

Last Name .....

First Name.....

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# Neural Networks and Biological Modelling Exam

## 23 June 2011

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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. .... / 10 pts

3. .... / 8 pts

4. .... / 12 pts

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Total: ..... / 40 pts

## 1 Adaptive Nonlinear Integrate-and-Fire Model (20 points)

A nonlinear integrate-and-fire neuron model with adaptation is described by the two differential equations

$$\frac{du}{dt} = \gamma [f(u) - w + I]$$

$$\begin{aligned} & (2) \\ \frac{dw}{dt} &= \epsilon (-w + u) \end{aligned} \tag{3}$$

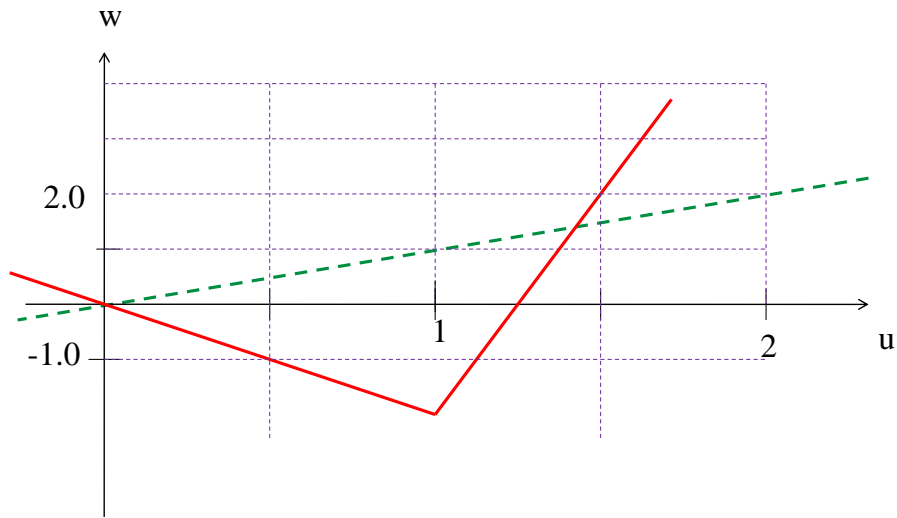
If  $u > 2$  the variable  $u$  is reset to  $u = 1.5$ . The variable  $w$  is increased by an amount of 1.5 during reset. The function  $f(u)$  is

$$f(u) = -2u \quad \text{for } u \leq 1 \tag{4}$$

$$f(u) = 4u - 6 \quad \text{for } u > 1 \tag{5}$$

The constants  $\gamma$  and  $\epsilon$  have appropriate units (You may assume  $\gamma = 0.5$  and  $\epsilon = 0.05$ ).

(a) Assume  $I = 0$  and annotate the two nullclines (by writing e.g.,  $u$ -nullcline or  $w$ -nullcline at the appropriate locations ) in the figure below.



number of points []1

(b) In the above graph, add representative arrows indicating QUALITATIVELY the flow on the nullclines AND in four different regions of the phase plane.

Keep in mind that  $\gamma = 0.5$  and  $\epsilon = 0.05$

number of points []4

(c) In the same graph, indicate a trajectory in the phase plane, after a stimulus  $I(t) = 0.8\delta(t)$  has been applied [ $\delta$  denotes the Dirac delta function]. (Note, if necessary, that there is a the reset condition) number of points []1

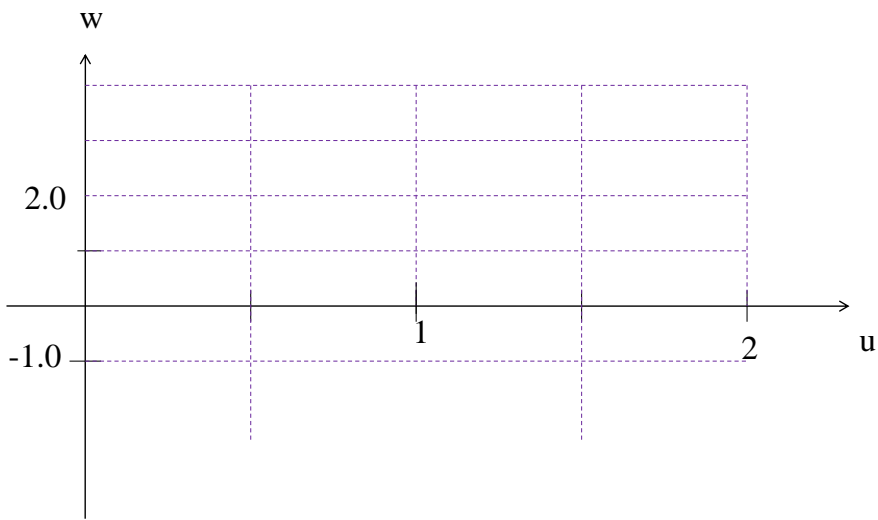
(d) Draw qualitatively (by hand) the voltage trajectory  $u(t)$  for the case in c in the space here: number of points []2

(e) Assume  $I = 0$  and determine the stability of the fixed point at  $u = w = 0$  number of points []3

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(f) At time  $t = 10$  the external input current is switched from  $I = 0$  to  $I = 3$ . Draw the two nullclines for  $t > 10$  in the figure below.

number of points []2



(g) With the step current stimulation of (f) the neuron model emits a series of spikes. As indicated at the beginning, after each spike, the membrane potential is reset **to** the value  $u = 1.5$  and the second variable is increased **by** an amount  $\Delta w = 1.5$ .

