# **Exercises**

# **Chapter 1**

- 1. Generate spike sequences with a constant firing rate  $r_0$  using a Poisson spike generator. Then, add a refractory period to the model by allowing the firing rate r(t) to depend on time. Initially,  $r(t) = r_0$ . After every spike, set r(t) to zero. Allow it to recover exponentially back to  $r_0$  by setting  $r(t + \Delta t) = r_0 + (r(t) r_0) \exp(-\Delta t/\tau_{ref})$  after every simulation time step  $\Delta t$  in which no spike occurs. The constant  $\tau_{ref}$  controls the refractory recovery rate. Initially, use  $\tau_{ref} = 10$  ms. Compute the Fano factor and coefficient of variation, and plot the interspike interval histogram for spike trains generated without a refractory period and with a refractory period determined by  $\tau_{ref}$  over the range from 1 to 20 ms.
- 2. Plot autocorrelation histograms of spike trains generated by a Poisson generator with A) a constant fire rate of 100 Hz, B) a constant firing rate of 100 Hz and a refractory period modeled as in exercise 1 with  $\tau_{ref} = 10$  ms, and C) a variable firing rate  $r(t) = 100(1 + \cos(2\pi t/25 \text{ ms}))$  Hz. Plot the histograms over a range from 0 to 100 ms.
- 3. Generate a Poisson spike train with a time-dependent firing rate  $r(t) = 100(1 + \cos(2\pi t/300 \text{ ms}))$  Hz. Approximate the firing rate from this spike train by making the update  $r_{approx} \rightarrow r_{approx} + 1/\tau_{approx}$  every time a spike occurs, and letting  $r_{approx}$  decay exponentially,  $r_{approx} \rightarrow r_{approx} \exp(-\Delta t)/\tau_{approx}$ ), if no spike occurs during a time step of size  $\Delta t$ . Make a plot the average squared error of the estimate,  $\int dt(r(t) r_{approx}(t))^2$  as a function of  $\tau_{approx}$  and find the value of  $\tau_{approx}$  that produces the most accurate estimate for this firing pattern.
- 4. Using the same spike trains as in exercise 3, construct estimates of the firing rate using square, Gaussian, and other types of window functions to see which gives the most accurate estimate.
- 5. For a constant rate Poisson process, every sequence of N spikes occurring during a given time interval is equally likely. This seems paradoxical because we certainly do not expect to see all N spikes appearing within the first 1% of the time interval. Yet this seems as likely as any other pattern. Resolve this paradox.
- 6. Build a white-noise stimulus. Plot its autocorrelation function and power spectrum, which should be flat. Discuss the range of relation of these results to those for an ideal white-noise stimulus given the value of  $\Delta t$  you used in constructing the stimulus.
- 7. Construct two spiking models using an estimate of the firing rate and a Poisson spike generator. In the first model, let the firing rate

be determined in terms of the stimulus *s* by  $r_{est}(t) = [s]_+$ . In the second model, the firing rate is determined instead by integrating the equation (see Appendix A of chapter 5 for a numerical integration method)

$$\tau_r \frac{d\mathbf{r}_{\text{est}}(t)}{dt} = [\mathbf{s}]_+ - \mathbf{r}_{\text{est}}(t) \tag{1}$$

with  $\tau_r = 10$  ms. In both cases, use a Poisson generator to produce spikes at the rate  $r_{est}(t)$ . Compare the responses of the two models to a variety of time-dependent stimuli including approximate white-noise, and study the responses to both slowly and rapidly varying stimuli.

8. Use the two models constructed in exercise 7, driven with an approximate white-noise stimulus, to generate spikes, and compute the spike-triggered average stimulus for each model. Show how the spike-triggered average depends on  $\tau_r$  in the second model by considering different values of  $\tau_r$ .

