Theoretical Neuroscience II
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Exercise 2: State Space Analysis

Introduction

The activity of neurons in a recurrent network always approaches the steady-state according to its current state. Considering a recurrent network as a linear system which the change of activity dependent on the connectivity (***A***, also A in the code), the activity (***v***, also v in the code) and the input of the population (***b***, also b in the code), it can be modeled as the following equation:

$$\frac{d\boldsymbol{v}}{d\boldsymbol{t}} = \boldsymbol{A} \cdot \boldsymbol{v} + \boldsymbol{b}$$

To understand the dynamic of activities under such a model, one may simplify it as a two-neuron network which can be mathematically described as:

$$\begin{pmatrix} dx/_{dt} \\ dy/_{dt} \end{pmatrix} = \begin{pmatrix} a_{xx} & a_{xy} \\ a_{yx} & a_{yy} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}$$

In the above equation, x and y represent the activities of the two neurons respectively; b_1 and b_2, the constant input; and the variable in the matrix, the synaptic strength of one to another. When one tries to analyse the system, there are a certain activity sets which gives one of the changes of activity to be 0. When they are plotted, a line is resulted which called an isocline or a nullcline. The point of intersect by two isoclines will be the steady-state(s) of a system, where any sets of activity that equals to it will not change anymore. To calculate the steady-state in the above system, it is the negative product of the inverse of ***A*** and ***b***. In case of the above system which the determinant of the matrix is not zero, in the absence of a constant input, this steady-state lies in the origin, i.e. both activities are 0. Also, since two isoclines are straight lines, a maximum of one steady-state can exist when simulated with a constant input. But in case of a non-linear network, since the isoclines can be curves and therefore multiple intersects and hence more than one steady-state is possible. Notably, not all steady-states are stable fixed points.

In this assignment, we are trying to investigate the properties and the time-development of a linear network, followed by an extra non-linear element, a sigmoidal activation function, putting on top of the responsiveness of the neurons.

Method

In this exercise, a recurrent network with 2 neurons was studied. The value of the connection matrix ***A*** and the steady-state $\boldsymbol{v}_{ss}$ was as followed:

$$\boldsymbol{A} = \begin{pmatrix} -2 & 3 \\ -3 & 2 \end{pmatrix} \qquad \boldsymbol{v}_{ss} = \begin{pmatrix} 10 \\ 10 \end{pmatrix}$$

In Task A, the constant input ***b***, the equations of isoclines and the point of intersection was determined analytically.

In Task B, based the characteristic polynomial of the given matrix, the eigenvalues were obtained analytically and hence the behaviour of the network was predicted. Using the provided function file *LinearOrder2.m*, the state space was mapped and used to plot the time-development of two different initial conditions.

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In Task C, a sigmoidal activation function was added to make the recurrent network non-linear. The network was modelled as

$$\frac{dv}{dt} = F(A \cdot v + b); \;\; F(x) = F_{max}\frac{x^2}{\kappa^2 + x^2}, \qquad x \geq 0$$

The sigmoidal function was computed using the provided function file *Factivation.m*. The function required inputs of F_{max} (defined as 40), κ (defined as $\in$ [2, 3, 4, 5, and 6]) and an activity. The initial activity vector was defined as:

$$v_0 = \binom{11}{9}$$

The activity vectors (v in the code) were computed over a period of time t = 10 with steps (dt in the code) of 0.01. To define activity vectors first the equilibrium state was determined using the following equation which is dependent on connectivity matrix (A), input vector (v_i) and constant input (b)

$$v_i^{ss} = F(A \cdot v_i + b)$$

After determining the equilibrium state, the next activity vector (v_{i+1}) is defined using this equation which allows the activity vector to reach an equilibrium based on the equilibrium state and time:

$$v_{i+1} = v_i^{ss} + (v_i - v_i^{ss})\exp(-\Delta t)$$

To plot the trajectory into the state space with the isoclines the code used was a modification of the LinearOrder2.m function provided. The function *plotstatespaceisoclines.m* was created based on said function and this was used to graph the trajectory. In order to do the time evolution in the state-space, tend parameter in the code (the finishing time of the simulation) was changed to values of 0.5, 1.5, 2 or 3.

