

**UNIVERSITY OF BRISTOL**

**May / June 2019 Examination Period**

**FACULTY OF ENGINEERING**

**Third Year / M Level Examination for the Degree of  
Bachelor of Science / Master of Engineering / Masters of Science**

**COMS 30127 / COMSM 2127  
Computational Neuroscience**

**TIME ALLOWED:  
2 hours**

**Answers to COMS 30127 / COMSM 2127: Computational  
Neuroscience**

**Intended Learning Outcomes:**

**Section A: short questions - answer all questions**

**Q1.** A substantial part of Henry Molaison's hippocampus was removed in an attempt to cure his epilepsy. What were the consequences of this damage to Henry Molaison? Henry Molaison was known as patient H.M.

**Solution:** He is unable to form new long term memories and had retrograde amnesia [2 marks for either answer].

**Q2.** What is the difference between *in vivo* and *in vitro* electrophysiology?

**Solution:** *In vitro* recordings are performed on cells in brain slices kept alive after the animal has been killed; *in vivo* recordings are recordings of neurons in the intact, or largely intact, brain of a living animal.

**Q3.** Why is the fourth order Runge-Kutta approximation better than the Euler approximation when solving differential equation?

**Solution:** The Runge-Kutta approximation includes more of the Taylor expansion; fourth order for example include the square, cubic and fourth order terms, and, therefore, has smaller errors than the Euler method.

**Q4.** Solve the differential equation

$$\frac{df}{dt} = 1 - f$$

with  $f(0) = -1$ .

**Solution:**

$$f(t) = 1 - 2e^{-t}$$

**Q5.** The hippocampus is important for encoding declarative memories (memories we can verbalise about). Name the two main subtypes of declarative memories.

**Solution:** Episodic (memories for places, people, events) and semantic (knowledge about facts and the world). [1 mark each correct answer. Partial marks if the gist is given without proper terminology].

**Q6.** What assumption does the idea of “rate coding” rely on?

**Solution:** That the timings of individual spikes are not relevant for brain dynamics or information processing, the only important variable is the rate of neural spiking over some time interval [2 marks].

**Q7.** What does “retinotopy” refer to in the visual regions of the brain?

**Solution:** Retinotopy is the property that anatomically nearby neurons in the brain tend to respond to stimuli in nearby parts of the visual field.

**Q8.** The left and right hemispheres of the brain respond to different aspects of the visual field. What part of the visual field does the brain's right hemisphere respond to?

**Solution:** The left side of the visual field (not the left eye).

**Q9.** There are several types of topographic map superimposed in visual cortex. Name two of the types.

**Solution:** Any two of: retinotopy; orientation tuning; motion direction tuning; spatial frequency tuning; ocular dominance. [1 mark each, up to two total.]

**Q10.** For a spike train with spike times  $\{t_1, t_2, \dots, t_n\}$  evoked by stimulus  $s(t)$  define the spike triggered average.

**Solution:**

$$S(\tau) = \frac{1}{n} \sum_i s(t_i - \tau)$$

**Q11.** Briefly describe the synaptic theory of working memory.

**Solution:** In the synaptic theory of working memory short-term facilitation [1 mark] encodes short lasting memory traces that can be read out a few seconds later on [1 mark].

**Q12.** Give the equations for the basic pairwise STDP model.

**Solution:** For LTP:  $\Delta W(\Delta t) = A_+ \exp(-x/\tau_+)$  for  $\Delta t > 0$  and for LTD:  $\delta W(\Delta t) = -A_- \exp(x/\tau_-)$  with  $\Delta t < 0$  [1 mark] for each.

**Q13.** Explain what is meant by detailed excitation-inhibition balance.

**Solution:** In detailed balance a given excitatory postsynaptic response is matched in amplitude and closely in time by an inhibitory synaptic response [2 marks].

