

Last Name .....

First Name.....

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# Biological Modelling of Neural Networks Exam

July 2, 2021

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- Write your name in legible letters on top of this page.
- The exam lasts 180 min.
- Write **all** your answers in a legible way on the exam (no extra sheets).
- No documentation is allowed apart from 1 sheet A5 of **handwritten** notes.
- No calculator is allowed.
- Have your student card displayed before you on your desk.
- Check that your exam has **12 pages**. Page 12 is empty.

Evaluation:

1. .... / 21 pts [Phase plane]
2. .... / 7 pts [Mean-field]
3. .... / 10 pts [Stochastic spike arrival]
4. .... / 6 pts (+2 BONUS points) [Separation of time scales]

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Total: .... / 44 pts (+ 2 BONUS points)

## 1 Phase Plane Analysis (21 points)

A model of a non-standard synapse describes the momentary configuration by the interaction of two molecules  $x$  and  $y$  with the following phenomenological equations:

$$\tau_x \frac{dx}{dt} = (1 - x) - xy \quad (1)$$

$$\tau_y \frac{dy}{dt} = -y + F(x) \quad (2)$$

where  $\tau_x$  and  $\tau_y$  are positive time constants and the function  $F$  is:

$$F(x) = -2(x - 1)(x - 3) \text{ for } x \leq 3 \text{ and}$$

$$F(x) = +2(x - 3)(x - 5) \text{ for } x > 3.$$

The value  $x > 0$  ('synaptic strength') is always positive but  $y$  can take positive or negative values.

The time constants are arbitrary, but for the plots in (b) - (i) below, you should choose  $\tau_x = \tau_y \approx 4$ .

(a) Calculate the two nullclines.

(a1)  $x$ -nullcline

.....

(a2)  $y$ -nullcline

.....

number of points: ...../2

(b) Plot the two nullclines in the figure on the next page. Annotate the nullclines by writing  $x$ -nullcline and  $y$ -nullcline.

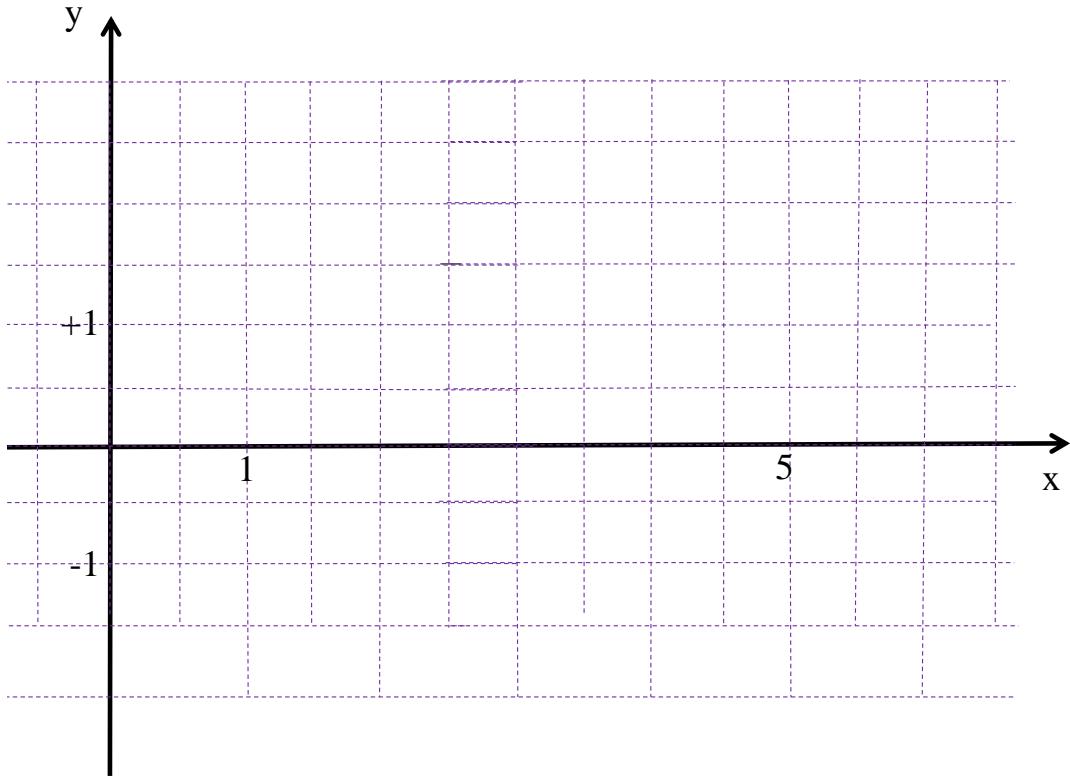
number of points: ...../2

(c) In the same graph, add arrows indicating the direction of flow at the points  $(x, y) = (3, -0.5)$  and  $(x, y) = (4, 0)$ .

number of points: ...../1

(d) Add, in the same graph, representative qualitative arrows indicating the flow in **at least six different regions** of the phase plane and **on all segments of the nullclines**

number of points: ...../3



Note: if you mess up this graph, you can use the reserve graph on the PAGE 5 instead.