Results and Discussion

Task A: Calculating the constant input and the equations of the isoclines of the system provided

1. For the constant input ***b***, when $0 = A \cdot v_{ss} + b$

$$0 = \begin{pmatrix} -2 & 3 \\ -3 & 2 \end{pmatrix} \cdot \binom{10}{10} + \boldsymbol{b}$$

$$0 = \binom{10}{-10} + \boldsymbol{b}$$

$$\boldsymbol{b} = \binom{-10}{10}$$

2. For the equations of both isoclines, when ${}^{dx}/_{dt} = 0 \; or \; {}^{dy}/_{dt} = 0$

$$a_{11}x + a_{12}y + b_1 = 0 \; or \; a_{21}x + a_{22}y + b_2$$

$$-2x + 3y - 10 = 0 \; or \; -3x + 2y + 10 = 0$$

3. For the point of intersection,

$$\begin{cases} -2x + 3y - 10 = 0 \\ -3x + 2y + 10 = 0 \end{cases}$$

$$\begin{cases} -6x = 30 - 9y \\ -6x = -20 - 4y \end{cases}$$

$$30 - 9y = -20 - 4y$$

$$50 = 5y$$

$$y = 10$$

$$-2x + 30 - 10 = 0$$

$$x = 10$$

Hence, the point of intersection is (10, 10) and equals to the chosen steady-state v_{ss}.

Task B: Stable behaviour of the system was observed

1. To solve the characteristic equation for eigenvalues λ_1 and λ_2,

$$|A - \lambda I| = \begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix} = (a_{11} - \lambda)(a_{22} - \lambda) - a_{12}a_{21} = 0$$

$$(-2 - \lambda)(2 - \lambda) - \big(3 \cdot (-3)\big) = 0$$

$$-4 + 2\lambda - 2\lambda + \lambda^2 + 9 = 0$$

$$\lambda^2 + 5 = 0$$

$$\boldsymbol{\lambda = \pm\sqrt{5}\, i}$$

Based on the eigenvalues, a neutrally stable spiralling behaviour is expected, since the real values are zero with both positive and negative imaginary parts. Thus, the trajectories should orbit around a fixed point.

The state-space and the time-developments of two initial conditions were plotted. For the first condition, $v_0 = \begin{pmatrix} 2 \\ 12 \end{pmatrix}$ (*Fig. 1a* and *1b*) while for the second condition $v_0 = \begin{pmatrix} 4 \\ 6 \end{pmatrix}$ (*Fig. 2a* and *2b*). For *Fig. 1a* and *2a*, the two isoclines of the system can be seen to intersect at the coordinate point (10, 10), and the trajectories are an ellipse which orbit around the point of intersection, meaning the system never reach steady-state. Furthermore, the trajectory in the state-space figure and the time-evolution system follows a similar pattern. For both initial inputs, as the trajectory moves from left to right, the graphs of time-evolution also rises. When the trajectory moves from right to left, the time-evolution graphs also slopes downwards. This pattern between trajectory and time evolution was repeated throughout.

On the other hand, the orbital in *Fig. 1a* and *1b* is more enlarged than in *Fig. 2a* and *2b*, since the first input condition is further away from the $\boldsymbol{v_{ss}}$. In addition, the frequencies of the time-evolutions in *Fig. 1b* were the same of *Fig. 2b*, but with greater amplitude. From this, we can say that increasing input argument causes an increase in the rate of change of trajectory.