#### Chapter 2

1. Build a model neuron (based on the electrosensory lateral-line lobe neuron discussed in chapter 1) using a Poisson generator firing at a rate predicted by equation **??** with  $r_0 = 50$  Hz and

$$D(\tau) = \cos\left(\frac{2\pi(\tau - 20 \text{ ms})}{140 \text{ ms}}\right) \exp\left(-\frac{\tau}{60 \text{ ms}}\right) \text{ Hz}.$$

Use a Gaussian white noise stimulus constructed using a time interval  $\Delta t = 10$  ms with  $\sigma_s^2 = 10$ . Compute the firing rate and spike train for a 10 s period. From these results, compute the spike-triggered average stimulus  $C(\tau)$  and the firing rate-stimulus correlation function  $Q_{rs}(\tau)$  and compare them with the linear kernel given above. Verify that the relations in equation **??** hold. Repeat this exercise with a static nonlinearity so that the firing rate is given by

$$r(t) = 10 \left| r_0 + \int_0^\infty d\tau D(\tau) s(t-\tau) \right|^{1/2}$$
 Hz

rather than by equation **??**. Show that  $C(\tau)$  and  $Q_{rs}(-\tau)$  are still proportional to  $D(\tau)$  in this case, though with a different proportionality constant.

2. For a Gaussian random variable *x* with zero mean and standard deviation  $\sigma$ , prove that

$$\langle xF(\alpha x)\rangle = \alpha\sigma^2 \langle F'(\alpha x)\rangle$$

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where  $\alpha$  is a constant, *F* is any function, *F* is its derivative,

$$\langle xF(\alpha x)\rangle = \int dx \frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{x^2}{2\sigma^2}\right) xF(\alpha x),$$

and similarly for  $\langle F(\alpha x) \rangle$ . By extending this basic result first to multivariant functions and then to the functionals, the identity **??** can be derived.

3. Using the inverses of equations ?? and ??

$$\epsilon = \epsilon_0 \left( \exp(X/\lambda) - 1 \right) \text{ and } a = -\frac{180^\circ(\epsilon_0 + \epsilon)Y}{\lambda \epsilon \pi}$$

map from cortical coordinates back to visual coordinates and determine what various patterns of activity in the primary visual cortex would 'look like'. Consider straight lines and bands of constant activity extending across the cortex at various angles. Ermentrout and Cowan (1979) used these results as a basis of a mathematical theory of visual hallucinations.

4. Compute the integrals in equations **??** and **??** for the case  $\sigma_x = \sigma_y = \sigma$  to obtain the results

$$L_{\rm s} = \frac{A}{2} \exp\left(-\frac{\sigma^2(k^2 + K^2)}{2}\right) \left(\cos(\phi - \Phi) \exp\left(\sigma^2 k K \cos(\Theta)\right) + \cos(\phi + \Phi) \exp\left(-\sigma^2 k K \cos(\Theta)\right)\right).$$

and

$$L_{\rm t}(t) = \frac{\alpha^6 |\omega| \sqrt{\omega^2 + 4\alpha^2}}{(\omega^2 + \alpha^2)^4} \cos(\omega t - \delta) \,.$$

with

$$\delta = \arctan\left(\frac{\omega}{\alpha}\right) + 8\arctan\left(\frac{2\alpha}{\omega}\right) - \pi$$

and verify the selectivity curves in figures **??** and **??**. In addition, plot  $\delta$  as a function or  $\omega$ . The integrals can be also be done numerically to obtain these curves directly.

5. Compute the response of a model simple cell with a separable spacetime receptive field to a moving grating

$$s(x, y, t) = \cos(Kx - \omega t) .$$

For  $D_s$  use equation ?? with  $\sigma_x = \sigma_y = 1^\circ$ ,  $\phi = 0$ , and  $1/k = 0.5^\circ$ . For  $D_t$  use equation ?? with  $\alpha = 1/(15 \text{ ms})$ . Compute the linear estimate of the response given by equation ?? and assume that the actual response is proportional to a rectified version of this linear response estimate. Plot the response as a function of time for  $1/K = 1/k = 0.5^\circ$  and  $\omega = 8\pi/s$ . Plot the response amplitude as a function of  $\omega$  for  $1/K = 1/k = 0.5^\circ$  and as a function of *K* for  $\omega = 8\pi/s$ .

