Last Name .... First Name..................

Biological Modelling of Neural Networks Exam
17 June 2014

- 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. .... / 7 pts
2. .... / 12 pts
3. .... / 6 pts
4. .... / 8 pts
5. .... / 9 pts
6. .... / 8 pts

Total: .... / 50 pts

1 Ion channel (7 points)

We consider the following model of a ion channel

$$I_{ion} = g_0\, x^p\, (u - E)$$

where u is the membrane potential. The parameters g_0, p and $E = 0$ are constants.

(a) What is the name of the variable E? ....

Why does it have this name, what does it signify (give answer in one short sentence)

....
....
number of points: 1

(b) The variable x follows the dynamics

$$\frac{dx}{dt} = -\frac{x - x_0(u)}{\tau}$$

where $x_0(u)$ is monotonically increasing and bounded between zero and one. Suppose we make a voltage step from a fixed value E to a new constant value u_0. Give the mathematical solution $x(t)$ for $t > 0$

$x(t) =$ ....
number of points: 2

An electrophysiologist tells you that he is able to apply voltage steps as in (b) and that by measuring the current he wants to determine the parameters g_0 and $x_0(u)$ of the ion channel in (a) and (b)

(c) How should he proceed to measure the parameter p? What would be different between the case p=1 and $p = 2$? You can sketch a little figure to illustrate your answer.

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

number of points: 2

(d) Under the assumption that $x_0(u)$ is bounded between zero and 1, how can he measure g_0?

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

number of points: 1

(e) Given the value of g_0 and p, how can he measure the value $x_0(u_1)$ at some arbitrary value u_1? If possible, give a mathematical expression to illustrate your explanation.

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

number of points: 1

2 Phase Plane Analysis (12 points)

We study a network of coupled rate neurons. However, we assume that the interaction weights w are subject to fatigue (also called synaptic depression) when they are used intensively. We write $w = J_0\, x$ with some variable x and a fixed parameter J_0 The system of equations is:

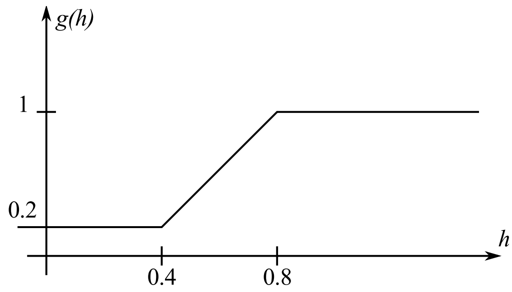
$$\tau \frac{dh}{dt} = -h + J_0\, x\, g(h) \qquad (1)$$

$$\tau_x \frac{dx}{dt} = 2.8 - x - 9.0\, x\, g(h) \qquad (2)$$

$\tau = 1$ and $\tau_x > \tau$ are time constants (arbitrary units). You may assume that $15 < \tau_x < 30$.

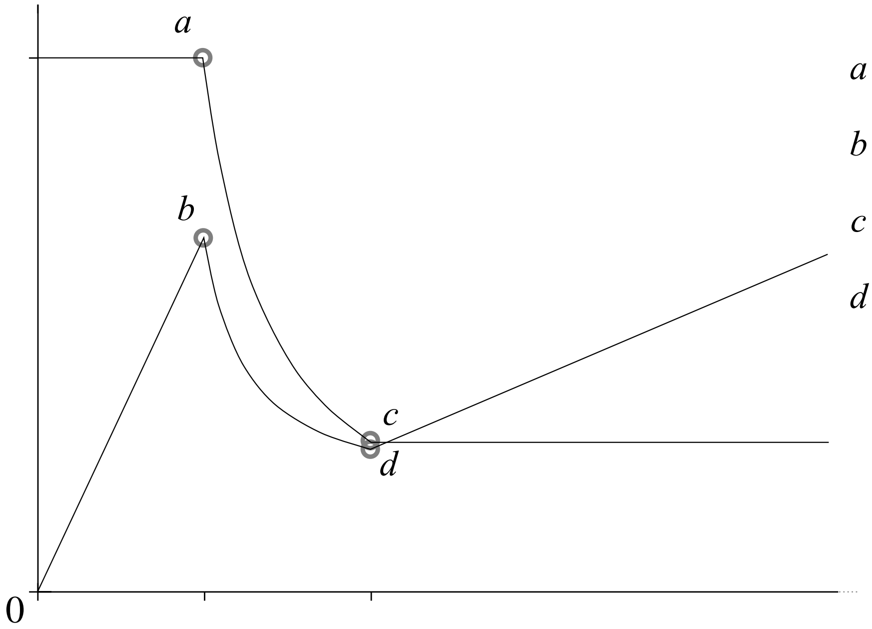
J_0 is a parameter (later we consider $J_0 = 3$).

