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

Biological Modelling of Neural Networks Exam
August 25, 2020

- 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 **13 pages**
- **Bonus points** typically involve longer calculations and should be attempted only if you have enough time.

Evaluation:

1. .... / 19 pts (+3 bonus points) [phase plane]
2. .... / 18 pts (+3 bonus points) [Hopfield model]
3. .... / 10 pts [Mean-field and 1-dim. equation]
4. .... / 8 pts (+3 bonus points) [Stochastic spike arrival]

Total: .... / 64 pts (= 55 points plus 9 bonus points)

1 Phase Plane Analysis and Epidemics (19 points + 3 bonus points)

Here are the two equations that we will study:

$$\frac{dx}{dt} = (1 - x - y)\,\alpha - \, x\,y\,\beta \tag{1}$$

$$\frac{dy}{dt} = (x - \frac{1}{R_0})\,y\,\beta \tag{2}$$

with fixed parameters α, β, R_0

(a) In the context of epidemics, x can be interpreted as the fraction of susceptible people and β as the rate of infections. Suggest a plausible interpretation of α and of $1 - x - y$.

$1{-}x{-}y$ can be interpreted as ....
α can be interpreted as ....

number of points: ...../1

(b)**Assume** $R_0 = 2.5$**,** $\beta = 1$**, and** $\alpha = 0.1$ Calculate the nullclines.

Answer:

Nullcline(s) with $dx/dt = 0$

....

Nullcline(s) with $dy/dt = 0$

....

number of points: ...../2

(c) **Plot all nullclines in the empty space on the next page. Annotate your lines by writing e.g.,** x**-nullcline or** y**-nullcline.**

Hint1: for a numerical evaluation it is useful to choose points $x = 0, x = 0.1, x = 0.4, x = 1$.

Hint2: Consider the range $0 \le x \le 1$ and $0 \le y \le 1$.

Hint3: It is also useful to plot in the same graph the curve $y = 1 - x$.

number of points: ...../2

Space for your phase plane graphics

(d) Calculate the flow arrows $(\Delta x, \Delta y)$ at the following points (x, y):

$(0, 0.5) \longrightarrow (\Delta x, \Delta y) =$ ....

$(0.1, 0.2) \longrightarrow (\Delta x, \Delta y) =$ ....

$(0.5, 0.5) \longrightarrow (\Delta x, \Delta y) =$ ....

$(0.9, 0.1) \longrightarrow (\Delta x, \Delta y) =$ ....

number of points: ...../2

(f) In the above graph, add a flow arrow indicating the direction of flow at the point $(x = 0.5, y = 0.5)$. Make the length of the arrow correspond to a suitable time step Δt such that $\Delta x = \Delta t(dx/dt)$ is in the order of 0.1 ... 0.2. Use the same time step to also draw the flow arrows at $(0, 0.5); (0.1, 0.2); (0.9, 0.1)$

number of points: ...../2

(g) Add 4 arrows on each of your nullclines with qualitatively consistent length.

number of points: ...../2

(h) Add 4 representative flow arrows in the empty space around the nullclines

number of points: ...../2

(i) Qualitatively construct in the phase plane the trajectory starting at $(0, 0.5)$.

number of points: ...../1

(j) Qualitatively construct in the phase the trajectory starting at $(0.2, 0)$

number of points: ...../1

(k) Assume now that $\alpha = 0.001$ while $R_0 = 2.5$, $\beta = 1$ as before.

Without replotting the nullclines, describe the new configuation of nullclines in the phase plane. Hint: What remains unchanged, what changes?

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

Also think about the size of the flow arrows. What is the consequence for epidemics?

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

What happens in the limit $\alpha \to 0$?

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

free space for calculations, do not write results here.

(l) **Bonus question (3pts)**. Return to the original set of parameters $\alpha = 0.1$ while $R_0 = 2.5$, $\beta = 1$. You see one or several fixed points (x_k, y_k).

If you see a saddle point, then make the following statements:

The saddle point is at location $(x_0, y_0) =$ ....

I am sure that it is a saddle point because

....

The attractive manifold of the saddle is the curve

....

If you see fixed point that is not a saddle point, then do the following:

The fixed point is at location $(x_0, y_0) =$ ....

Rewrite the equations with new variables $x' = x - x_0; y' = y - y_0$ after linearlization around (x_0, y_0)

....

....

and make a linear stability analysis for small x', y'.

The stability analysis gives Eigenvalues with real parts that are

both positive/both negative/mixed (circle the correct answer)

Therefore the fixed point is stable/unstable/neutral (circle the correct answer)

The Eigenvalues are

$\lambda_1 =$ ....

$\lambda_2 =$ ....

number of points: ...../3

free space for calculations, do not write results here.

2 Hopfield model (18 points + 3 bonus points)

Consider a network of $N = 50000$ neurons that has stored 10 patterns

$\xi^1 = \{\xi_1^1, \dots \xi_N^1\}, \quad \xi^2 = \{\xi_1^2, \dots \xi_N^2\}, \quad \xi^3 = \{\xi_1^3 \dots \xi_N^3\}, \quad ... \ \xi^{10} = \{\xi_1^{10} \dots \xi_N^{10}\}$

using the synaptic update rule

$$w_{ij} = \frac{J}{(1-a^2)N} \sum_{\mu} (\xi_i^\mu)(\xi_j^\mu - a) \tag{3}$$

where $J > 0$ is a parameter.

