Exercises

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 σ_r^2 are chosen so that these distributions produce negative rates rarely enough that we can integrate over r values over the entire range $-\infty < r < \infty$. Suppose that you base discrimination of the plus and minus stimuli on whether the evoked firing rate is greater or less than a threshold z. Show that the size and power, $\alpha(z)$ and $\beta(z)$ of this test are given by

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

Show that the probability of a correct answer in the associated two-alternative forced choice task involving discriminating between plus-then-minus and minus-then-plus presentations of the two stimuli is given by equation 3.10. Also, derive the result of equation 3.17. 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 the two-alternative forced choice task. Show that the fractions of correct answer for different values of d' are equal to the areas under the corresponding ROC curves.

2. Simulate the random-dot discrimination experiment. Denote the stimulus by plus or minus, corresponding to the two directions of motion. On each trial, choose the stimulus randomly with equal probability for the two cases. When the minus stimulus is chosen, generate the responses of the neuron as 20 Hz plus a random Gaussian term with a standard deviation of 10 Hz (set any rates that come out negative to zero). When the plus stimulus is chosen, generate the responses as $20 + 10d$ Hz plus a random Gaussian term with a standard deviation of 10 Hz, where d is the discriminability (again, set any rates that come out negative to zero). First, choose a threshold $z = 20 + 5d$, which is half-way between the means of the two response distributions. Whenever $r \geq z$ guess "plus", otherwise guess "minus". Over a large number of trials (1000, for example) determine how often you get the right answer for different d values. Plot

the percent correct as a function of d over the range $0 \leq d \leq 10$. Next, by allowing z to vary over a range, plot ROC curves for several values of d (starting with $d = 2$). To do this, determine how frequently the guess is "plus" when the stimulus is, in fact, plus (this is β), and how often the guess is "plus" when the real stimulus is minus (this is α). Then, plot β versus α for z over the range $0 \leq z \leq 140$.

3. Simulate the responses of four interneurons in the cercal system of the cricket and check the accuracy of a vector decoding scheme. For a true wind direction θ, the average firing rates of the four interneurons should be generated as

$$\langle r_i \rangle = [50 \, \text{Hz} \cos{(\theta - \theta_i)}]_+ \,,$$

where $[\ ]_+$ indicates half-wave rectification, and $\theta_i = \pi/4$, $3\pi/4$, $5\pi/4$, $7\pi/4$ for $i = 1, 2, 3, 4$. The actual rates, r_i, are then obtained by adding to these mean rates a random number chosen from a Gaussian distribution with zero mean and a standard deviation of 5 Hz (set any rates the come out negative to zero). From these rates, construct the x and y components of the population vector

$$x = \sum_{i=1}^{4} r_i \cos{(\theta_i)} \quad \text{and} \quad y = \sum_{i=1}^{4} r_i \sin{(\theta_i)}$$

and, from the direction of this vector, compute an estimate θ_{est} of the wind direction. Average the squared difference $(\theta - \theta_{\text{est}})^2$ over 1000 trials. The square root of of this quantity is the error. Plot the error as a function of θ over the range $-90° \leq \theta \leq 90°$.

4. Show that if an infinite number of unit vectors $\vec{c}_a$ is chosen uniformly 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?

5. 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 of the distribution $p[s|\mathbf{r}]$, given by equation 3.27. Also show that the estimate that arises from minimizing the expected loss function $L(s, s_{\text{bayes}}) = |s - s_{\text{bayes}}|$ is the median of $p[s|\mathbf{r}]$.

6. Show that the equations for the Fisher information in equation 3.42 can also be written as in equation 3.43,

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

or as

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

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

7. The discriminability for the variable Z defined in equation 3.19 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 Δs, $\langle \Delta Z \rangle = I_\mathrm{F}(s) \, \Delta s$. 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 $I_\mathrm{F}(s)$. Computing the ratio, we find from these results that $d' = \Delta s \sqrt{I_\mathrm{F}(s)}$ which matches the discriminability 3.49 of the ML estimator.

8. Extend equation 3.46 to the case of neurons encoding a D-dimensional vector stimulus $\vec{s}$ with tuning curves given by

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

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 3.48.

9. Derive equation 3.54 by minimizing the expression 3.53. Use the methods of appendix A of chapter 2.

10. MATLAB® program `c3p10.m` performs acausal decoding using signal processing techniques to construct an approximate solution of equation 3.54, while suppressing unwanted effects of noise (for an illustration of these effects, see part (e) of this exercise). The program is called as `[est,K,ind]=ch3ex10(stim,spk,nfft)`, where `stim` and `spk` are the stimulus and response respectively, `nfft` is the length of a discrete Fourier transform (suitable values are `nfft`$= 2^{10} = 1024$ or $2^{11} = 2048$), K is the acausal kernel, `est` is the resulting stimulus estimate, and `ind` is a vector of indices that specifies the range over which the estimate and stimulus should be compared. Specifically, `est` provides an estimate of `stim(ind)`.

a) Compute an estimated firing rate r_est from equation 2.1 with $r_0 = 50$ Hz and

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

in response to an approximate white noise stimulus (roughly 500 seconds long) calculated by choosing at each time step (with $\Delta t = 10$ ms) a stimulus value from a Gaussian distribution with mean 0 and variance 2. Generate a kernel and estimate for this stimulus using

`c3p10.m` with r_{est} playing the role of the argument `spk`. Verify that `est` and `stim(ind)` are closely related, and describe the relationship between the coding kernel D and the decoding kernel `K`.

b) Repeat (a) with a rectification non-linearity, so that $[r_{est}]_+$ is used in place of r_{est}. Measure the effect of the nonlinearity by comparing the average (over time) of the squared difference between `est` and `stim(ind)`, divided by the variance of `stim`, for the rectified and nonrectified cases. What is the effect of rectification on the optimal decoding kernel `K`, and why? Assess the accuracy with which different frequency components in `stim` are captured in `est` by considering the power spectrum of the average squared difference between `est` and `stim(ind)`.

c) Generate a spike sequence `spk` from the rectified firing rate $[r_{est}]_+$ using a Poisson generator. The sequence `spk` should consist of a one or a zero at each time step, depending on whether or not a spike occurred. Recompute the acausal kernel as in part (a), but using `spk` as the response rather than r_{est}. How accurate is the resulting decoding, and what is the effect of using spikes rather than rates on the decoding kernel `K`?

d) What happens to decoding accuracy as the value of Δt, which defines the approximation to a white noise stimulus, increases and why? In the general case, the approximate white noise should be generated by choosing a stimulus value at each time step from a Gaussian distribution with mean 0 and variance $20 \text{ ms}/\Delta t$.

e) Attempt to repeat the decoding in (a) using the cross-correlation function `xcorr` and the fast Fourier transform `fft` to solve equation 3.54. Why is the answer so noisy?