The gain function is:
$g(h) = 0.2$ for $h < 0.4$
$g(h) = 2h - 0.6$ for $0.4 \leq h \leq 0.8$
$g(h) = 1$ for $h > 0.8$
(as shown on the right)



a) Assume $J_0 = 3$. The nullclines are shown below, without axis labels or scale.

- Add the axis labels.
- Label the 2 nullclines.
- Give the numerical values for the 4 circled points a, b, c and d. number of points: 3



$a = (\quad ; \quad)$

$b = (\quad ; \quad)$

$c = (\quad ; \quad)$

$d = (\quad ; \quad)$

c) Evaluate the differential equations at $(h, x) = (0, 1)$ and draw an arrow in the above graph. (The direction of the arrow should qualitatively point in the right direction, i.e. towards the right quadrant). number of points: 1

d) Add in your graph flow arrows along the nullclines (at least four on each nullcline). number of points: 2

e) Draw two trajectories. One starting at (1,0) and another one starting at (0,1). number of points: 2

f) Determine analytically the stability of the fixed point, using Equations 1 and 2 repeated here for convenience:

$$\frac{dh}{dt} = \frac{1}{\tau}\left[-h + J_0\, x\, g(h)\right] \tag{3}$$

$$\frac{dx}{dt} = \frac{1}{\tau_x}\left[2.8 - x - 9.0\, x\, g(h)\right] \tag{4}$$

Give the two eigenvalues.

Result: The fixed point is (stable/unstable/saddle)...........................
number of points: 2

(3pts) The two eigenvalues are ....

number of points: 3

(Space for calculations)

3 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

$$\tau \frac{d}{dt} p(x,t) = -\frac{d}{dx} J(x,t) + r(t)\, \delta(x - x_0) \tag{5}$$

(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?

....

....

number of points: 1

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

....

....

number of points: 1

(d) We now specify the model in Eq. (5) 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
the neuron model ....

....

....

the noise ....

....

....

the input ....

....

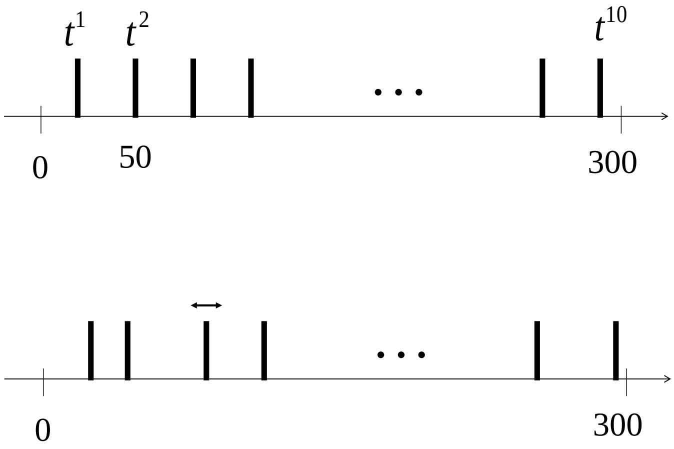
....

number of points: 3

4 Spike Train Statistics (8 points)

A neuron has received a constant stimulus during the time $0 < t < 300$ms and generated a spike train $S(t) = \sum_{f=1}^{10} \delta(t - t^f)$ with 10 spikes at times $t^1, t^2, \ldots t^{10}$. 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 Δ^{abs}. Spikes occur with stochastic intensity

$$\rho(t) = 0 \qquad \text{for} \quad t^f < t < t^f + \Delta^{\mathrm{abs}} \tag{6}$$

$$\rho(t) = \rho_0 \qquad \text{for} \quad t \geq t^f + \Delta^{\mathrm{abs}} \tag{7}$$

Write down the likelihood that an observed spike train with spike times $t^1 \ldots t^{10}$ could have been generated by the model. The right-hand side of your equation should contain the parameters Δ^{abs} and ρ_0.

....

....

number of points: 3

(c) Observed spikes have occurred at times $20, 50, 80, 110, \ldots, 290$ms (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 $\Delta^{\text{abs}} = 10$ms.

What is the most likely value of the parameter ρ_0?

$\rho_0 =$ ....

number of points: 2

space for calculations, if necessary

(d) Suppose that, in a second trial, each of the spikes is jittered by ± 5ms 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 ρ_0. The result is

$\rho_0 =$..