**Q14.** What causes the imbalance of ion concentrations across the neuron membrane?

**Solution:** There is a pump powered by ATP which pumps ions across the membrane.

**Q15.** According to the Hodgkin-Huxley equation the conductance of the potassium gate is proportional to  $n^4$  where

$$\frac{dn}{dt} = \alpha(1 - n) - \beta n$$

What is the usual interpretation of  $\alpha$  and  $\beta$ ? Show how the equation can be rewritten in the form

$$\tau \frac{dn}{dt} = n_{\infty} - n$$

**Solution:**  $\alpha$  and  $\beta$  are the opening and closing rates; rewrite as

$$\frac{dn}{dt} = \alpha - (\alpha + \beta)n$$

then divide across by  $\alpha + \beta$  to get

$$\frac{1}{\alpha + \beta} \frac{dn}{dt} = \frac{\alpha}{\alpha + \beta} - n$$

which has the required form if  $\tau = 1/(\alpha + \beta)$  and  $n_{\infty} = \alpha/(\alpha + \beta)$ .

## Section B: long questions - answer two questions

**Q1.** This question is about the leaky integrate-and-fire neuron.

(a) The voltage in the integrate-and-fire neuron satisfies:

$$\tau_m \frac{dV}{dt} = E_L - V + RI$$

However this is not the whole model; what must be added to give the integrate and fire model? [3 marks]

(b) How is the membrane time constant  $\tau_m$  related to the electrical properties of the cell membrane? [3 marks]

(c) Sketch a plot of the absolute impedance of the subthreshold voltage of the integrate-and-fire neuron. [4 marks]

(d) Derive a formula for the interspike interval for this neuron when there is a constant current large enough to cause spiking. [7 marks]

(e) There are a few common extensions to the integrate-and-fire model used to make it more realistic. Name one example of such an extension. [3 marks]

**Solution:** a) It needs a spike-and-reset mechanism. Whenever the voltage hits some threshold value, the voltage value is instantaneously reset to a lower voltage and a spike is said to have occurred. [3 marks]

b)  $\tau = R_m C_m$ , it is the product of the membrane capacitance with the membrane resistance. [3 marks]

c) The impedance curve should follow

$$A(\omega) \propto \frac{\tau_m}{1 + i\omega\tau_m}$$

, so the plot should look like a straight horizontal line that bends downwards at some point before dropping as  $1/\omega$ , where  $\omega$  is the input current frequency. [4 marks]

d) In the model

$$\tau_m \frac{dV}{dt} = E_L - V + R_m I_e$$

which we can solve from our study of odes, it gives

$$V(t) = E_L + R_m I_e + [V(0) - E_L - R_m I_e]e^{-t/\tau_m}$$

[2 marks] so if the neuron has spiked and is reset at time  $t = 0$  and reaches threshold at time  $t = T$ , assume  $V_R = E_L$  we have [2 marks]

$$V_T = E_L + R_m I_e - R_m I_e e^{-T/\tau_m}$$

[1 mark] so

$$e^{-T/\tau_m} = \frac{E_L + R_m I_e - V_T}{R_m I_e}$$

[1 mark] Taking the log of both sides we get

$$T = \tau_m \log \left[ \frac{R_m I_e}{E_L + R_m I_e - V_T} \right]$$

[2 marks]

e) Any one of: a mechanism for spike frequency adaptation; a refractory period; a dynamic threshold; a more realistic spiking mechanism. [3 marks]

**Q2.** This question is part about inhibitory plasticity and part about Hopfield networks.

(a) Give the learning rule used by Vogels et al. Science 2011 to achieve excitation-inhibitory balance in recurrent networks. [3 marks]

(b) Give the expression to which the weight converges for the above rule and explain its meaning. [7 marks]

(c) What aspect of the Hopfield network learning rule might be described as Hebbian? [3 marks]

- (d) Imagine a Hopfield network with three neurons, and two patterns to store:  $(-1, 1, -1)$  and  $(1, 1, -1)$ . Compute the synaptic weights between the three neurons:  $w_{12}$ ,  $w_{13}$  and  $w_{23}$ . [4 marks]
- (e) Assume the neurons have a threshold value  $\theta = 1/2$ . If the same network were initialised in state  $(-1, -1, -1)$ , and you did a synchronous update on all the neurons' states, what would the network state be at the next timestep? [3 marks]

**Solution:** a)  $\Delta w = \eta(\text{pre} \times \text{post} - p_o \text{pre})$  or similarly  $\Delta w = \eta(xy - p_o x)$  [3 marks] b) By setting  $\Delta w = 0$  we find the point of convergence which is  $\text{post} = p_o$  [4 marks], this means that the learning rule stops when the postsynaptic rate is equal to a target value (which is predefined)  $p_o$  [3 marks; 7 marks in total].

