BE 521: Homework 5

Vision

Spring 2015

42 points

Due: 3/03/2015

Objective: Visual responses and likelihood

Homework Policy

1. Piazza should be used for peer discussion for all questions related to course material. Please also use Piazza to contact teaching staff for all questions. TA's will be available to help during office hours and occasionally on Piazza.

2. Submit LaTeX write-up (pdf) and Matlab code to Canvas as pennkey_hwx.pdf, .m before listed deadline.

3. Assignments will be returned electronically on Canvas.

4. Collaboration is encouraged but individual write-ups are required. Please list any collaborators. Honor code will be strictly enforced. Note: submitted code is routinely passed through a plagiarism checker.

5. Late Policy: 5% per day. **No homework is accepted after the 5th late day.** (e.g. If originally due Tuesday, 11:59PM, last day to turn in is Sunday, 11:59 PM).

V1 Dataset

In this homework, you will work with data from 18 cells recorded from mouse primary visual cortex (also known as V1). Cells in this area are responsive to specific angles. Hence, a common stimulation paradigm is to show the subject a sinusoidal grating drifting at a specific angle (see Figure 1).

This data was collected and graciously provided by Daniel Denman in the Contreras Lab, University of Pennsylvania. The file `mouseV1.mat` contains two variables: `neurons`, a cell array

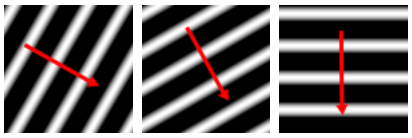

Figure 1: Example sinusoidal drifting grating at (in order left to right) 30, 60, and 90 degrees, where the red arrows shows the direction of the drift.

representing all the times that each of the 18 cells fired a spike during the approximately 4 minute long experiment, and `stimuli`, which provides the time (first column, in milliseconds) that a given angle (second column) was presented in this experiment. Note that each stimulus in `stimuli` is presented for exactly 2 seconds, after which a gray screen is presented for approximately 1.5 seconds (therefore each trial is approximately 3.5 seconds in duration.)

1 Stimulus Response (11 pts)

In this section, you will explore the response of the cells to different stimulus angles.

1. How many unique grating angles are there in `stimuli`? (1 pt)

2. A *tuning curve* is frequently used to study the response of a neuron to a given range of input stimuli. To create tuning curves for this data, calculate the average number of spikes each cell fires in response to each grating angle. Store the result in an $18 \times m$ dimensional matrix, where each element represents the response of a single neuron to a particular input stimulus angle, with each neuron assigned a row and each angle assigned a column. In a 2×2 Matlab subplot, plot the tuning curve for the first four cells. Place the stimulus angle on the x-axis and the number of spikes on the y-axis. (6 pts)

   (a) Look through the tuning response curves of each of the 18 cells. How reasonable is it to assume that the response of a given cell to angle θ is the same as its response to angle $\theta + 180$? Include at least a few tuning curves to back up your answer. (2 pts)

   (b) Does this assumption have any physiological justification (given what you know about the types of cells in V1)? (2 pts)

2 Neural Decoding (31 pts)

Suppose we would like to work backwards - that is, for a given neural response, can we predict what the grating angle was? This process is called "neural decoding," and is especially of interest to the BCI motor control community (as we'll see in a later homework). In this section, we will try

out a relatively straightforward decoding approach which is detailed in Jazayeri & Movshon 2006 (*Nature Neuroscience*)[1].

A brief detour: The method we will use involves conditional probabilities, also known as likelihoods, of the data. For example, if you have a fair coin with $P(heads) = \theta = .5$, and you observe 5 heads in a row, then the likelihood of your data $P(y|\theta) = \prod_{i=1}^{5} P(y_i = H|\theta) = 0.5^5 = 0.03125$. This means that your data is unlikely if $P(heads) = 0.5$, which argues for a different value for θ. We used here a Bernoulli distribution with parameter θ.

For us, the data is the number of spikes s_i that cell i fires when the subject sees a stimulus with grating angle θ. One way to think about our likelihood function is to ask the question "given a stimulus angle θ, how many spikes would I expect this cell to fire?" We can represent this number of spikes s_i using a Poisson process with parameter $f_i(\theta)$ for a stimulus θ, where $f_i(\theta)$ represents the neuron's tuning function. A Poisson distribution is often used to model count data that occurs at a constant rate, and in this case the rate is given by $f_i(\theta)$. In math terms, our likelihood function $L_i(\theta)$ for each neuron i is the probability $p(s_i|\theta)$ of neuron i firing s_i spikes for a given value of θ, ranging from 0 to 330.