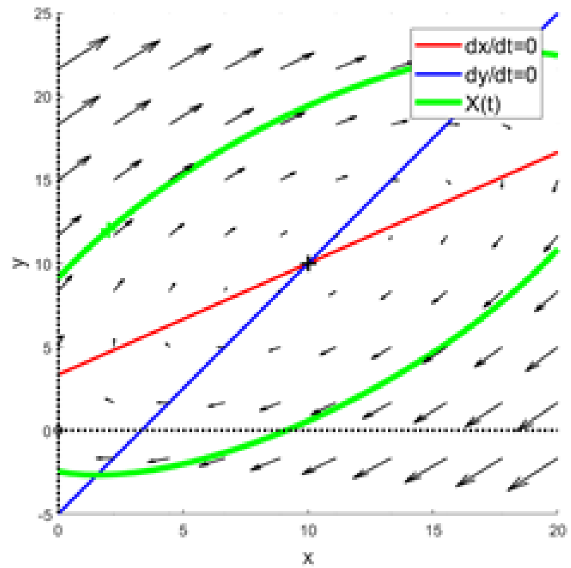

Fig. 1a The state-space and trajectory of the system for input of $\boldsymbol{v_0} = \binom{2}{12}$. X(t) denoted the trajectory of ***v***, whereas the blue and the red lines indicated the two isoclines. Arrows represented the relative size of $\frac{\boldsymbol{dv}}{dt}$.

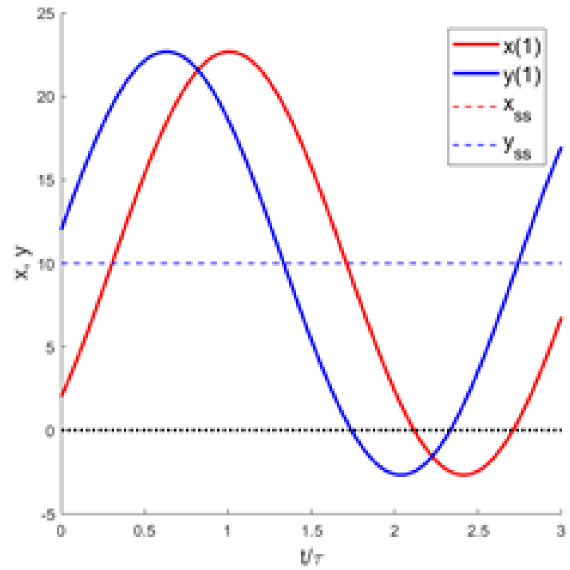

Fig. 1b The time-evolution of the system for input of $v_0 = \binom{2}{12}$. x(1) and y(1) indicated the time evolution of the two systems and x_{ss} and y_{ss} indicates their steady-states.

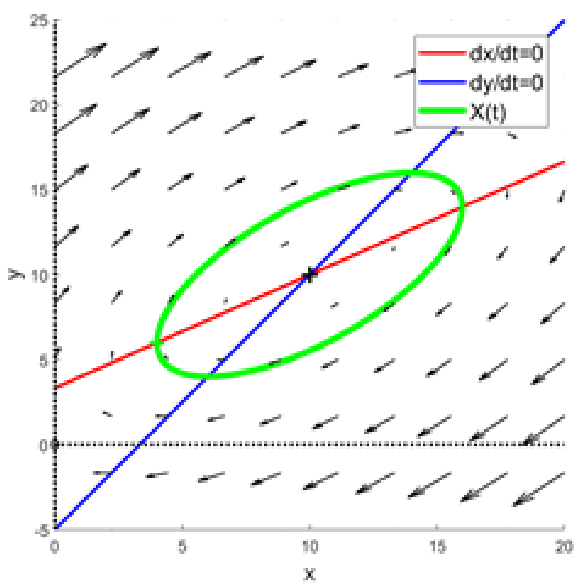

Fig. 2a The state-space and trajectory of the system for input of $\boldsymbol{v_0} = \binom{4}{6}$. X(t) denoted the trajectory of ***v***, whereas the blue and the red lines indicated the two isoclines. Arrows represented the relative size of $\frac{\boldsymbol{dv}}{dt}$.