- 6. Construct a model simple cell with the nonseparable space-time receptive field described in the caption of figure **??**B. Compute its response to the moving grating of exercise 4. Plot the amplitude of the response as a function of the velocity of the grating,  $\omega/K$ , using  $\omega = 8\pi/s$  and varying *K* to obtain a range of both positive and negative velocity values (use negative *K* values for this).
- 7. Compute the response of a model complex cell to the moving grating of exercise 5. The complex cell should be modeled by squaring the linear response estimate of the simple cell used in exercise 5, and adding this to the square of the response of a second simple cell with identical properties except that its spatial phase preference is  $\phi = -\pi/2$  instead of  $\phi = 0$ . Plot the response as a function of time for  $1/K = 1/k = 0.5^{\circ}$  and  $\omega = 8\pi/s$ . Plot the response amplitude as a function of  $\omega$  for  $1/K = 1/k = 0.5^{\circ}$  and as a function of *K* for  $\omega = 8\pi/s$ .
- 8. Construct a model complex cell that is disparity tuned but insensitive to the absolute position of a grating. The complex cell is constructed by summing the squares of the responses of two simple cells, but disparity effects are now included. For this exercise, we ignore temporal factors and only consider the spatial dependence of the response. Each simple cell response is composed of two terms that correspond to inputs coming from the left and right eyes. Because of disparity, the spatial phases of the image of a grating in the two eyes,  $\Phi_L$  and  $\Phi_R$ , may be different. We write the spatial part of the linear response estimate for a grating with the preferred spatial frequency (k = K) and orientation ( $\Theta = \theta = 0$ ) as

$$L_1 = \frac{A}{2} \left( \cos(\Phi_L) + \cos(\Phi_R) \right)$$

assuming that  $\phi = 0$  (this equation is a generalization of **??**). Let the complex cell response be proportional to  $L_1^2 + L_2^2$  where  $L_2$  is similar to  $L_1$  but with the cosine functions replaced by sine functions. Show that the response of this neuron is tuned to the disparity,  $\Phi_L - \Phi_R$ , and is independent of the absolute spatial phase of the grating,  $\Phi_L + \Phi_R$ . Plot the response tuning curve as a function of disparity. (See Ohzawa *et al*, 1991).

- 9. Determine the selectivity of the LGN receptive field of equation ?? to spatial frequency and of the temporal response function for LGN neurons, equation ??, to temporal frequency by computing their integrals when multiplied by cosine functions of space or time respectively. Use  $\sigma_c = 0.3^\circ$ ,  $\sigma_s = 1.5^\circ$ , B = 5,  $1/\alpha = 16$  ms, and  $1/\beta = 64$  ms. Plot the resulting spatial and temporal frequency tuning curves.
- 10. Construct the Hubel-Wiesel simple and complex cell models of figure ??. Use difference-of-Gaussian and Gabor functions to model the LGN and simple cell response. Plot the spatial receptive field of the

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simple cell constructed in this way. Compare the result of summing appropriately placed LGN center-surround receptive fields (figure ??A) with the results of the Gabor filter model of the simple cell that uses the spatial kernel of equation ??. Compare the responses of a complex cell constructed by linearly summing the outputs of simple cells (figure ??B) with different spatial phase preferences with the complex cell model obtained by squaring and summing two simple cell responses with spatial phases 90° apart as in equation ??.

### **Chapter 3**

1. Suppose that the probabilities that a neuron responds with a firing rate between *r* and  $r + \Delta r$  to two stimuli labeled plus and minus are  $p[r|\pm]\Delta r$  where

$$p[r|\pm] = \frac{1}{\sqrt{2\pi}\sigma_r} \exp\left(-\frac{1}{2}\left(\frac{r-\langle r\rangle_{\pm}}{\sigma_r}\right)^2\right).$$

Assume that the two mean rate parameters  $\langle r \rangle_+$  and  $\langle r \rangle_-$  and the single variance  $\sigma_r^2$  are chosen so that these distributions produce negative rates rarely enough that we can ignore this problem. Show that

$$\alpha(z) = \frac{1}{2} \operatorname{erfc}\left(\frac{z - \langle r \rangle_{-}}{\sqrt{2}\sigma_{r}}\right) \quad \text{and} \quad \beta(z) = \frac{1}{2} \operatorname{erfc}\left(\frac{z - \langle r \rangle_{+}}{\sqrt{2}\sigma_{r}}\right)$$

and that the probability of a correct answer in a two-alternative forced choice task is given by equation **??**. Derive the result of equation **??**. Plot ROC curves for different values of the discriminability

$$d' = \frac{\langle r \rangle_+ - \langle r \rangle_-}{\sigma_r}$$

By simulation, determine the fraction of correct discriminations that can be made in a two-alternative forced choice task involving discriminating between plus-then-minus and minus-then-plus presentations of two stimuli. Show that the fractions of correct answer for different values of d are equal to the areas under the corresponding ROC curves.

