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Due Friday, 28 April 2017, uploaded to Gradescope.
Covers material up to Poisson Processes I.
100 points total.

1. (15 pts) True / False. Determine if the following statements are true or false. If a statement is false, please correct the statement to receive full credit. Note that we use "spike" and "action potential" interchangeably. Each statement is worth 1 point.

   (a) When an action potential is fired, there is first a larger current attributable to K^+ channels opening before Na^+ channels.

   Solution: False. Na^+ channels open first, leading to larger currents through Na^+ channels.

   Na^+

   (b) During an action potential, Na^+ currents and K^+ currents both serve to depolarize the cell.

   K^+ out polarize K^+

   Solution: False. K^+ currents hyperpolarizes the cell after Na^+ channel inactivation.

   (c) The patch-clamp allows experimenters to measure the current flowing through a single ion channel.

   Solution: True.

   (d) It is possible to record action potentials with electroencephalograms (EEG).

   Solution: False. To measure action potentials requires intra-cellular neural recordings at the soma.

   (e) Imagine a neuron perfectly modeled by a Poisson process with a homogeneous firing rate of 1 spike per second. Consider two scenarios. In scenario (a), the last spike occurred 100 ms ago. In scenario (b), the last spike occurred 1.2 s ago. It is more likely that in the next 100 ms, a spike will fire in scenario (b) than it will in scenario (a).

   Solution: False. They are equally likely to happen, as the interspike interval distribution is exponential and depends only on the rate, and not how much time has elapsed since the last spike.

   (f) If the Fano factor of a neuron is greater than 1, then its firing rate mean is greater than its firing rate variance.

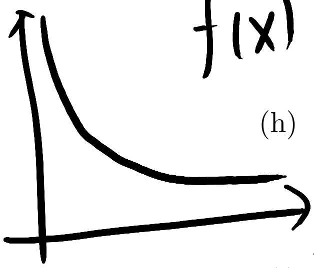
   Solution: False. If the Fano factor is greater than 1, the variance is larger than the mean.

   (g) A Poisson process will *always* have a Fano factor of 1.

   Solution: True.

Fano factor = $\frac{var(X)}{E(X)}$

$$f(x) = \begin{cases} \lambda e^{-\lambda x} & x \geq 0 \\ 0 & \text{otherwise} \end{cases}$$



(h) An exponential interspike interval distribution models the refractory period well.

Solution: False. An exponential interspike interval distribution predicts that spikes are most probable during the refractory period.

(i) Chronic, multi-site electrode arrays allow the measurement of action potentials from several neurons at millisecond resolution.

Solution: True.

(j) There is stimulation electrode technology that can remain functional and effective in humans for years.

Solution: True.

(k) Using single-electrode technology, it is possible to record spikes from different neurons at the same time.

Solution: True.

(l) To accurately and reliably detect action potentials from a single neuron using a static threshold, a high-pass filter, which removes DC and low-frequency components of raw electrode voltage waveforms, is required.

Solution: True.

(m) Convolving spike trains with a Gaussian kernel to approximate a spike rate, $r(t)$, is a type of high-pass filtering.

Solution: False. It is a type of low-pass filtering.

(n) Tuning curves describe neural activity in the visual and motor systems well.

time-varying signals of motor system

Solution: False. While tuning curves describe neural activity in the visual system well, it does not well-describe neural activity in the motor system, where preferred directions change through time, at different speeds, or with different movement extents.

(o) During the relative refractory period, it is impossible for a spike to be generated.

Solution: False. It is possible to generate a spike by applying a large enough voltage.

2. (30 points) Tuning curves. One way to model the firing rate of motor cortical neurons is with tuning curves. The tuning curve models the average firing rate, $f(\theta)$, for a neuron when a reach is made in the direction θ. The cosine tuning model asserts that:

$$f(\theta) = c_0 + c_1 \cos(\theta - \theta_0)$$

In this question, we will learn how to derive values for the parameters c_0, c_1, and θ_0 given that we know the average firing rates for reaches in certain directions.

(a) (1 point) Show that θ_0 is the *preferred direction* of the neuron. The preferred direction is the direction for which the neuron fires most.