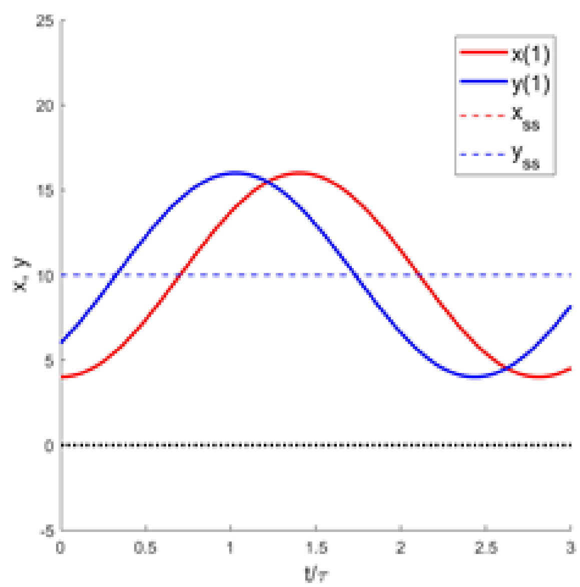

Fig. 2b The time-evolution of the system for input of $v_0 = \binom{4}{6}$. x(1) and y(1) indicated the time evolution of the two systems and x_{ss} and y_{ss} indicates their steady-states.

Detailed the time-evolution of the trajectory can be seen in *Fig. 3*.

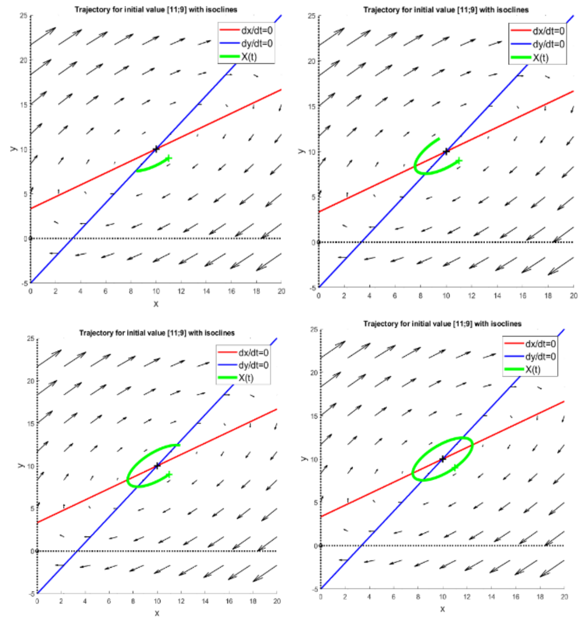

Fig.3 Time evolution of trajectory in the state space. The trajectory follows the directional property and the gradient and did not reach the stable point.

Task C

For the non-linear recurrent network, a sigmoidal activation function was added to model the behaviour of the system. For κ = 2 (*Fig. 4*, upper panel), the system did not reach a steady state and it just fluctuates between states. The amplitude and frequency were diminishing as time went by, and after a certain time it reached a point in which there was no observable change in the oscillation.

As the value of κ increased till 4, the initial states which did not matter for the smallest κ seem to be differentiating for this κ. The general appearance of the graph is maintained, amplitude and frequency diminished inversely with respect to time and the system reached the same constant oscillation state.

For κ = 5 or 6, the dampening of the oscillation was much more noticeable and each activity reached a steady state equal. The frequency and amplitude were both decreasing with time. There were oscillations but with more time it was very likely that it would reach a steady state of activity.