Assumption 1: Each pattern has values $\xi_i^\mu = \pm 1$ so that exactly $(a+1)N/2$ neurons in a pattern have $\xi_i^\mu = +1$. We call these the 'active neurons of pattern μ'.

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

$$Prob\{S_i(t+1) = +1 | h_i(t)\} = 0.5[1 + g(h_i(t))] \tag{4}$$

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 (4) by introducting an overlap
$m^\mu(t) = [1/(N(1-a^2))] \sum_j (\xi_j^\mu - a)\, S_j(t)$.

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

and evaluate

$[1/(N(1-a^2))] \sum_j (\xi_j^\mu - a)\, \xi_j^\mu =$ ....
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) **Assumption 2: The ten patterns are orthogonal**,
i.e., $\sum_i (\xi_i^\mu)(\xi_i^\nu - a) = 0$ if $\mu \neq \nu$.

Assumption 3: The overlap with pattern 4 at $t = 0$ has a value of $m^4(0) = M$ 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 takes a value $S_i(t) = 1$ in time step 1? Give first the formula for arbitrary J and $m^4(0) = M$ and then evaluate then for $J = 1$ and $M = 0.2$.

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

What is the probability that another neuron k with $\xi_k^4 = +1$ takes a value $S_i(t) = 1$ in time step 1? Give first the formula for arbitrary J, M and evaluate then for $J = 1, M = 0.2$.

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

number of points: ...../4

(d) For the same assumptions as in (c) with $J = 1, M = 0.2$, what is the expected overlap for $< m^4(t) >$ and for $< m^1(t) >$ after the first time step.

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

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

number of points: ...../3

(e) In question (d) you calculated the EXPECTATION $< m^4 >$. The exact value might fluctuate around $< m^4 >$. Do you believe that fluctuations will disappear in the limit of $N \to \infty$? Justify your answer in two sentences.

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

number of points: ...../1

(f) In the limit of $N \to \infty$, evaluate the final state of the network. What is the final overlap of pattern 4 and pattern 1?

The final overlap of pattern 4 is ....
The final overlap of pattern 1 is ....

How many time steps does it take until the final value of the overlap is reached? Sketch the evolution of $m^4(t)$ and $m^1(t)$ as a function of time in the space here.

Hint: horizontal axis should show discrete time steps, 1,2,3, ... 10 and the vertical axis the overlap on a suitable scale.

number of points: ...../3

(g) **Assumption 4.** $N \to \infty$ **as in f.** We work with assumptions 1-3 as before, but now we change the weights so that

$$w_{ij} = \frac{J_0}{(1-a^2)N} \sum_{\mu} (\xi_i^{\mu})(\xi_j^{\mu} - a) + \frac{J_1}{(1-a^2)N} \sum_{\mu} (\xi_i^{\mu+1})(\xi_j^{\mu} - a) \tag{5}$$

where we have defined $\xi_i^{11} = \xi_i^1$ (patterns form a cycle). We simplify and **set** $J_0 = 0$ **and choose** $J_1 = 1$**.**

Express the expected overlap for the following patterns in the first time step assuming that $m^4(0) = M = 0.5$ and all other patterns have initial overlap zero.

Hint: Adapt your results from (a) to (d).

$m^1(1)$..
$m^4(1)$..
$m^5(1)$..
$m^6(1)$..

number of points: ...../3

(h) BONUS (3 points).

Analyze the model in (g) with values $J_0 = 1$, $J_1 = 0.2$ and $a = -0.8$. The initial overlap at time $t = 0$ is $m^4(0) = 0.5$. All other overlaps are zero.

We add neuronal **adaptation**: a neuron that has been active 5 times during the last 10 time steps can not become active during the next 10 time steps:

$$Prob\,\{S_i(t+1) = +1|h_i(t)\} = 0.5[1 + g(h_i(t))] \quad \text{if} \quad \sum_{k=0}^{9} S_i(t-k) < 5 \qquad (6)$$

and zero otherwise. The function g is the same as before.

We assume that none of the neurons has been active before $t = 1$.

Sketch in the limit of $N \to \infty$ the overlap as a function of time for $m^1(t), m^4(t), m^5(t), m^6(t)$ during 20 time steps.

Sketch goes here. Make sure that values along the vertical axis are correctly indicated.

Hint1: Exploit that $a = -0.8$

Hint2: Consider how adaptation affects these four groups of neurons:

group 1 contains neurons that are active in pattern 4 and active in pattern 5;
group 2 contains neurons that are active in pattern 4 and inactive in pattern 5;
group 3 contains neurons that are inactive in pattern 4 and active in pattern 5;
group 4 contains neurons that are inactive in pattern 4 and inactive in pattern 5.

number of points: ...../3

3 Mean-field and 1-dimensional nonlinear equations (10pts)

We consider the population activity $A = g(h)$ of a single population, where the input potential h evolves according to the differential equation

$$\tau \frac{dh}{dt} = -h + J\, g(h) + h_0 \tag{7}$$

with a coupling weight J.

