

Last Name .....

First Name.....

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# Biological Modelling of Neural Networks Exam

## 17 June 2013

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- Write your name in legible letters on top of this page.
- The exam lasts 160 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.

Evaluation:

1. .... / 20 pts

2. .... / 6pts

3. .... / 8 pts

4. .... / 12 pts (+ 4 Bonus)

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Total: .... / 46pts (+4 Bonus)

# 1 Synaptic Plasticity and Phase Plane Analysis (20 points)

Suppose that a pair of neurons is coupled with weights  $w_{12}$  (from neuron 2 to neuron 1) and  $w_{21}$  (from neuron 1 to neuron 2). The two neurons fire with rates  $\nu_1$  and  $\nu_2$ , respectively. Weight values and rates are given in unit-free numbers.

The weights are not fixed but plastic and can change in the range  $0 \leq w_{12}, w_{21} \leq 1$ . If they are not at the lower bound of zero or at the upper bound of one, weights are subject to synaptic plasticity according to the rule

$$\frac{dw_{21}}{dt} = a \nu_1 \nu_2 + b w_{21} \nu_1 - c w_{12} \tag{1}$$

$$\frac{dw_{12}}{dt} = a \nu_1 \nu_2 + b w_{12} \nu_2 - c w_{21} \tag{2}$$

(a) Is the above synaptic plasticity rule a Hebbian rule? Give a reason or condition.

YES, it is a Hebbian rule if/because .....

NO, it is NOT a Hebbian rule if/because .....

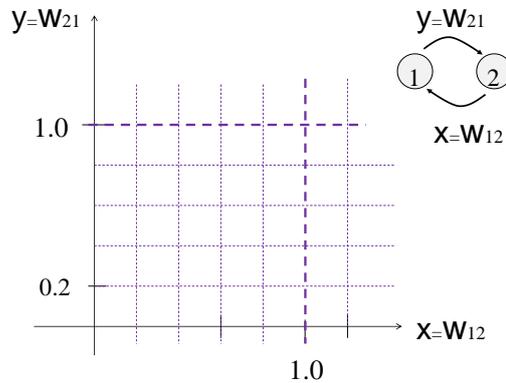
number of points: 1

(b) Phase plane analysis:

Study the case

$a = -0.4$  and

$b = c = \nu_1 = \nu_2 = 1$



(b1) In the above graph, draw the nullclines.

number of points: 2

(b2) In the above graph, draw the direction of flow at  $x = 0 = y$ .

number of points: 1

(b3) In the above graph, draw the direction of flow on the nullclines.

number of points: 2

(b4) In the above graph, add representative arrows indicating QUALITATIVELY the flow in three different regions.

number of points: 2

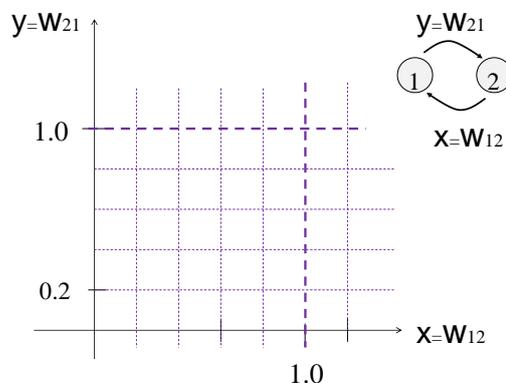
(b5) Draw, for each typical solution a sample trajectory. Interpret your result in

terms of final resulting connectivity pattern and tick correct answers below.

number of points: 2

$y = W_{21} = 1$  $X = W_{12} = 1$	$y = W_{21} = 1$  $X = W_{12} = 0$	$y = W_{21} = 0$  $X = W_{12} = 1$	$y = W_{21} = 0$  $X = W_{12} = 0$
<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>A</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>B</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>C</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>D</b>

(c) Study now the case  $a = -0.4$  and  $b = c = \nu_1 = 1$ , but in contrast to before take  $\nu_2 = 3$ .



(c1) In the above graph, draw the nullclines and annotate your graph with flow arrows.