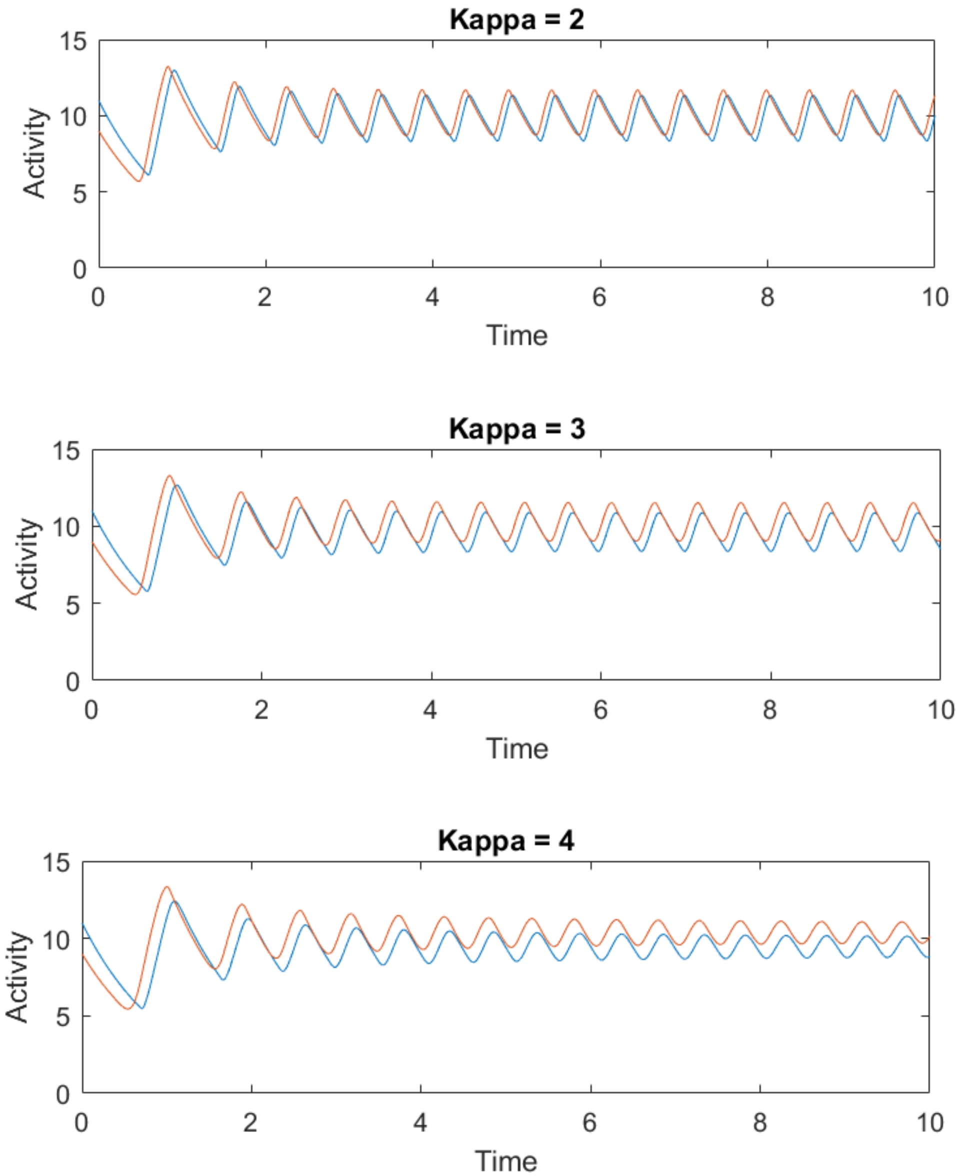

Fig.*4 Activity as a function of time for κ = 2, 3 and 4.* The amplitude and frequency gradually decreased and stabilised to a state of constant oscillation.

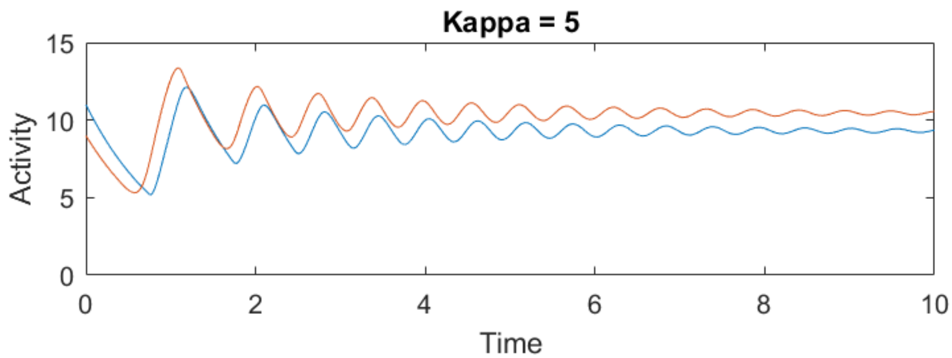

Fig.5 Differential equation of activity as a function of time for κ = 5. Dampening effect could be seen and a steady state of no oscillation seemed possible to attain. Amplitude and frequency decreased with time.