(a) What is the meaning of the parameters h_0 and J?

h_0 represents ....

J represents ....

number of points: ...../1

(b) What are the assumptions and/or approximations necessary to arrive at the above equation, starting from a population of integrate-and-fire neurons.

....

....

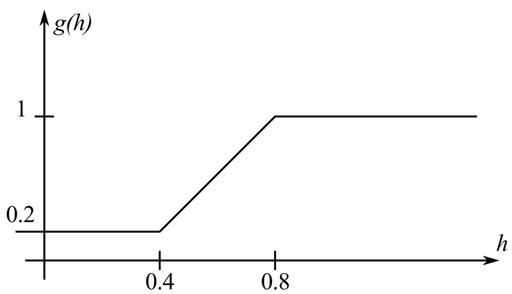
....

....

number of points: ...../2

(c) Set $h_0 = 0$ and $J = 1$. Determine analytically the position of the fixed point or fixed points and give the value of each fixed point using as shown on the right

Assume (as shown on the right)
$g(h) = 0.2$ for $h < 0.4$
$g(h) = 2h - 0.6$ for $0.4 \leq h \leq 0.8$
$g(h) = 1$ for $h > 0.8$



....

....

....

....

number of points: ...../2

(d) With parameters as before, plot in the space below:

- Plot dh/dt as a function of h.
- Draw arrows for the flow.
- Determine graphically the stability of the fixed point or fixed points, and mark the result on the plot (write "S" for stable and "U" for unstable).

number of points: ...../3

(e) Still with same conditions, draw qualitatively the function $A(t) = g(h(t))$, on the axes below. Use four different initial conditions, that enable you to characterize the behavior of the system. Assume $\tau = 3$.

number of points: ...../2

4 Stochastic Spike Arrivals and Spiking Probability (8 points + 3 bonus points)

There are certain types of neurons that communicate with 'doublets' of spikes: Whenever the firing threshold is crossed, the neuron emits two spikes, at a fixed interval t_0. (Later we will use t_0=2ms).

Suppose that **each of the two spikes of the doublet** causes a postsynaptic depolarization of standard exponential shape:

(i) Upon spike arrival the membrane potential of the postsynaptic neuron jumps by an amount b (later we will use b=2mV).

(ii) Thereafter it decays with a time constant τ_m. (Later we will use $\tau_m = 5$ms.)

Consider a postsynaptic neuron that receives input from K presynaptic neurons where each of the presynaptic neuron fires doublets of spikes. Suppose that, in each of the K neurons, a **spike doublet occurs stochastically at a constant rate** ν_0. (Later we consider ν_0=0.5Hz.)

The total input potential of the postsynaptic neuron is

$$u(t) = \sum_{k=1}^{K} \sum_{f} \alpha(t - t_k^f) \tag{8}$$

where α is defined above by the sentences explaining the shape of the depolarization and t_k^f denotes the spike arrival times.

(a) Determine the mean input potential of the postsynaptic neuron. (Assuming K presynaptic neurons, each one generating spike doublets at rate ν_0.) Express your result as an explicit function of the parameters t_0, b, τ_m, ν_0, K; no integral signs should be left.

$< u >=$

....

number of points: ...../2

(b1) Evaluate the mean input potential for $t_0 = 2ms; b = 2mV; \tau_m = 5ms; K = 1000; \nu_0 = 0.5Hz$. Pay attention to the units

$< u >=$ ....

number of points: ...../1

(b2) Knowing that the typical distance between resting potential and threshold is in the range of 20-30 mV, and assuming that the membrane potential is reset to rest after each spike, do you expect the neuron to fire *regularly* when driven with the input spikes as defined above?

Yes/No because ....

number of points: ...../1

(c) How would the mean input potential change if instead of each neuron firing doublets at rate ν_0, it would fire single spikes at rate $\nu = 4\nu_0$?

....

Give an intuitive or mathematical reason.

....

number of points: ...../2

(d) How would the standard deviation of the input potential change if instead of each neuron firing doublets at rate ν_0, it would fire single spikes at rate $\nu = 2\nu_0$?

....

Give an intuitive or mathematical reason. You may want to consider the limiting cases $t_0 \to 0$ and $t_0 \gg \tau_m$.

....

number of points: ...../2

(e) **BONUS (3pts).**

(e1) Determine mathematically the variance of the input potential of the postsynaptic neuron. Express your result as a function of the parameters t_0, b, τ_m, ν_0, K; no integral signs should be left.

$< (\Delta u)^2 >=$ ....

number of points: ...../2

(e2) Using your results of (a) and (e), evaluate the standard deviation of the membrane potential for $t_0 = 5ms; b = 1mV; \tau_m = 10ms; K = 1000; \nu_0 = 1Hz$. Pay attention to the units.

$< (\Delta u(t))^2 >^{0.5}=$ ....

number of points: ...../1