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.

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

② *Total input current – Particular case : Uniform input*

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

$$\begin{aligned} I(\theta) &= h_0 + \frac{1}{2\pi} \int_0^{2\pi} \left(J_0 + J_1 \cos(\theta - \theta')\right) m_0 \, \mathrm{d}\theta' \\ &= h_0 + \frac{m_0}{2\pi} \left(J_0 \underbrace{\int_0^{2\pi} \mathrm{d}\theta'}_{2\pi} + J_1 \underbrace{\int_0^{2\pi} \cos(\theta - \theta') \, \mathrm{d}\theta'}_{0} \right) \\ &= h_0 + J_0 m_0 \end{aligned}$$

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

$$\frac{\mathrm{d}m(\theta, t)}{\mathrm{d}t} = -m_0 + f[I(\theta)] = 0 \implies m_0 = f(\underbrace{h_0 + J_0 m_0}_{>0 \text{ (assumption)}}) = h_0 + J_0 m_0 \quad \Rightarrow \quad m_0 = \frac{h_0}{1 - J_0}$$

• The mean network activity m_0 is positive by assumption, which entails for $J_0 < 1$. The mean activity goes to 0 for $J_0 \to -\infty$ and diverges to $+\infty$ for $J_0 \to 1^-$.

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 :

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

- The perturbation does not feature any bump :

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

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3 Bumpy perturbation

⑤ *Values of M and C*

- The average deviation is null with a cosine perturbation :

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

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

$$\begin{aligned}
C(t) &= \frac{1}{2\pi}\int_0^{2\pi} \epsilon\cos(\theta' - \phi)e^{i\theta'}\,\mathrm{d}\theta' \\
&= \frac{\epsilon}{2\pi}\int_0^{2\pi} \frac{e^{i(\theta'-\phi)} + e^{-i(\theta'-\phi)}}{2}e^{i\theta'}\,\mathrm{d}\theta' \quad \text{by Euler's formula} \\
&= \frac{\epsilon}{2}\frac{1}{2\pi}\int_0^{2\pi}(e^{i\theta'}e^{-i\phi} + e^{-i\theta'}e^{i\phi})e^{i\theta'}\,\mathrm{d}\theta' \\
&= \frac{\epsilon}{2}\frac{1}{2\pi}\left[e^{-i\phi}\underbrace{\int_0^{2\pi} e^{i2\theta'}\,\mathrm{d}\theta'}_{0} + e^{i\phi}\underbrace{\int_0^{2\pi}\mathrm{d}\theta'}_{2\pi}\right] \\
&= \frac{\epsilon}{2}e^{i\phi}
\end{aligned}$$

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 :

$$\begin{aligned}
\frac{\mathrm{d}\delta_m(\theta,t)}{\mathrm{d}t} = \frac{\mathrm{d}(m(\theta,t) - m_0)}{\mathrm{d}t} = \frac{\mathrm{d}m(\theta,t)}{\mathrm{d}t} &= -m(\theta,t) + f[I(\theta,t)] \\
&= -m(\theta,t) + I(\theta,t) \\
&\text{Indeed : } I(m_0) > 0 \text{ and by continuity, } I(m_0 + \delta m) > 0 \\
&= -m(\theta,t) + \int_0^{2\pi}(J_0 + J_1\cos(\theta - \theta'))m(\theta',t)\,\mathrm{d}\theta'
\end{aligned}$$

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 ▷[*TD*] :

$$\begin{aligned}
\frac{\mathrm{d}\delta_m(\theta,t)}{\mathrm{d}t} &= -(m_0 + \delta_m(\theta,t)) + h_0 + \frac{1}{2\pi}\int_0^{2\pi}(J_0 + J_1\cos(\theta - \theta'))(m_0 + \delta_m(\theta',t))\,\mathrm{d}\theta' \\
&= \underbrace{-m_0 + h_0 + \frac{1}{2\pi}\int_0^{2\pi}(J_0 + J_1\cos(\theta - \theta'))m_0\,\mathrm{d}\theta'}_{0 \quad \text{(equilirbium)}} - \delta_m(\theta,t) + \frac{1}{2\pi}\int_0^{2\pi}(J_0 + J_1\cos(\theta - \theta'))\delta_m(\theta',t))\,\mathrm{d}\theta'
\end{aligned}$$

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

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

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

$$\begin{aligned}
\frac{\mathrm{d}M}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{2\pi}\int_0^{2\pi}\delta_m(\theta',t)\,\mathrm{d}\theta'\right) \\
&= \frac{1}{2\pi}\int_0^{2\pi}\frac{\mathrm{d}\delta_m(\theta',t)}{\mathrm{d}t}\,\mathrm{d}\theta' \\
&= \frac{1}{2\pi}\int_0^{2\pi}\left[-\delta_m(\theta',t) + J_0 M(t) + J_1\frac{e^{i\theta'}\overline{C(t)} + e^{-i\theta'}C(t)}{2}\right]\mathrm{d}\theta' \\
&= -\underbrace{\frac{1}{2\pi}\int_0^{2\pi}\delta_m(\theta',t)\,\mathrm{d}\theta'}_{M(t)} + \frac{J_0 M(t)}{2\pi}\underbrace{\int_0^{2\pi}\mathrm{d}\theta'}_{2\pi} + \frac{J_1}{2}\left(\frac{\overline{C(t)}}{2\pi}\underbrace{\int_0^{2\pi} e^{i\theta'}\,\mathrm{d}\theta'}_{0} + \frac{C(t)}{2\pi}\underbrace{\int_0^{2\pi} e^{-i\theta'}\,\mathrm{d}\theta'}_{0}\right) \\
&= (J_0 - 1)\, M
\end{aligned}$$