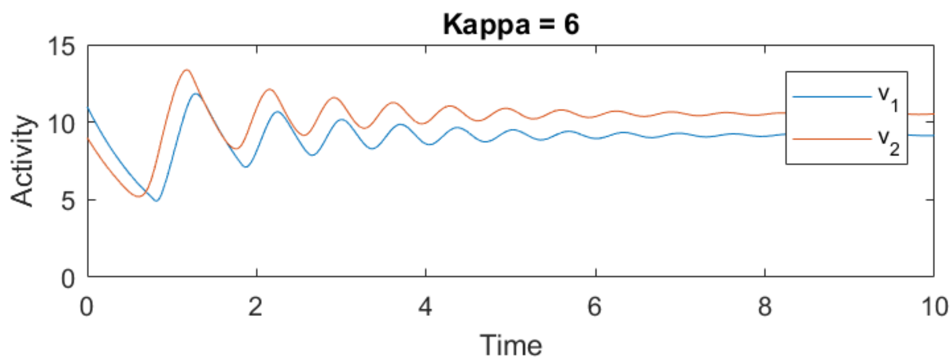

Fig. 6 Differential equation of activity as a function of time for κ = 6. A steady state reached with no oscillation in the observable time. Dampening effect was clear, amplitude and frequency reached zero.

The κ is a very important parameter of the function as it has a direct effect on whether and how soon can a system reach a steady state. It is possible for any of the systems plotted (with varying κ) to reach steady state, since they were modelled after the same equation independent of the κ, however as we can see there is no noticeable dampening for smaller κ which would mean a much longer period of time before the system can in reality reach a steady state, for a small enough κ it would be virtually infinite. Dampening effect is related to the value of κ.

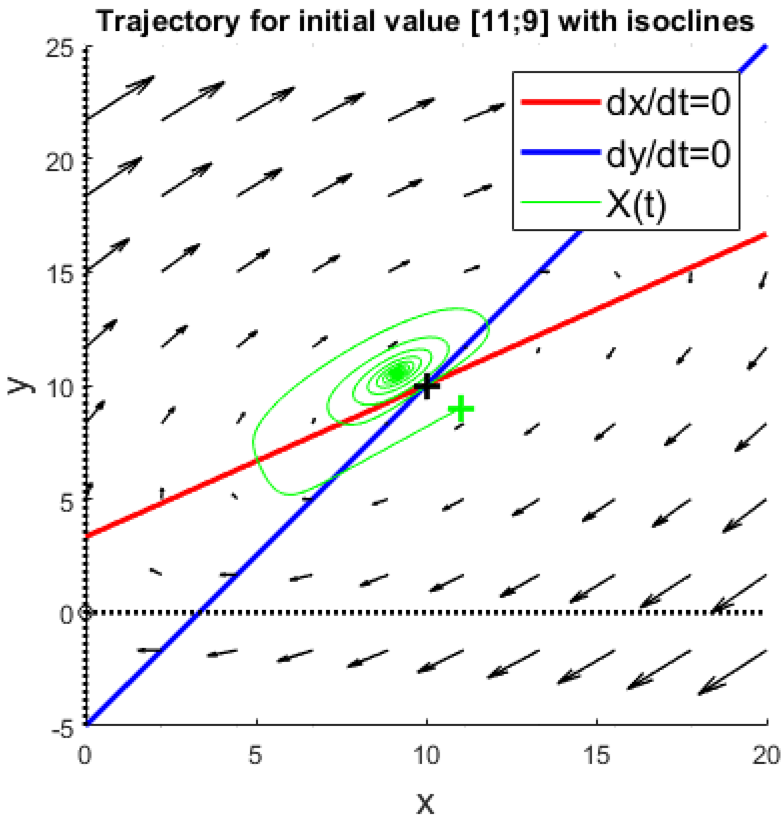

Fig. 7 Trajectory of activity as a function of time for κ = 6. A steady state reached with a spiral pattern.