Neural Networks and Biological Modeling

Professor Wulfram Gerstner
Laboratory of Computational Neuroscience

Answers – Question set 13

Exercise 1: Low-dimensional dynamics in a field model

Note: we use the shorthand notation $D\boldsymbol{z} = \rho(\boldsymbol{z})d\boldsymbol{z}$ for the integral with respect to the density of neurons.

1.1 If the field is given by the linear combination:

$$h(t, \boldsymbol{z}) = \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\kappa_\mu(t) \tag{1}$$

then by projection on the function f_μ, we obtain:

$$\begin{aligned}\int_V f_\mu(\boldsymbol{z})h(t,\boldsymbol{z})D\boldsymbol{z} &= \int_V f_\mu(\boldsymbol{z}) \sum_{\mu'=1}^{D} f_{\mu'}(\boldsymbol{z})\kappa_{\mu'}(t)D\boldsymbol{z} = \sum_{\mu'=1}^{D} \kappa_{\mu'}(t) \int_V f_\mu(\boldsymbol{z})f_{\mu'}(\boldsymbol{z})D\boldsymbol{z} \\ &= \sum_{\mu'=1}^{D} \kappa_{\mu'}(t)\delta_{\mu\mu'} = \kappa_\mu(t)\end{aligned} \tag{2}$$

due to the orthonormality of the functions f_μ.

Thus, $\kappa_\mu(t) = \int_V f_\mu(\boldsymbol{z})h(t,\boldsymbol{z})D\boldsymbol{z}$ is the projection of the field $h(t,\cdot)$ on the function f_μ.

1.2

The steady-state $h(t,\boldsymbol{z}) = \bar{h}(\boldsymbol{z})$ is obtained by setting the time derivative $\frac{d}{dt}h(t,\boldsymbol{z})$ to zero:

$$\frac{d}{dt}\bar{h}(\boldsymbol{z}) = 0 = -\frac{1}{\tau}\bar{h}(\boldsymbol{z}) + J \int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}' \tag{3}$$

which gives us:

$$\begin{aligned}\bar{h}(\boldsymbol{z}) &= \tau J \int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}' \\ &= \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z}) \left(\tau J \int_V g_\mu(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}'\right) = \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\bar{\kappa}_\mu\end{aligned} \tag{4}$$

Method 1. The steady-state coefficients $\bar{\kappa}_\mu$ are obtained by identification: $\bar{\kappa}_\mu = \tau J \int_V g_\mu(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}$.

Method 2. Alternatively, the same expression for $\bar{\kappa}_\mu$ is obtained by projecting Eq.(4) onto f_μ:

$$\begin{aligned}\bar{\kappa}_\mu &= \int_V f_\mu(\boldsymbol{z})\bar{h}(\boldsymbol{z})D\boldsymbol{z} = \int_V f_\mu(\boldsymbol{z}) \sum_{\mu'=1}^{D} f_{\mu'}(\boldsymbol{z}) \left(\tau J \int_V g_{\mu'}(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}'\right) D\boldsymbol{z} \\ &= \sum_{\mu'=1}^{D} \left(\int_V f_\mu(\boldsymbol{z})f_{\mu'}(\boldsymbol{z})D\boldsymbol{z}\right) \left(\tau J \int_V g_{\mu'}(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}'\right) \\ &= \sum_{\mu'=1}^{D} \delta_{\mu\mu'} \left(\tau J \int_V g_{\mu'}(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}'\right) = \tau J \int_V g_\mu(\boldsymbol{z}')\phi(\bar{h}(\boldsymbol{z}'))D\boldsymbol{z}'\end{aligned} \tag{5}$$

Moreover, the field $\bar{h}(\boldsymbol{z})$ in the integral can be replaced by the linear combination: $\bar{h}(\boldsymbol{z}) = \sum_{\nu=1}^{D} f_\nu(\boldsymbol{z})\bar{\kappa}_\nu$, hence giving the closed-form expression:

$$\bar{\kappa}_\mu = \tau J \int_V g_\mu(\boldsymbol{z})\phi(\bar{h}(\boldsymbol{z}))D\boldsymbol{z} = \tau J \int_V g_\mu(\boldsymbol{z})\phi\left(\sum_{\nu=1}^{D} f_\nu(\boldsymbol{z})\bar{\kappa}_\nu\right) D\boldsymbol{z} \tag{6}$$