Solution: Since $c_1 > 0$, the maximum value that $f(\theta)$ can attain is $c_0 + c_1$ and it is attained at $\theta = \theta_0$. Therfore the neuron fires the most at θ_0. This is the definition of preferred direction.

(b) (3 points) Your colleague writes a script to find the values of c_0, c_1, and θ_0 given some neural data. He runs it and finds that $c_0 = -11$, $c_1 = 8$, and $\theta_0 = 125°$. Do you tell him "Great job! This is a completely reasonable model!" or do you tell him "You've made a mistake." Why?

Solution: Your colleague has made a mistake, as the firing rate of the neuron cannot be negative. While, due to fitting noisy data, it's possible that the tuning curve may dip negative, this tuning curve has the neuron's firing rate always negative. That is really dubious and is hinting at a bug in the code.

(c) (3 points) You decide to take a stab at writing a script that will find the parameters of the tuning model. However, you're going to go about it a different way than your colleagues. You're first going to simplify the term $\cos(\theta - \theta_0)$. By using Euler's formula, $e^{j\theta} = \cos(\theta) + j\sin(\theta)$, derive the formula:

$$\cos(\theta - \theta_0) = \cos(\theta)\cos(\theta_0) + \sin(\theta)\sin(\theta_0).$$

Solution: From Euler's formula, we have that

$$\begin{aligned}
\cos(\theta - \theta_0) &= \frac{e^{j(\theta-\theta_0)} + e^{-j(\theta-\theta_0)}}{2} \\
&= \frac{e^{j\theta}e^{-j\theta_0} + e^{-j\theta}e^{j\theta_0}}{2} \\
&= \frac{1}{2}\left[(\cos(\theta + j\sin(\theta))\,(\cos(\theta_0) - j\sin(\theta_0)) + \dots\right. \\
&\quad \left.\dots + (\cos(\theta - j\sin(\theta))\,(\cos(\theta_0) + j\sin(\theta_0))\right] \\
&= \cos(\theta)\cos(\theta_0) - j\cos(\theta)\sin(\theta_0) + j\sin(\theta)\cos(\theta_0) + \sin(\theta)\sin(\theta_0) + \dots \\
&\quad \dots + \cos(\theta)\cos(\theta_0) - j\sin(\theta)\cos(\theta_0) + j\cos(\theta)\sin(\theta_0) + \sin(\theta)\sin(\theta_0) \\
&= \cos(\theta)\cos(\theta_0) + \sin(\theta)\sin(\theta_0)
\end{aligned}$$

(d) (3 points) To simplify our parameter estimation, we will re-write $f(\theta)$ as

$$f(\theta) = k_0 + k_1\sin(\theta) + k_2\cos(\theta).$$

Find k_0, k_1, and k_2 in terms of c_0, c_1, and θ_0.

Solution: We re-write $f(\theta)$ using the result of part (c).

$$\begin{aligned}
f(\theta) &= c_0 + c_1\cos(\theta - \theta_0) \\
&= c_0 + c_1\left(\cos(\theta)\cos(\theta_0) + \sin(\theta)\sin(\theta_0)\right) \\
&= c_0 + (c_1\sin(\theta_0))\sin(\theta) + (c_1\cos(\theta_0))\cos(\theta) \\
&= k_0 + k_1\sin(\theta) + k_2\cos(\theta)
\end{aligned}$$

and by inspection, $k_0 = c_0$, $k_1 = c_1\sin(\theta_0)$, and $k_2 = c_1\cos(\theta_0)$.

(e) (5 points) We define y_θ to be the measured average firing rates for a reach in direction θ. For simplicity in this question, assume that we've only measured the firing rate when the monkey reaches to three unique directions: y_0 for the reach at an angle of 0° (i.e., to the right), y_{120} for the reach to 120° (up and to the left) and y_{240} for the reach to 240° (down and to the left). Find k_0, k_1, and k_2 in terms of y_0, y_{120} and y_{240}.