2. Model the responses of the cercal system of the cricket by using the tuning curves of equation ?? to determine mean response rates and generating spikes with a Poisson generator. Simulate a large number of responses for a variety of wind directions randomly, use the vector method to decode them on the basis of spike counts over a predefined trial period, and compare the decoded direction with the actual direction used to generated the responses to determine the decoding accuracy. Plot the root-mean-square decoding error as a function of wind direction for several different trial durations. The results may not match those of figure ?? because a different model of variability was used in that analysis.

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- 3. Show that if an infinite number of unit vectors  $\vec{c}_a$  is chosen from a probability distribution that is independent of direction,  $\sum (\vec{v} \cdot \vec{c}_a)\vec{c}_a \propto \vec{v}$  for any vector  $\vec{v}$ . How does the sum approach this limit for a finite number of terms?
- 4. Show that the Bayesian estimator that minimizes the expected average value of the the loss function  $L(s, s_{\text{bayes}}) = (s s_{\text{bayes}})^2$  is the mean given by equation ?? and that the median corresponds to minimizing the expected loss function  $L(s, s_{\text{bayes}}) = |s s_{\text{bayes}}|$ .
- 5. Simulate the response of a set of M1 neurons to a variety of arm movement directions using the tuning curves of equation ?? with randomly chosen preferred directions, and a Poisson spike generator. Choose the arm movement directions and preferred directions to lie in a plane so that they are characterized by a single angle. Study how the accuracy of the vector decoding method depends on the number of neurons used. Compare these results with those obtained using the ML method by solving equation ?? numerically.
- 6. Show that the formulas for the Fisher information in equation **??** and also be written as

$$I_{\rm F}(s) = \left\langle \left(\frac{\partial \ln p[\mathbf{r}|s]}{\partial s}\right)^2 \right\rangle = \int d\mathbf{r} \, p[\mathbf{r}|s] \left(\frac{\partial \ln p[\mathbf{r}|s]}{\partial s}\right)^2$$

or

$$I_{\rm F}(s) = \int d\mathbf{r} \, \frac{1}{p[\mathbf{r}|s]} \left( \frac{\partial p[\mathbf{r}|s]}{\partial s} \right)^2 \, .$$

Use the fact that  $\int d\mathbf{r} p[\mathbf{r}|s] = 1$ .

7. The discriminability for the variable *Z* defined in equation **??** is the difference between the average *Z* values for the two stimuli  $s + \Delta s$  and *s* divided by the standard deviation of *Z*. The average of the difference in *Z* values is

$$\langle \Delta Z \rangle = \int d\mathbf{r} \, \frac{\partial \ln p[\mathbf{r}|s]}{\partial s} \left( p[\mathbf{r}|s + \Delta s] - p[\mathbf{r}|s] \right) \,.$$

Show that for small  $\Delta s$ ,  $\langle \Delta Z \rangle = I_F(s) \Delta s$ . Also prove that the average value of *Z*,

$$\langle Z \rangle = \int d\mathbf{r} \, p[\mathbf{r}|s] \frac{\partial \ln p[\mathbf{r}|s]}{\partial s}$$

is zero and that the variance of Z is  $I_{\rm F}(s)$ . Computing the ratio, we find from these results that  $d = \Delta s \sqrt{I_{\rm F}(s)}$  which matches the discriminability **??** of the ML estimator.

8. Extend equation **??** to the case of neurons encoding a *D*-dimensional vector stimulus  $\vec{s}$  with tuning curves given by

$$f_a(\vec{s}) = r_{\max} \exp\left(-\frac{|\vec{s} - \vec{s}_a|^2}{2\sigma_r^2}\right)$$

and perform the sum by approximating it as an integral over uniformly and densely distributed values of  $\vec{s}_a$  to derive the result in equation ??.

- 9. Derive equation ?? by minimizing the expression ??. Use the methods of Appendix A in chapter 2.
- 10. Use the electric fish model from problem 1 of chapter 2 to generate a spike train response to a stimulus s(t) of your choosing. Decode the spike train and reconstruct the stimulus using an optimal linear filter. Compare the optimal decoding filter with the optimal kernel for rate prediction,  $D(\tau)$ . Determine the average squared error of your reconstruction of the stimulus. Examine the effect that various static nonlinearities in the model for the firing rate that generates the spikes have on the accuracy of the decoding.