- Variable C

$$\begin{aligned}
\frac{\mathrm{d}C}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{2\pi}\int_0^{2\pi}\delta_m(\theta',t)e^{i\theta'}\,\mathrm{d}\theta'\right) \\
&= \frac{1}{2\pi}\int_0^{2\pi}\frac{\mathrm{d}\delta_m(\theta',t)}{\mathrm{d}t}e^{i\theta'}\,\mathrm{d}\theta' \\
&= \frac{1}{2\pi}\int_0^{2\pi}\left[-\delta_m(\theta',t) + J_0 M(t) + J_1\frac{e^{i\theta'}\overline{C(t)} + e^{-i\theta'}C(t)}{2}\right]e^{i\theta'}\,\mathrm{d}\theta' \\
&= -\underbrace{\frac{1}{2\pi}\int_0^{2\pi}\delta_m(\theta',t)e^{i\theta'}\,\mathrm{d}\theta'}_{C(t)} + \frac{J_0 M(t)}{2\pi}\underbrace{\int_0^{2\pi} e^{i\theta'}\,\mathrm{d}\theta'}_{0} + \frac{J_1}{2}\left(\frac{\overline{C(t)}}{2\pi}\underbrace{\int_0^{2\pi} e^{2i\theta'}\,\mathrm{d}\theta'}_{0} + \frac{C(t)}{2\pi}\underbrace{\int_0^{2\pi}\mathrm{d}\theta'}_{2\pi}\right) \\
&= \left(\frac{J_1}{2} - 1\right) C(t)
\end{aligned}$$

⑧ *Conditions for stability*

The variables M and C follow linear first order equations, whose solutions are exponential functions. Therefore, the network activity is stable under two conditions :

- $M(t) = M(0)e^{(J_0-1)t} \to 0 \iff J_0 - 1 < 0 \iff J_0 < 1$
  In this case, the perturbation vanishes. Otherwise, any perturbation leads to exponentially amplifying deviation from the equilibrium.
- $C(t) = C(0)e^{\left(\frac{J_1}{2}-1\right)t} \to 0 \iff J_1 < 2$
  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 $h(\theta)$:

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

Therefore, the same results apply with an additional term in the expressions.
For the derivative of the perturbation $\frac{\mathrm{d}\delta_m(\theta,t)}{\mathrm{d}t}$:

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

For $\frac{\mathrm{d}M}{\mathrm{d}t}$, it induces an additional term $\frac{1}{2\pi}\int_0^{2\pi}\epsilon\cos(\theta')\,\mathrm{d}\theta' = 0$, which does not change the expression.
For $\frac{\mathrm{d}C}{\mathrm{d}t}$, it induces an additional term $\frac{1}{2\pi}\int_0^{2\pi}\epsilon\underbrace{\cos(\theta')}_{\frac{e^{i\theta'}+e^{-i\theta'}}{2}}e^{i\theta'}\,\mathrm{d}\theta' = \frac{\epsilon}{2}\frac{1}{2\pi}\int_0^{2\pi}(e^{2i\theta'}+1)\,\mathrm{d}\theta' = \frac{\epsilon}{2}$.

Thus the dynamics of the order parameters become :

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

10 *Activity profile at equilibrium*

- Under the conditions $J_0 < 1$, $J_1 < 2$, 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 :

$$\frac{\mathrm{d}C}{\mathrm{d}t} = 0 \implies C^* = \frac{\epsilon/2}{1 - J_1/2}$$

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.

- The parameters m_0 and h_0 are related by the expression of the equilibrium state (question 2) :

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

- The parameters m_1 and ϵ can be related through the expression of the equilibrium C^* :

On the one hand, the equation of its dynamics gives $C^* = \frac{\epsilon/2}{1 - J_1/2}$ (question 10).
On the other hand, integrating its definition (involving the parameter m_1) gives :

$$C = \frac{1}{2\pi}\int_0^{2\pi}(m_0 + m_1\cos(\theta'))e^{i\theta'}\,\mathrm{d}\theta' = \underbrace{\frac{1}{2\pi}\int_0^{2\pi}m_0 e^{i\theta'}\,\mathrm{d}\theta'}_{0} + \frac{1}{2\pi}\int_0^{2\pi}m_1\frac{e^{i\theta'}+e^{-i\theta'}}{2}e^{i\theta'}\,\mathrm{d}\theta' = \frac{m_1}{2} \quad \text{(as before)}$$

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. $J_1 > 2J_0$.