Justify your answer in words:

....

number of points: 2

5 Mean-field and population activity (9 points)

Consider a population of N identical neurons. If driven by an input $I(t)$, each neuron fires independently and stochastically with a Poisson firing rate $\nu(t) = g(I(t))$.

The input $I = I^{\text{ext}} + I^{\text{syn}}$ has a fixed external component I^{ext} as well as a synaptic component I^{syn}.

(a) Suppose that each neuron receives spike input from all other neurons. Spike arrival at time $t = 0$ evokes a response $w_0[\exp(-t/\tau_2) - \exp(-t/\tau_1)]$ with $0 < \tau_1 < \tau_2$.

Write down the total input $I(t_0)$ to a specific neuron i assuming that you know the spike times for $t < t_0$.

....

number of points: 1

(b) Based on your result in (a), calculate the expected value of the input assuming that all neurons fire independently at the same constant frequency ν_0. The result should be expressed in a simple formula containing the relevant parameters.

....

number of points: 2

space for calculations, if necessary

(c) even for constant firing rates, the input will fluctuate around the mean input calculated above. Assume that $w_0 = 5/N$.

How does the standard deviation of these fluctuations scale with the number of neurons N?

....

How does the expected input scale with the number of neurons N?

....

number of points: 2

(d) Assume that the gain function $g(I)$ is piecewise linear with $g(I)$=0 for $I \leq 1$, $g(I) = 2I - 1$ for $1 < I \leq 2$, and $g(I) = 1$ for $I > 2$.

Furthermore set $\tau_2 = 1$ and $\tau_1 = 0$ and $w_0 = 5/N$, as before. Consider the limit $N \to \infty$ and dermine graphically the fixed points of the population activity $A(t)$. Make a graph in the space here:

number of points: 2

(e) What is the number of fixed points in the above graph? Exists there a value for I^{ext} where the number of fixed points changes?

....

....

number of points: 2

6 Hopfield model (8 points)

Consider a network of $N = 20000$ neurons that has stored 4 patterns

$\xi^1 = \{\xi_1^1, \dots \xi_N^1\}$
$\xi^2 = \{\xi_1^2, \dots \xi_N^2\}$
$\xi^3 = \{\xi_1^3 \dots \xi_N^3\}$
$\xi^4 = \{\xi_1^4 \dots \xi_N^4\}$

using the synaptic update rule $w_{ij} = (J/N) \sum_\mu \xi_i^\mu \xi_j^\mu$ where $J > 0$ is a parameter. **Each pattern has values $\xi_i^\mu = \pm 1$ so that exactly 50 percent of neurons in a pattern have $\xi_i^\mu = +1$.**

Assume stochastic dynamics: neurons receive an input $h_i(t) = \sum_j w_{ij} S_j(t)$ where $S_j(t) = \pm 1$ is the state of neuron j. Neurons update their state

$$Prob\,\{S_i(t+1) = +1 | h_i(t)\} = 0.5[1 + g(h_i(t))] \tag{8}$$

where g is an **odd and monotonically increasing function**: $g(h) = 4h$ for $|h| < 0.25$ and $g(h) = 1$ for $h \geq 0.25$ and $g(h) = -1$ for $h \leq -0.25$.

(a) Rewrite the righ-hand-side of equation (8) by introducting an overlap $m^\mu(t) = (1/N) \sum_j \xi_j^\mu S_j(t)$.

....

number of points: 1

(b) What is the significance of the overlap? Describe its meaning in one sentence; give examples if necessary.

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

number of points: 1

(c) Assume that the four patterns are orthogonal, i.e., $\sum_i \xi_i^\mu \xi_i^\nu = 0$ if $\mu \neq \nu$. **Assume that the overlap with pattern 4 at $t = 0$ has a value of 0.25 and $m^\mu(0) = 0$ for all other patterns.**

Suppose that neuron i is a neuron with $\xi_i^4 = -1$.

What is the probability that neuron i fires in time step 1? Give the formula for arbitrary J and evaluate then for $J = 1$.

....

What is the probability that another neuron k with $\xi_k^4 = +1$ fires in time step 1? Give the formula for arbitrary J and evaluate then for $J = 1$.

....

number of points: 2

(d) For the same assumptions as in (c), what is the expected overlap for $< m^4(t) >$ after the first time step.

$< m^4(1) >=$...

....

number of points: 2

(e) In question (d) you calculated the EXPECTATION $< m^4 >$. Can we drop the expectation sign in the limit of $N \to \infty$? Justify your answer in two sentences.

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number of points: 2