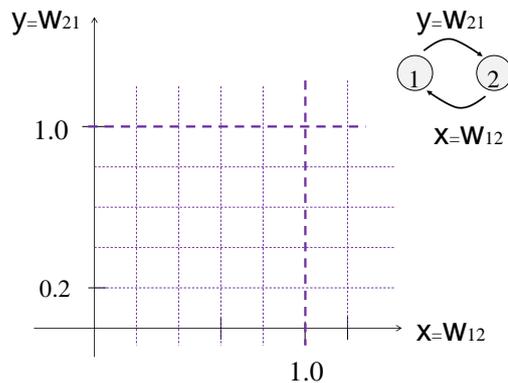
number of points: 2

(c2) Draw, for each typical solution a sample trajectory. Interpret your result in terms of final resulting connectivity pattern and tick correct answers below.

number of points: 2

$y = W_{21} = 1$  $X = W_{12} = 1$	$y = W_{21} = 1$  $X = W_{12} = 0$	$y = W_{21} = 0$  $X = W_{12} = 1$	$y = W_{21} = 0$  $X = W_{12} = 0$
<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>A</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>B</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>C</b>	<input type="checkbox"/> is excluded <input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>D</b>

(d) Study now the case  $a = -0.4$  and  $b = \nu_1 = \nu_2 = 1$ , but in contrast to the first scenario, take  $c = 0.5$ .



(d1) In the above graph, draw the nullclines and annotate your graph with flow arrows.

number of points: 2

(d2) Draw, for each typical solution a sample trajectory. Interpret your result in terms of final resulting connectivity pattern and tick correct answers below.

number of points: 2

$y=W_{21}=1$  $x=W_{12}=1$	$y=W_{21}=1$  $x=W_{12}=0$	$y=W_{21}=0$  $x=W_{12}=1$	$y=W_{21}=0$  $x=W_{12}=0$
<input type="checkbox"/> is excluded			
<input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>A</b>	<input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>B</b>	<input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>C</b>	<input type="checkbox"/> may occur. I have drawn a sample trajectory labeled <b>D</b>

(e) Summarize and interpret your results from (b) - (d) by answering the following question:

Assuming the synaptic plasticity in the brain is well described by the above learning rule, is it possible or excluded that stable reciprocal connections develop? Give a reason for your answer.

number of points: 2

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## 2 Continuity equation (6pts)

In a population of integrate-and-fire neurons with firing threshold  $x = \vartheta$  the distribution of membrane potentials  $p(x, t)$  for  $x < \vartheta$  evolves according to

$$\tau \frac{d}{dt} p(x, t) = -\frac{d}{dx} J(x, t) + r(t) \delta(x - x_0) \quad (3)$$

(a) What is the meaning of the term  $r(t)$ , why do we need this term?

.....  
 .....

number of points: 1

(b) What is the meaning of the parameter  $x_0$ , why do we need this term?

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 .....

number of points: 1

(c) How do you calculate  $r(t)$ ?

.....  
 .....

number of points: 1

(d) We now specify the model in Eq. (3) and study a nonlinear integrate-and-fire model which is driven by an external input (that does not depend on the potential). For our specific model, the flux term is

$$J(x, t) = p(x, t) \{-x(t) + x_1 + x_2 \exp[x(t)/x_3] + x_4 \sin(\omega t)\}$$

where  $x_1, x_2, x_3, x_4$  are fixed parameters.

What can you say about each term in particular with respect to the neuron model .....

.....  
 .....

the noise .....

.....  
 .....

the input .....

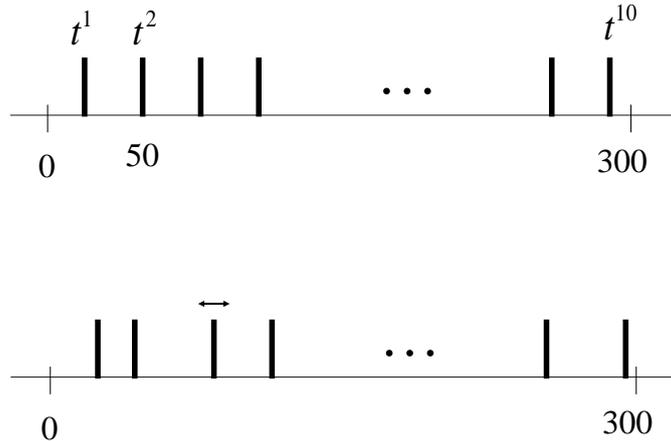
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number of points: 3

### 3 Spike Train Statistics (8 points)

A neuron has received a constant stimulus during the time  $0 < t < 300\text{ms}$  and generated a spike train  $S(t) = \sum_{f=1}^{10} \delta(t - t^f)$  with 10 spikes at times  $t^1, t^2, \dots, t^{10}$ . There were no spikes for  $t < 0$ .