Indicate the trajectory in the phase plane of the above figure in (f) up to the emission of the **fourth** spike, by exploiting the fact that  $\gamma = 0.5$  and  $\epsilon = 0.05$ .

number of points []4

(h) Draw qualitatively the voltage trajectory as a function of time in the space below.

number of points [2]

(i) Interpret your result. What is the resulting firing pattern?

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number of points [1]

## 2 Stochastic Spike Arrivals (10 points)

A stochastic spike train is transmitted along a sensory pathway from the receptors to neurons in the brain. Each spike evoked at the receptors generates, ten milliseconds later, an excitatory input current of amplitude 1 and duration  $\tau$  followed immediately afterwards by an input at an inhibitory synapse of amplitude 0.5 and duration  $2\tau$ . Therefore each input spike at time  $t^f$  causes a net input current

$$I(t - t^f) = e^{-(t-t^f)/\tau} - 0.5 e^{-(t-t^f)/2\tau} \quad (6)$$

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In the following we assume the spikes arrive stochastically with rate  $\nu$  (i.e., a Poisson process).

(a) Determine the mean input current.

number of points [2] .....

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(b) Determine the variance of the input current.

number of points [2] .....

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(c) The input current (generated by the stochastic spike arrivals) drives a neuron

in the sub-threshold regime, governed by the passive membrane equation

$$\tau \frac{du}{dt} = -u + RI(t) \tag{7}$$

Determine the mean of the membrane voltage.

number of points [2] .....

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(d) Suppose the autocorrelation of the input current can be approximated by

$$\langle I(t) I(t') \rangle = a e^{-t/\tau} \cos(t/\tau) = a \operatorname{Re}\left\{\exp\left[-\frac{(1+i)t}{\tau}\right]\right\} \tag{8}$$

with some parameter  $a$ . Calculate the variance of the membrane voltage defined in c.

number of points [2] .....

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(e) Suppose the firing threshold of the neuron is at a value  $\vartheta = 1$ ,  $\tau = 10\text{ms}$  and  $\nu = 1\text{kHz}$  and consider three cases:  $a = 0.01$ ,  $a = 1$ ,  $a = 100$ . Do you expect that the neuron fires in an observation period of 1 second? Justify your answer.

number of points [2] .....

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### 3 Spike Train Statistics (6 points)

We assume that during stimulation with a stationary stimulus, interspike intervals in a long spike train are independent and given by the distribution

$$P(t|t') = \frac{(t - t')}{\tau^2} \exp\left(-\frac{t - t'}{\tau}\right) \quad (9)$$

(a) Calculate the hazard function  $\rho(t|t')$ , that is, the stochastic intensity that the neuron fires, given that its last spike was at  $t'$ .

number of points  $\square 2$

$$\rho(t|t') = \dots\dots\dots$$

(b) Calculate the survivor function  $S(t|t')$ , i.e. the probability that the neuron survives from time  $t'$  to  $t$  without firing.

number of points  $\square 2$

$$S(t|t') = \dots\dots\dots$$

(c) A spike train starts at time 0 and we have observed a first spike at time  $t_1$ . We are interested in the probability that the  $n$ th spike occurs around time  $t_n = t_1 + s$ , if the first spike occurs at time  $t_1$ . With this definition of spike labels, calculate the probability density  $P(t_3|t_1)$  that the third spike occurs around time  $t_3$ .

number of points  $\square 4$

$$P(t_3|t_1) = \dots\dots\dots$$

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

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

$$\tau_e \frac{de}{dt} = -e + f(I) - s \quad (10)$$

with

$$f(i) = \gamma I \quad \text{for } I > 0 \quad \text{and else } f(I) = 0 \quad (11)$$

Inhibitory neurons have a firing rate  $s$

$$\tau_s \frac{ds}{dt} = -s + g(I) + e \quad (12)$$

with

$$g(i) = \gamma (I - 1)^2 \quad \text{for } I > 1 \quad \text{and else } f(i) = 0 \quad (13)$$

(a) Consider a pair consisting of one excitatory neuron coupled to one inhibitory neuron. 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

(b) Write the result in the form

$$\tau_e \frac{de}{dt} = -e + F(I) \quad (14)$$

and plot the function  $F(I)$  here.

number of points []2

(c) Assume that we have a large network of  $N \gg 1$  pairs of excitatory and inhibitory

neurons, where each pair of excitatory and inhibitory neurons is described by Eq. (14). The input to neuron pair  $i$  is

$$I_i(t) = I_0 + \sum_{k=1}^N \frac{w}{N} e_k \quad (15)$$

Here  $e_k$  is the rate of excitatory neuron  $k$ .

Solve graphically for the stationary state of the activity in the network, for two *qualitatively different* regimes which you choose. Free parameters are the coupling  $w$  and the external input  $I$ .

number of points  $\square 4$

First regime, show graph in the space above.

Second regime, show graph in the space above.

(d) Give the analytical solution for the steady state of the network, under the assumptions mentioned in c. If there are several solutions, indicate stability of each of these.

number of points  $\square 4$