$ a function to be determined.
- The differential equation (9) for the variable $C(t)$ shows that C admits a non-null fixed point $\frac{\epsilon/2}{1-J_1/2}$ (obtained by setting $\frac{dC}{dt} = 0$ as in previous TDs). Thus, the variable $C(t)$ converges to a *real* number, which is equivalent to a complex number of phase 0. This means that the activity profile of the network evolves towards a bump centered on 0. This could likely be written with a cosine function (assuming the most simple expression for a 'bump', in view of the formula of the input $h(\theta)$ and the network's dynamics) :

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

(11) Conditions for amplification

The goal is to find a relation between the parameters m_0 , m_1 , h_0 , ϵ .

- A first expression relates m_0 and h_0 (question (2)) :

$$m_0 = \frac{h_0}{1 - J_0}$$

- A second expression can be found for relating m_1 and ϵ :

On the one hand, at the equilibrium, the network's activity displays a bump such that $C(t) = \frac{\epsilon/2}{1-J_1/2}$ (question (10)).

On the other hand, another expression for this variable can be obtained by integrating its expression involving the parameter m_1 :

$$C = \frac{1}{2\pi} \int_0^{2\pi} (m_0 + m_1 \cos(\theta')) e^{i\theta'} d\theta' = \underbrace{\frac{1}{2\pi} \int_0^{2\pi} m_0 e^{i\theta'} d\theta'}_0 + \frac{1}{2\pi} \int_0^{2\pi} m_1 \frac{e^{i\theta'} + e^{-i\theta'}}{2} e^{i\theta'} d\theta' = \frac{m_1}{2} \quad (\text{as before})$$

Therefore :

$$\frac{\epsilon/2}{1 - J_1/2} = \frac{m_1}{2} \implies m_1 = \frac{\epsilon}{1 - J_1/2}$$

- Gathering both relations leads to :

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

The network amplifies the input if $\frac{m_1}{m_0} > \frac{\epsilon}{h_0}$, which imposes $\frac{1-J_0}{1-J_1/2} > 1$, i.e. $J_1 > 2J_0$.