The following graph sketches the situation with two example spike trains.



(a) What is the mean firing rate of the neuron, during the period of stimulation?

.....

number of points: 1

(b) Suppose that the spike train has been generated by a stochastic neuron model with absolute refractory period  $\Delta^{\text{abs}}$ . Spikes occur with stochastic intensity

$$\rho(t) = 0 \quad \text{for } t^f < t < t^f + \Delta^{\text{abs}} \quad (4)$$

$$\rho(t) = \rho_0 \quad \text{for } t \geq t^f + \Delta^{\text{abs}} \quad (5)$$

Write down the likelihood that an observed spike train with spike times  $t^1 \dots t^{10}$  could have been generated by the model. The right-hand side of your equation should contain the parameters  $\Delta^{\text{abs}}$  and  $\rho_0$ .

.....  
 .....

number of points: 3

(c) Observed spikes have occurred at times 20, 50, 80, 110, . . . , 290ms (see the first of the two sample spike trains in the graph on the left).

Try to explain the observed sequence of spike by the model with absolute refractoriness. Set  $\Delta^{\text{abs}} = 10\text{ms}$ .

What is the most likely value of the parameter  $\rho_0$ ?

$\rho_0 = \dots\dots\dots$

number of points: 2

space for calculations, if necessary

(d) Suppose that, in a second trial, each of the spikes is jittered by  $\pm 5\text{ms}$  compared to the first trial. (see the second of the two sample spike trains in the graph on the left, e.g. spikes occur at 25,45,85,105 ... ms.)

Redo the estimation of  $\rho_0$ . The result is

$\rho_0 = \dots\dots\dots$

Justify your answer in words:

.....

number of points: 2

#### 4 Mean-field in a Network of Rate Models (12 points + 4 Bonus)

We study a network of excitatory and inhibitory neurons. Each excitatory neuron has a firing rate  $e_k$

$$\tau_e \frac{de_k}{dt} = -e_k + f(I - s) \quad (6)$$

with

$$f(x) = 2(x - 0.5) \quad \text{for } x > 0.5 \quad \text{and else } f(x) = 0 \quad (7)$$

Inhibitory neurons have a firing rate  $s$

$$\tau_s \frac{ds}{dt} = -s + g(e) \quad (8)$$

with

$$g(x) = x^2/4 \quad \text{for } x > 0 \quad \text{and else } g(x) = 0 \quad (9)$$

(a) We start with a network of excitatory neurons (no inhibition, hence  $s = 0$ ). Assume that we have a large network of  $N \gg 1$  excitatory neurons, described by Eq. (6). The input to neuron  $i$  is

$$I_i(t) = \sum_{k=1}^N \frac{w}{N} e_k \quad (10)$$

Here  $e_k$  is the rate of excitatory neuron  $k$ . There is no additional external input.

(a1) Assume that all  $N$  excitatory neurons have the same firing rate and write down the resulting dynamics for the population activity  $e = (1/N) \sum_{k=1}^N e_k$  in a single equation for  $e$ .

.....

number of points: 2

(a2) Solve graphically for the stationary state(s) of the activity in the network. Make two different graphs for the choices  $w = 0.5$  and  $w = 1$ .

number of points: 2

(a3) In your graph, circle the steady state(s), if there are any. For each steady state that you find, indicate its stability directly in the graph (s=stable, u=unstable).  
 number of points: 2

(b) Now we add inhibition. Assume that there is a common pool of inhibitory neurons with population activity  $s$  given by Eq. (8). Assume a separation of time scales  $\tau_s \ll \tau_e$  and reduce the number of equations from two to one. Give the resulting single equation.

.....  
 number of points: 2

(c) Write the result in the form

$$\tau_e \frac{de}{dt} = -e + F_w(e) = G_w(e) \tag{11}$$

and plot either the function  $F_w(e)$  or the function  $G_w(e)$  for two different choices of the parameter  $w$ , i.e.  $w = 0.5$  and  $w = 2$ .

number of points: 3

(c) For each of the two parameter choices, are there stationary states? Are they stable?

.....  
 number of points: 1

(d) **Bonus:** (d1) Given your results from (a) - (c) what can you say about the role of inhibition in neural networks.

number of points: 1

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 (d2) Give the analytical solution for the steady state(s) of the network of coupled excitatory and inhibitory neurons in the case of  $w = 2$ .

number of points: 3

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