### **Chapter 4**

- 1. Show that the distribution that maximizes the entropy when the firing rate is constrained to lie in the range  $0 \le r \le r_{\text{max}}$  is given by equation ?? and its entropy for a fixed resolution  $\Delta r$  is given by equation ??. Use a Lagrange multiplier (chapter 12) to constrain the integral of p[r] to one.
- 2. Show that the distribution that maximizes the entropy when the mean of the firing rate is held fixed is an exponential, and compute its entropy for a fixed resolution  $\Delta r$ . Assume that the firing rate can fall anywhere in the range from zero to infinity. Use Lagrange multipliers (chapter 12) to constrain the integral of p[r] to one and the integral of p[r]r to the fixed average firing rate.
- 3. Show that the distribution that maximizes the entropy when the mean and variance of the firing rate are held fixed is a Gaussian, and compute its entropy for a fixed resolution  $\Delta r$ . To simplify the mathematics, allow the firing rate to take any value between minus and plus infinity. Use Lagrange multipliers (chapter 12) to constrain the integral of p[r] to one, the integral of p[r]r to the fixed average firing rate, and the integral of  $p[r](r \langle r \rangle)^2$  to the fixed variance.
- 4. Using Fourier transforms solve equation **??** to obtain the result of equation **??**.

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5. Suppose the filter  $L_{s}(\vec{a})$  has a correlation function that satisfies equation ??. We write a new filter in terms of this old one by

$$L'_{\rm s}(\vec{a}) = \int d\vec{c} \, U(\vec{a}, \vec{c}) \, L_{\rm s}(\vec{c}) \,. \tag{2}$$

Show that if  $U(\vec{a}, \vec{c})$  satisfies the condition of an orthogonal transformation.

$$\int d\vec{c} U(\vec{a}, \vec{c}) U(\vec{b}, \vec{c}) = \delta(\vec{a} - \vec{b}), \qquad (3)$$

the correlation function for this new filter also satisfies equation ??.

6. Construct an integrate-and-fire neuron model, and drive it with an injected current consisting of the sum of two or more sine waves with incommensurate frequencies. Compute the rate of information about the injected current contained in the spike train produced by this model neuron the method discussed in the text.

### Chapter 5

- 1. Write down the analytic solution of equation ?? when  $I_{e}(t)$  is an arbitrary function of time. The solution will involve integrals that cannot be performed unless  $I_{\rm e}(t)$  is specified.
- 2. Construct the model of two, coupled integrate-and-fire model neurons of figure ??. Show how the pattern of firing for the two neurons depends on the strength, type (excitatory or inhibitory), and time constant of the reciprocal synaptic connection (see Van Vreeswijk et al. 1994).
- 3. Plot the firing frequency as a function of constant electrode current for the Hodgkin-Huxley model. Show that the firing rate jumps discontinuously from zero to a finite value when the current passes through the minimum value required to produce sustained firing.
- 4. Demonstrate postinhibitory rebound in the Hodgkin-Huxley model.
- 5. The Nernst equation was derived in this chapter under the assumption that the membrane potential was negative and the ion being considered was positively charged. Rederive the Nernst equation, ??, for a negatively charged ion and for the case when *E* is positive to verify that it applies in all these cases.
- 6. Compute the value of the release probability  $P_{\rm rel}$  at the time of each presynaptic spike for a regular, periodic, constant-frequency presynaptic spike train as a function of the presynaptic firing rate. Do this for both the depression and facilitation models discussed in the text.

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- 7. Verify that the state probabilities listed after equation **??** are actually a solution of these equations if *n* satisfies equation **??**. Show that an arbitrary set of initial values for these probabilities, will ultimately settle into this solution.
- 8. Construct and simulate the K<sup>+</sup> channel model of figure ??. Plot the mean squared deviation between the current produced by *N* such model channels and the Hodgkin-Huxley current as a function of *N*, matching the amplitude of the Hodgkin-Huxley model so that the mean currents are the same.
- 9. Construct and simulate the Na<sup>+</sup> channel model of figure ??. Compare the current through 100 such channels with the current predicted by the Hodgkin-Huxley model at very short times after a step-like depolarization of the membrane potential. What are the differences and why do they occur?

# **Chapter 6**

Chapter 7

**Chapter 8** 

**Chapter 9** 

**Chapter 10** 

Chapter 11

Chapter 12