The idea in this method is to calculate the log likelihood[2] function of each neuron and then add them all together to get the log likelihood function of the entire population of (n) neurons. We often work with the *log* likelihood because it allows adding of probabilities instead of multiplying, which can lead to numerical problems.

$$
\begin{aligned}
p(s_i|\theta) \sim Pois(f_i(\theta)) &= \frac{f_i(\theta)^{s_i}}{s_i!} e^{-f_i(\theta)} && \text{(Poisson probability density)} \\
Ł_i(\theta) &= p(s_i|\theta) && \text{(Likelihood of a given neuron firing at } s_i\text{)} \\
Ł(\theta) &= \prod_{i=1}^{n} p(s_i|\theta) && \text{(Joint likelihood of all n neurons)} \\
\log Ł(\theta) &= \sum_{i=1}^{n} \log L_i(\theta) = \sum_{i=1}^{n} \log p(s_i|\theta) && \text{(Take log)} \\
&\propto \sum_{i=1}^{n} s_i \log f_i(\theta) && \text{(evaluation of PDF and simplifying)}
\end{aligned}
$$

Thus, we can define the log likelihood for each neuron i as the log of its tuning curve $f_i(\theta)$ times the number of spikes s_i it fires for a particular stimulus θ, and the population log likelihood is simply the summation across all cells. This tells us that, given a set of tuning curves $f_i(\theta)$, we can compute the likelihood of observing our data s.

But we already have those tuning curves for each cell from question 1.2, so all we need to know

[1] A copy of this paper is included if you are curious, but we walk you through the method in this homework.

[2] log = natural log unless otherwise specified

for a new (hidden) stimulus is how many spikes each neuron fires. Let $\mathbf{s}$ be the n-dimensional column vector of the number of spikes each cell fires after the subject is presented with a new stimulus θ' and let $\mathbf{F}$ be the $n \times m$ matrix representing the tuning curves of each neuron at each of the m stimuli (for us, m is the number of stimuli between 0 and 150 degrees because we assume that all neurons respond equally to θ and $\theta + 180$ degrees.) We can then compute the log likelihood of the new stimulus θ' easily using the inner product of $\mathbf{s}$ and $\mathbf{F}$: `L = s'*log(F)`.

1. Compute the matrix `F` by recalculating the tuning curves you calculated in question 1.2 using only the **first 70** trials (this is akin to our "training" data). You will use the remaining 50 trials (as "testing" data) to make predictions. Make a histogram of the number of stimulation angles for the first 70 trials to ensure that each angle (0 to 150) is presented at least a few times. (3 pts)

2. For the 50 "testing" trials, compute a $n \times 50$ matrix `S` where each element represents the number of spikes each of the n neurons fired in response to a given input angle, with rows corresponding to neurons and columns corresponding to the grating angle for a given trial. With this, you can easily compute the log likelihood functions for all the trials at once with the command: `L_test = S'*log(F)`. (Hint: what can you do to avoid taking the log of any zero values you might have in `F`, which would result in some infinite output values in `L_test`?)

   (a) Plot the likelihood functions for the first four testing trials in a 2×2 subplot. In the title of each plot, give the trial number (1, 2, 3, or 4) and the true stimulation angle. Make sure to label your axes correctly. (5 pts)

   (b) How well do these four likelihood functions seem to match the true stimulation angle? Explain in a few sentences. (3 pts)

   (c) Compute the maximum likelihood estimate (abbreviated MLE) for each of the 50 trials. This is another way of asking which angle θ has the highest probability, or in math terms,

   $$\hat{\theta}_{MLE} = \arg\max_{\theta} \; L(\theta) = \arg\max_{\theta} \; \log L(\theta)$$

   In what percentage of the 50 trials did your MLE correctly predict the stimulation angle [0-150]? (5 pts)

   (d) In a few sentences, discuss how well this method worked for predicting the input angle from the response of the 18 neurons. What might you change in the experimental protocol to try and get a better prediction? (3 pts)

3. It is important to show that your findings are not a result of chance. One way to demonstrate this is using a "permutation test." Here, we will perform a permutation test by randomly reassigning new grid angles to the 50 test responses and then calculating how often the new grid angles match the true stimulation angles.

(a) Simulate the chance prediction (the "null" distribution) by randomly reassigning the stimulation angles 1000 times. For each permutation, calculate the percent accuracy of each label (this is called a permutation test). Create a histogram of the 1000 accuracy measurements for the null distribution. Add a red vertical line with the accuracy calculated from using the Jazayeri method above. (5 pts)

(b) What is the probability that your actual accuracy measurement comes from the null-distribution? That is, calculate the fraction of permutation samples with accuracy *more extreme* relative to the mean of the null distribution (less than your measurement if your value is less than the mean, or more than your measurement if your value is more than the mean). (2 pts)

(c) What is this value typically called? (1 pt)

4. The tuning curves and neuron responses to a new trial were calculated using the number of spikes each neuron fired after the stimulation. But what if a particular neuron just happens to fire a lot and fires even more when it gets a stimulus to which it's tuned? Those neurons could "swamp" the log likelihood estimate given in Equation 1 by virtue of just having a larger average s_i and $f_i(\theta)$. How might we correct for this type of behavior? Suggest a possible method. (4 pts)