(e) Show that the **left-most fixed point** is STABLE by calculating the two Eigenvalues as a function of the parameter  $\tau := \tau_x = \tau_y$ .

The two Eigenvalues are

$$\lambda_1 = \dots$$

$$\lambda_2 = \dots$$

number of points: ...../4

(f) For every saddle point in the graph, add four representative trajectories, two starting in the saddle and two ending in the saddle.

number of points: ...../2

(g) Add, in the above graph, a trajectory starting at  $(x_1, y_1) = (\epsilon, 2)$  for  $\epsilon \ll 1$

number of points: ...../1

(h) Add, in the above graph, a trajectory starting at  $(x_2, y_2) = (2, 0)$ .

number of points: ...../1

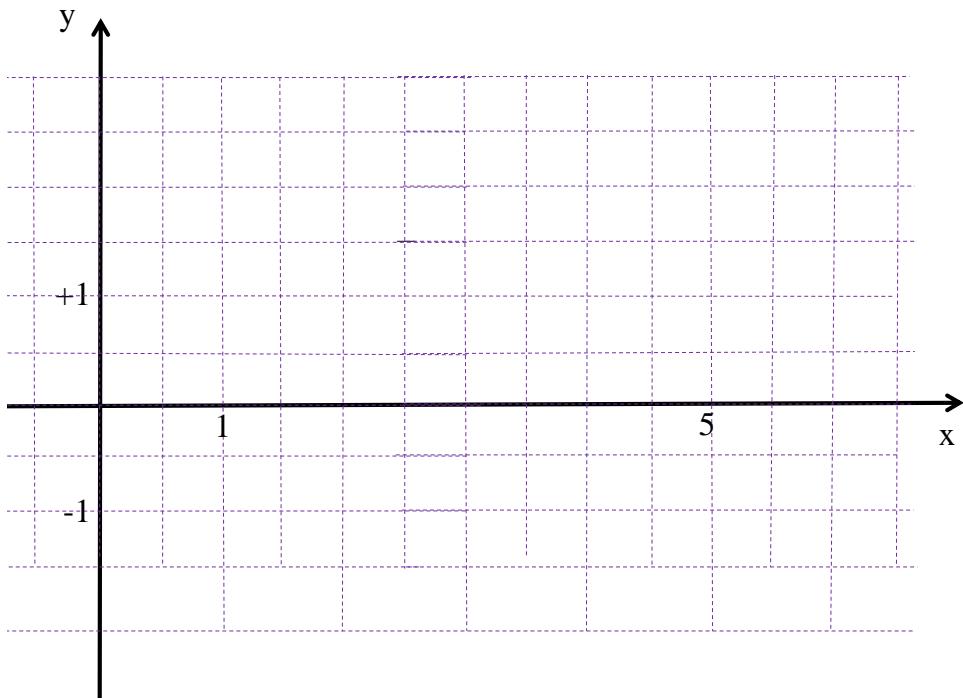
(i) Add, in the above graph, 4 trajectories starting at  $(x_3, y_3) = (3, 0)$ ;  $(x_4, y_4) = (4, 0)$ ;  $(x_5, y_5) = (5, 0)$ ; and  $(x_6, y_6) = (6, 0)$ .

number of points: ...../2

(j) Repeat in the graph below the figure of the nullclines, but for the case  $\tau_x \ll \tau_y$  and add two trajectories starting at  $(x_7, y_7) = (4, 1)$  and  $(x_8, y_8) = (2, -0.52)$ .

Hint: Make sure that both nullclines pass through their correct  $y$ -values at  $x = 4$  and  $x = 2$ .