1.3

From the expression of the linear combination (Eq.(1)), we have:

$$\frac{d}{dt}h(t,\boldsymbol{z}) = \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\frac{d}{dt}\kappa_\mu(t) \tag{7}$$

On the other hand, the derivative of the field is given by:

$$\frac{d}{dt}h(t,\boldsymbol{z}) = -\frac{1}{\tau}h(t,\boldsymbol{z}) + J\int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}' \tag{8}$$

Replacing h by Eq.(1), we get:

$$\begin{aligned}\frac{d}{dt}h(t,\boldsymbol{z}) &= -\frac{1}{\tau}\sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\kappa_\mu(t) + J\int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}' \\ &= \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\left(-\frac{1}{\tau}\kappa_\mu(t) + J\int_V g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}'\right)\end{aligned} \tag{9}$$

By identification of Eqs.(7) and (9), one gets directly:

$$\frac{d}{dt}\kappa_\mu(t) = -\frac{1}{\tau}\kappa_\mu(t) + J\int_V g_\mu(\boldsymbol{z})\phi(h(t,\boldsymbol{z}))D\boldsymbol{z} \tag{10}$$

Again, the field $h(t,\boldsymbol{z})$ in the integral can be replaced by the linear combination: $h(t,\boldsymbol{z}) = \sum_{\nu=1}^{D} f_\nu(\boldsymbol{z})\kappa_\nu(t)$ to obtain a closed-form expression for the dynamics of the coefficients κ_μ.

1.4

Let $h(t,\boldsymbol{z}) = \sum_\mu f_\mu(\boldsymbol{z})\kappa_\mu(t) + \Delta h(t,\boldsymbol{z})$. Thus, we have:

$$\frac{d}{dt}h(t,\boldsymbol{z}) = \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\frac{d}{dt}\kappa_\mu(t) + \frac{d}{dt}\Delta h(t,\boldsymbol{z}) \tag{11}$$

On the other hand, the dynamics are given by:

$$\begin{aligned}\frac{d}{dt}h(t,\boldsymbol{z}) &= -\frac{1}{\tau}\left(\sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\kappa_\mu(t) + \Delta h(t,\boldsymbol{z})\right) + J\int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}' \\ &= \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\left(-\frac{1}{\tau}\kappa_\mu(t) + J\int_V g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}'\right) - \frac{1}{\tau}\Delta h(t,\boldsymbol{z})\end{aligned} \tag{12}$$

By identification of Eqs.(11) and (12), one gets:

$$\frac{d}{dt}\Delta h(t,\boldsymbol{z}) = -\frac{1}{\tau}\Delta h(t,\boldsymbol{z}) \quad \Rightarrow \quad \Delta h(t,\boldsymbol{z}) = e^{-t/\tau}\Delta h(0,\boldsymbol{z})$$

Thus, in the general case: $h(t,\boldsymbol{z}) = \sum_\mu f_\mu(\boldsymbol{z})\kappa_\mu(t) + e^{-t/\tau}\Delta h(0,\boldsymbol{z})$.

For any initial condition, the field asymptotically becomes a linear combination of the functions f_μ, and the residual term $\Delta h(t, \boldsymbol{z})$ decays exponentially. This is why Eq.(1) is a good assumption.

1.5 Coming back to Eq.(9), the dynamics can now be written (with the new terms highlighted in blue):

$$\begin{aligned}\frac{d}{dt}h(t,\boldsymbol{z}) &= -\frac{1}{\tau}\sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\kappa_\mu(t) + J\int_V \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}' + \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})I_\mu(t) \\ &= \sum_{\mu=1}^{D} f_\mu(\boldsymbol{z})\left(-\frac{1}{\tau}\kappa_\mu(t) + J\int_V g_\mu(\boldsymbol{z}')\phi(h(t,\boldsymbol{z}'))D\boldsymbol{z}' + I_\mu(t)\right)\end{aligned} \tag{13}$$

so that we get the dynamics:

$$\frac{d}{dt}\kappa_\mu(t) = -\frac{1}{\tau}\kappa_\mu(t) + J\int_V g_\mu(\boldsymbol{z})\phi(h(t,\boldsymbol{z}))D\boldsymbol{z} + I_\mu(t) \tag{14}$$