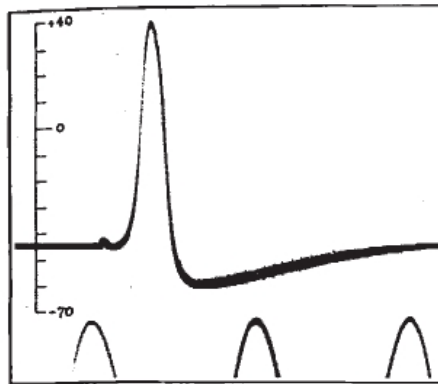
c) The fact that the rule involves the product of pre and post-synaptic activity. [3 marks]

d) The weight setting rule is  $w_{ij} = 1/2 \sum_a x_i^a x_j^a$  where  $a$  indexes the patterns, so  $w_{12} = 0$ ,  $w_{13} = 0$ ,  $w_{23} = -1$ . [4 marks]

e) The update rule is  $x_i(t+1) = \text{sign}(\sum_{j \neq i} w_{ij} x_j(t) - \theta)$  so after one timestep the network state will be  $(-1, 1, 1)$ . [3 marks]

**Q3.** This question is about models of spiking neurons.

- (a) The figure shows a recording made by Hodgkin and Huxley of an action potential.



- What ion flow accounts for the upswing and downswing in the voltage. [4 marks]
- (b) Write down the Hodgkin-Huxley equation for the voltage; include the relationship between the conductances and the gating variables  $n$ ,  $m$  and  $h$ ; there is no need to include equations for the gating variables. Take care to define the various constants. [6 marks]
- (c) Sketch the asymptotic values of  $n$ ,  $m$  and  $h$  and describe the role they play in forming the spike. [5 marks]
- (d) What assumptions are made to roughly derive the Morris-Lecar model from the Hodgkin-Huxley one. [5 marks]

**Solution:** a) The upswing is due to the influx of sodium, the downswing, the outflux of potassium [2 marks each]

b) The equation is

$$C_m \frac{dV}{dt} = g_l(E_l - V) + g_n(E_n - V) + g_k(E_k - V) + I$$

where  $E_l$ ,  $E_n$  and  $E_k$  are the leak, sodium and potassium reversal potentials,  $g_l$ ,  $g_n$  and  $g_k$  are the leak, sodium and potassium conductances,  $C_m$  is the membrane capacitance and  $I$  is an input current. [2 marks for eqns, 2 marks for constants]. The conductances are [2 marks]

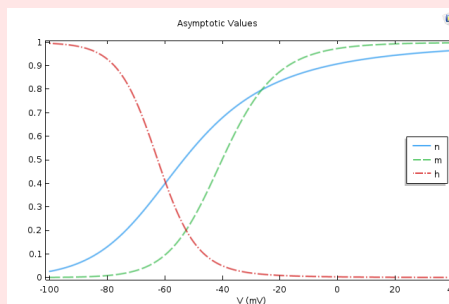
$$g_n = \bar{g}_n m^3 h$$

and

$$g_k = \bar{g}_k n^4$$

The second of these actually appears in the short questions.

c) The picture should look like plot below. The key aspect is that curves should be sigmoid functions of voltage,  $m$  and  $n$  are monotonically increasing with  $V$  while  $h$  is monotonically decreasing with  $V$  [2 marks]



As the voltage increases, the asymptotic value for  $m$  increases, opening the gates and allowing sodium in, driving up the voltage, at this increased voltage value  $h$  falls, cutting off the sodium while the potassium follows its increased asymptotic value; potassium flows out bringing the voltage back down.

d) The dynamics of the  $m$  sodium variable is assumed to be instantaneous [2 marks], reducing the model to two equations [1 mark], the  $h$  variable is ignored and all powers are dropped in the conductances.[2 marks]