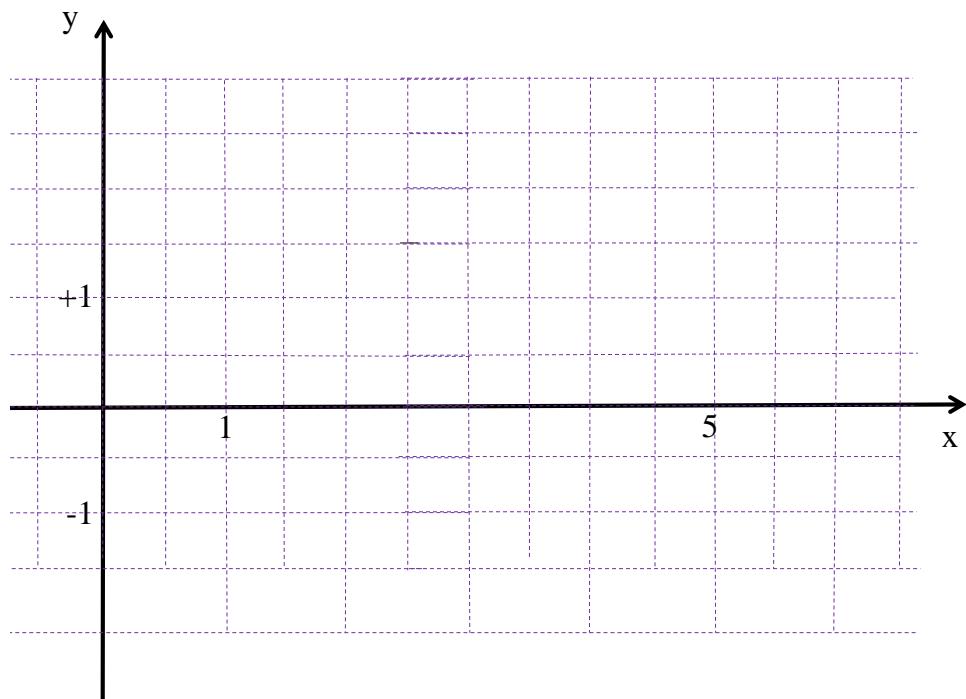
number of points: ...../3



**Free space for your calculations, do not use to write down solutions/answers.**

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Here is the alternative grid (reserve) for the graph of Section 1.



Space for your calculations. Do not use to write answers

## 2 Mean-field (7pts)

We consider a population of  $N$  fully connected inhibitory spiking neurons that are connected with each other with identical negative weights characterized by a parameter  $w_{II} < 0$ . Each neuron also receives an input current  $I(t)$  from other areas in the brain.

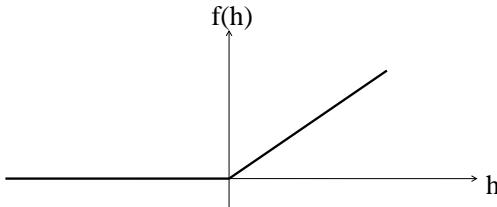
The membrane potential of a neuron  $i$  in the inhibitory population is given by

$$\tau_I \frac{d}{dt} h_i = -h_i + R I(t) + \tau_I \frac{1}{N} w_{II} \sum_{k=1}^N \sum_n \delta(t - t_k^n) \quad (3)$$

where  $t_k^n$  is the  $n$ th firing time of neuron  $k$ . The parameter  $\tau_I$  has units of time and  $R$  has units of resistance. Given the membrane potential  $h_k$ , neuron  $k$  fires stochastically (inhomogeneous Poisson process) with stochastic intensity

$$\rho_k(t) = f(h_k(t)) \quad (4)$$

where  $f(h) = h/(\tau_I h_0)$  for  $h > 0$  and  $f(h) = 0$  otherwise (see Figure). There is no reset of the membrane potential after the spike. The parameter  $h_0$  has units of voltage.



(a) Rewrite the right-hand-side of Eq. (3) in terms of the population activity  $A(t)$ .

$$\tau_I \frac{d}{dt} h_i =$$

.....

number of points: ...../1

(b) At time  $t = 0$  all variables  $h_i$  have been initialized at zero. Assume that we know time course of  $I(t)$  and  $A(t)$  for  $0 < t' < t$ . Integrate your equation so as to write down the membrane potential of neuron  $i$  at time  $t$  (the solution still contains integral signs)

$$h_i(t) =$$

.....

number of points: ...../2

(c) Consider two different neurons of the inhibitory population, say  $i = 17$  and  $i = 966$ . Do they have the same or different values for the membrane potential? Give a reason:

The same/different because

.....  
.....

number of points: ..../1

(d) Now we consider the limit  $N \rightarrow \infty$ . Use Eq. (4) as well as your results from (a) and (b) and write down the population activity  $A(t)$  at time  $t$  as an integral over the past. You may assume  $h_i(t) > 0$  for all  $i$  and all  $0 < t' < t$ .

$A(t) =$

.....

number of points: ..../3

**Space for your calculations. Do not write any answers here.**

### 3 Stochastic Spike Arrivals and synaptic currents (10 points)

We consider a point neuron model that receives stochastically arriving spikes from  $2K$  presynaptic neurons. Each individual spike causes a current pulse  $\alpha(s|d) = H(s)H(d-s)[1 - (s/d)]$  where  $H(x)$  denotes the Heaviside step function with  $H(x) = 1$  for  $x > 0$  and zero otherwise. There are two groups of synapses, which have a different duration of the respective input pulses.

