

## Question 1

You are sitting in a room waiting for an auditory signal. The probability per unit time for the signal to appear is  $\gamma$ , and once it appears it stays there forever.

1. The signal has not appeared at time 0. What is the probability that it will appear at time  $t$ ? What is the probability it will not appear in the interval  $[0, T]$ ? (2 marks)
2. A neuron with firing rate  $\nu(t)$  and refractory period  $\Delta t$  emits spikes as follows: the probability that the neuron fires in a small interval  $dt$  around  $t$  is  $\nu(t)dt$  if the neuron fired no previous spikes in the interval  $[t - \Delta t, t]$  and zero otherwise. If  $\nu(t) = \nu = \text{constant}$ , what is the mean firing rate of this neuron? (3 marks)
3. A neuron in auditory cortex fires at a background rate of  $\nu_0$  before the signal in part 1 appears and jumps to rate  $\nu_1$  (and stays there) after it appears. As in part 2, the neuron has an absolute refractory period of  $\Delta t$ . You observe spikes at times  $t_1, t_2, \dots, t_n$ . Write down the probability distribution that the signal came on at time  $t_s$  given the spikes, denoted  $p(t_s|\text{spikes})$ . Include the probability that the signal never came on. The normalization that appears in this problem will involve an integral – don't do it! (5 marks)
4. You observe spikes in the interval  $[0, T]$ . Assume the signal came on at time  $t_0$ . Sketch  $\langle \log p(t_s|\text{spikes}) \rangle$  versus  $t_s$  where the average is over ensembles of spike trains. (10 marks)
5. Based on this plot, give a back of the envelope estimate of the value of  $t_0$  at which you will say that no signal occurred; that is, estimate the value of  $t_0$  such that  $\int dt_s p(t_s|\text{spikes})$  is larger, on average, than  $p(\text{no signal}|\text{spikes})$ .

## Question 2

Consider a network of  $N$  analog neurons that obey the time-evolution equations

$$\tau \dot{x}_i = \phi(J\bar{x} - \theta) - x_i \quad (1)$$

where “dot” denotes a time derivative,  $\bar{x} \equiv N^{-1} \sum_i x_i$  is the mean firing rate, and  $\phi(z)$  is the gain function. We will demand that the gain function be threshold-concave-nonincreasing, meaning

$$\begin{aligned} z < 0 : \quad & \phi(z) = 0 \\ z \geq 0 : \quad & \phi'(z) \geq 0 \text{ and } \phi''(z) \leq 0. \end{aligned}$$

1. Write down the time evolution equation for  $\bar{x}$ . (1 mark)
2. Find the equilibria graphically in a regime in which there are three. Which of the equilibria are stable and which are unstable? (2 marks)
3. There are two main models for network bursting in the literature: synaptic depression and spike-frequency adaptation.
  - (a) What biophysical mechanism is thought to be responsible for synaptic depression? (2 marks)
  - (b) What biophysical mechanism is thought to be responsible for spike-frequency adaptation? (2 marks)
4. To model these two mechanisms, one typically lets  $J$  or  $\theta$  have slow, activity dependent dynamics. For synaptic depression,

$$\tau_0 \dot{J} = -(J - J_0(\bar{x})), \quad (2)$$

while for spike-frequency adaptation,

$$\tau_0 \dot{\theta} = -(\theta - \theta_0(\bar{x})). \quad (3)$$

In both cases these variables evolve slowly, meaning  $\tau_0 \gg \tau$ . If Eqs. (2) and (3) are to provide adaptation, how must  $J_0$  and  $\theta_0$  depend on  $\bar{x}$ ? (Essentially, what is the slope of  $J_0(\bar{x})$  and  $\theta_0(\bar{x})$ ?) Sketch the two functions. (4 marks)

5. Given our model, including the properties of  $\phi$ , which of these two mechanisms, if either, can lead to network bursting, and why? Assume  $\tau_0 \gg \tau$ , so that the  $x_i$  relax essentially instantaneously to their equilibria. For the model(s) that show bursting, sketch the trajectories of  $\bar{x}$  and either  $J$  or  $\theta$  versus time. (8 marks)
6. Let the threshold,  $\theta$ , be a random variable,

$$\tau \dot{x}_i = \phi(J\bar{x} - \theta_i) - x_i$$

where the  $\theta_i$  are drawn i.i.d. from a Gaussian distribution with mean  $\theta$  and variance  $\sigma^2$ .

- (a) Derive a time evolution equation for  $\bar{x}$  in the large  $N$  limit. (4 marks)
- (b) Sketch the resulting effective gain function. (3 marks)
- (c) With this new model with variable thresholds, which of the mechanisms can produce bursting? (4 marks)