The external input thus only results in an external drive to the dynamics of the hidden variables κ_μ. This affects the fixed points: the steady state equation (Eq.(6)) is now:

$$\bar{\kappa}_\mu = \tau J\int_V g_\mu(\boldsymbol{z})\phi\left(\sum_{\nu=1}^{D} f_\nu(\boldsymbol{z})\bar{\kappa}_\nu\right)D\boldsymbol{z} + I_\mu(t) \tag{15}$$

Exercise 2: Application: ring model

2.1 The density of neurons is given by $\rho(z) = 1/(2\pi)$. The measure of the distribution is thus: $Dz = \rho(z)dz = \frac{dz}{2\pi}$. The orthonormality is satisfied:

$$\int_0^{2\pi} f_1^2 Dz = \int_0^{2\pi} f_2^2 Dz = \int_0^{2\pi} 2\cos(z)^2\frac{dz}{2\pi} = 1 \quad ; \quad \int_0^{2\pi} f_1 f_2 Dz = \int_0^{2\pi} 2\cos(z)\sin(z)\frac{dz}{2\pi} = 0$$

2.2 We look for a steady-state in the form of $\bar{h}(z) = A\cos(z) = A/\sqrt{2}f_1(z)$, i.e. $\bar{\kappa}_1 = A/\sqrt{2}$, $\bar{\kappa}_2 = 0$. The steady-state equation, Eq.(6), writes:

$$\begin{aligned}\bar{\kappa}_1 = A/\sqrt{2} &= \tau J\int_0^{2\pi}\sqrt{2}\cos(z)\phi(A\cos z)\frac{dz}{2\pi} \\ &= \tau J\int_{-\pi/2}^{\pi/2}\sqrt{2}\cos(z)R\frac{dz}{2\pi} = \sqrt{2}\tau JR\frac{1}{2\pi}\underbrace{\int_{-\pi/2}^{\pi/2}\cos(z)dz}_{2} \\ \Rightarrow \quad & A = 2\tau JR/\pi\end{aligned} \tag{16}$$

where we used the fact that $\phi(A\cos(z)) = R\mathbf{1}\{A\cos(z) > 0\} = R\mathbf{1}\{-\pi/2 < z < \pi/2\}$ for $A > 0$. For $\bar{\kappa}_2$, we get the self-consistent equation:

$$0 = \bar{\kappa}_2 = \tau J\int_0^{2\pi}\sqrt{2}\sin(z)\phi(A\cos z)\frac{dz}{2\pi} = \tau J\int_{-\pi/2}^{\pi/2}\sqrt{2}\sin(z)R\frac{dz}{2\pi} = 0 \tag{17}$$

Thus, $\bar{h}(z) = 2\tau JR\cos(z)/\pi = \bar{\kappa}_1 f_1(z) + 0\cdot f_2(z)$ is a steady-state of the field dynamics.

2.3 We have seen that $\kappa_2(t) = 0$ is a steady-state. Thus, we look for a solution of the form: $h(t,z) = A(t)\cos(z) = \kappa_1(t)\sqrt{2}\cos(z)$, with $\kappa_2 = 0$ and initial condition $\kappa_1(0) = A_0/\sqrt{2}$.

From Eq.(10), one obtains:

$$\begin{aligned}\frac{d}{dt}\kappa_1 &= -\frac{1}{\tau}\kappa_1 + J\int_0^{2\pi}\sqrt{2}\cos(z)\phi(\sqrt{2}\kappa_1\cos z)\frac{dz}{2\pi} = -\frac{1}{\tau}\kappa_1 + J\int_{-\pi/2}^{\pi/2}\sqrt{2}\cos(z)R\frac{dz}{2\pi} \\ &= -\frac{1}{\tau}\kappa_1 + \sqrt{2}JR/\pi\end{aligned} \tag{18}$$

Given $A(t) = \sqrt{2}\kappa_1(t)$ and the initial condition $A(0) = A_0$, we obtain $A(t) = A_0 + (1 - e^{-t/\tau})(\bar{A} - A_0)$, where $\bar{A} = 2\tau JR/\pi$.

The exact same computations can be done for $h(t, z) = A(t)\sin(z)$, except that now, $\kappa_1(t) = 0$ is a steady-state, and $A(t) = \sqrt{2}\kappa_2(t)$ follows the exact same dynamics as Eq.(18).