The total input current driving the postsynaptic neuron is

$$I(t) = \sum_{k=1}^K \sum_f w_1 \alpha(t - t_k^f | d_1) + \sum_{k=K+1}^{2K} \sum_f w_2 \alpha(t - t_k^f | d_2) \quad (5)$$

where  $\alpha$  is defined above and  $t_k^f$  denotes the spike arrival times.

(a) Determine the mean input current driving the postsynaptic neuron assuming that the spikes of each neuron in groups 1 and 2 are generated by independent Poisson processes with rates  $\nu_1$  and  $\nu_2$ , respectively.

Express your result as an explicit function of the parameters  $d_1, d_2, w_1, w_2, \nu_1, \nu_2$ ; no integral signs should be left.

$\langle I \rangle =$

.....

number of points: ...../2

(b) Evaluate the mean input current for  $K = 1000, w_1 = 1\mu A, d_1 = 1ms, \nu_1 = 5Hz$  and  $w_2 = -0.2\mu A, d_2 = 10ms, \nu_2 = 2.5Hz$

Pay attention to the units

$\langle I \rangle =$

.....

number of points: ...../1

(c) Evaluate the mean input current for  $K = 1000, w_1 = 1\mu A, d_1 = 1ms, \nu_1 = 5Hz$  and  $w_2 = -0.2\mu A, d_2 = 10ms, \nu_2 = 10Hz$

Pay attention to the units

$\langle I \rangle =$

.....

number of points: ...../1

(d) Determine mathematically the variance of the input current of the postsynaptic neuron under the assumption that the mean of the effective input current vanishes. Express your result as a function of the parameters; no integral signs should be left.

$$<(\Delta I)^2> =$$

.....

number of points: ...../3

(e) By which factor does the standard deviation change (compared to the outcome with parameters as in (b)),

(i) if both  $w_1$  and  $w_2$  increase by a factor of two?

.....

(ii) if both  $\nu_1$  and  $\nu_2$  increase by a factor of two?

.....

(iii) if both  $d_1$  and  $d_2$  increase by a factor of two?

.....

number of points: ...../3

**Space for calculations. Do not use to write down answers**

#### 4 Separation of time scales (6 points + 2 BONUS points)

We study a simplified version of the two-dimensional model in section 1,

$$\tau_x \frac{dx}{dt} = (3/7)(1-x) - y \quad (6)$$

$$\tau_y \frac{dy}{dt} = -y + F(x) \quad (7)$$

where  $\tau_x$  and  $\tau_y$  are positive time constants and the function  $F$  is  $F(x) = F_1(x) = -2(x-1)(x-3)$  for  $x \leq 3$  and  $F(x) = F_2(x) = +2(x-3)(x-5)$  for  $x > 3$ .

Your task is to perform analytically a separation of time scales under the assumption  $\tau_x \ll \tau_y$  and reduce the two variables to a single variable.

(a) The resulting differential equation for the remaining variable  $var$  is of the form  $dvar/dt = g(var)$ . Give this equation here:

.....  
number of points: ...../2

(b) Without doing any long calculations, plot qualitatively  $g(var)$  as a function of  $var$ . HINT: evaluate  $g(var)$  at points  $var_1 = \epsilon \ll 1$ ,  $var_2 = 0$ ,  $var_3 = -3/7$ ,  $var_4 = -9/7$ ,  $var_5 = -3/2$ ,  $var_6 = -12/7$ . For the first three points you use the branch  $F_1$  and for the last three points the branch  $F_2$ .

.....  
number of points: ...../2

**Space for your calculations. Do not use to write answers**

(c) Even if we do not know the exact location of fixed points, we can still label them according to their stability. Based on your figure give qualitative arguments on the stability of the fixed point(s). If there is more than one fixed point, label the fixed points in the graph, and give answers of the form: the fixed point with index ... is (stable/unstable) because ....

.....  
.....  
.....  
.....  
.....

number of points: ..../2

(d) **BONUS** What is the approximate mapping of the above qualitative analysis to the situation of Section 1, question (j)? Can you relate the position of your fixed point(s) in (b) with the position of your fixed point(s) in Section 1? To structure your answer, please respond to the following specific points:

- (i) What is the relation (mapping) of the fixed points between the two sections?
- (ii) What is a relation of the FLOW in the two sections?
- (iii) Explain why we had to select the specific branches  $F_1$ ,  $F_2$  for the qualitative plot in (b)?

HINT: Think about the configuration in the two-dimensional phase plane.

(i) .....

.....

(ii) .....

.....

(iii) .....

.....

number of points: ..../2

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