2.4 Let $(r(t), \theta(t))$ be the polar coordinates of the two-dimensional vector $\boldsymbol{\kappa}(t) = (\kappa_1(t), \kappa_2(t))$, and $(\hat{e}_r, \hat{e}_\theta)$ be the (time-dependent) unit vectors of the polar coordinate system associated with $\boldsymbol{\kappa}$. In this polar coordinate system, we have:

$$\boldsymbol{\kappa} = r\hat{e}_r \ , \dot{\boldsymbol{\kappa}} = \dot{r}\hat{e}_r + r\dot{\theta}\hat{e}_\theta$$

where the dot denotes the time derivative. The vector $\boldsymbol{f}(z) = \boldsymbol{g}(z) = \sqrt{2}(\cos(z), \sin(z))$ is:

$$\boldsymbol{f}(z) = \boldsymbol{g}(z) = \sqrt{2}\cos(z - \theta)\hat{e}_r + \sqrt{2}\sin(z - \theta)\hat{e}_\theta$$

Finally, the field is given by the scalar product:

$$h(t, z) = \boldsymbol{f}(z) \cdot \boldsymbol{\kappa}(t) = \sqrt{2}r(t)\cos(z - \theta(t))$$

In vector form, the dynamics of $\boldsymbol{\kappa}$ (Eq.(10)) read:

$$\dot{\boldsymbol{\kappa}} = -\frac{1}{\tau}\boldsymbol{\kappa} + J\int_0^{2\pi} \boldsymbol{g}(z)\phi(h(t, z))\frac{dz}{2\pi}$$

By identification of the components along $\hat{e}_r$ and $\hat{e}_\theta$, we get:

$$\begin{aligned}
\text{on } \hat{e}_r : \qquad \dot{r} &= -\frac{1}{\tau}r + J\int_0^{2\pi} \sqrt{2}\cos(z-\theta)\phi(\sqrt{2}r\cos(z-\theta))\frac{dz}{2\pi} \\
&= -\frac{1}{\tau}r + J\int_0^{2\pi} \sqrt{2}\cos(z)\phi(\sqrt{2}r\cos(z))\frac{dz}{2\pi} \\
&= -\frac{1}{\tau}r + \sqrt{2}JR/\pi \\
\text{on } \hat{e}_\theta : \qquad r\dot{\theta} &= J\int_0^{2\pi} \sqrt{2}\sin(z-\theta)\phi(\sqrt{2}r\cos(z-\theta))\frac{dz}{2\pi} \\
&= J\int_0^{2\pi} \sqrt{2}\sin(z)\phi(\sqrt{2}r\cos(z))\frac{dz}{2\pi} = 0
\end{aligned} \tag{19}$$

where we used again the results of Eqs.(16) and (17).

Thus, given any initial condition $(r(0), \theta(0))$, the vector $\boldsymbol{\kappa}(t)$ converges to a point on the circle of radius $\bar{r} = \sqrt{2}\tau JR/\pi$, according to:

$$r(t) = r(0) + (1 - e^{-t/\tau})(\bar{r} - r(0))$$

while the angle $\theta(t) = \theta(0)$ stays constant.

The flow of the dynamics in the phase plane of (κ_1, κ_2) is shown on fig.1.

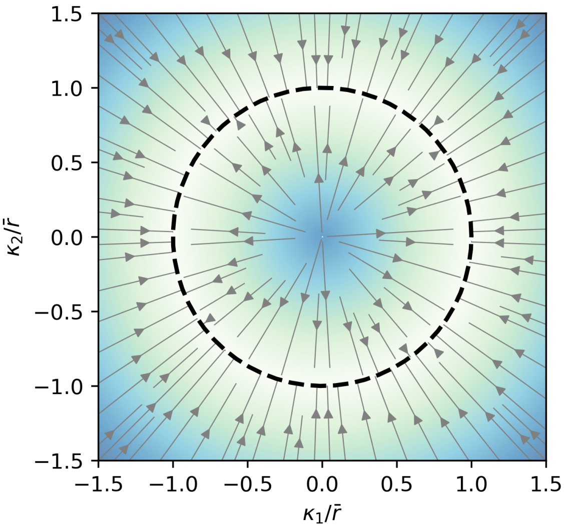

Figure 1: Flow of the dynamics in the phase plane of (κ_1, κ_2) for the ring model. The continuous set of attractors forms a circle (dashed black line).