Solution: We have the following three equations from plugging in θ.

$$\begin{aligned} y_0 &= k_0 + k_2 \\ y_{120} &= k_0 + \frac{\sqrt{3}}{2}k_1 - \frac{1}{2}k_2 \\ y_{240} &= k_0 - \frac{\sqrt{3}}{2}k_1 - \frac{1}{2}k_2. \end{aligned}$$

We have three equations for three unknowns. Adding y_{120} and y_{240}, we get

$$y_{120} + y_{240} = 2k_0 - k_2, \tag{1}$$

and substituting $k_2 = y_0 - k_0$, we have that

$$k_0 = \frac{1}{3}(y_0 + y_{120} + y_{240}). \tag{2}$$

Substituting equation 2 into equation 1, we arrive at

$$\begin{aligned} k_2 &= \frac{2}{3}(y_0 + y_{120} + y_{240}) - y_{120} - y_{240} \\ &= \frac{2}{3}y_0 - \frac{1}{3}(y_{120} + y_{240}) \end{aligned}$$

And finally we can subtract y_{240} from y_{120} to find

$$y_{120} - y_{240} = \sqrt{3}k_1,$$

so that

$$k_1 = \frac{1}{\sqrt{3}}(y_{120} - y_{240})$$

(f) (5 points) Plot the tuning curve, $f(\theta)$, when $y_0 = 25$, $y_{120} = 70$, and $y_{240} = 10$. Also include y_0, y_{120}, and y_{240} on the plot. Finally, provide the values of c_0, c_1, and θ_0.

Solution: By running the code below, we see that $c_0 = 35$, $c_1 = 36.05$, and $\theta_0 = 106.1°$. **NOTE**: The tuning curve as defined here will produce negative values. Since we cannot have negative firing rates, we know that this is not an accurate description. This is a good example of two things: the difficulty of modelling complex processes with very simple models and the reduction in model quality when limited to only a few sample points. If your model in reality still produced this effect, you would simply treat those areas as zero. The code produces Figure 1.

```

function [f, c0, c1, theta0] = ptc(y0, y1, y2);

```

```
%PTC plots the tuning curve given average firing rates for
%certain directions.
%   [F, C0, C1, THETA0] = PTC(Y0, Y1, Y2) takes three inputs
%   corresponding to the average firing rate of a neuron
%   during a reach to 0 degrees (y0), 120 degrees (y1) and
%   240 degrees (y2).  It computes the tuning model,
%       f(theta) = c0 + c1 cos(theta - theta0).
%   Thus, the outputs, c0, c1, and theta0 are the parameters
%   of the tuning model.  f is a figure handle to the
%   generated plot.
%
%   This script was written for EE 239AS.2, question #2.

    assert(nargin == 3, 'You have not provided the three average firing rate inputs.');


    % find the values of the k's
    k0  = mean([y0, y1, y2]);
    k1  = 1/sqrt(3) * (y1 - y2);
    k2  = 2/3 * y0 - 1/3 * (y1 + y2);

    % find the value's of the c's
    theta0  = atan2d(k1,k2)  % Return the value in degrees.
    theta0r = atan2(k1,k2);  % Use radians for calculation

    c0      = k0;
    c1      = k1 / sin(theta0r);

    % plot
    theta   = linspace(0,2*pi,80);
    f = figure;
    hold on;
    plot([0 120 240], [y0, y1, y2], 'linestyle', 'none', 'marker', '*', 'markersize', 10, 'color', 'r');
    plot(theta * 180 / pi, c0 + c1 * cos(theta - theta0r), 'linewidth', 2, 'color', 'b');
    xlim([-10 370]);
    ylim([0 80]);
    xlabel('$\theta$ (degrees)', 'interpreter', 'latex');
    ylabel('$f(\theta)$', 'interpreter', 'latex');
end
```

(g) (10 points) Now consider that we sampled the workspace much more effectively. We now have the following data:

$y_0 = 25$, $y_{60} = 40$, $y_{120} = 70$, $y_{180} = 30$, $y_{240} = 10$ and $y_{300} = 15$.

Report the values of c_0, c_1, and θ_0 that minimize the mean-square error between the tuning curve and the observed data.

Solution: It is given that $y_0 = 25$, $y_{60} = 40$, $y_{120} = 70$, $y_{180} = 30$, $y_{240} = 10$ and $y_{300} = 15$. We know that the turning curve is modeled as $f(\theta) = k_0 + k_1 \sin(\theta) + k_2 \cos(\theta)$. We have to determine parameters $W = [k_0, k_1, k_2]^T$ with the goal of minimizing the

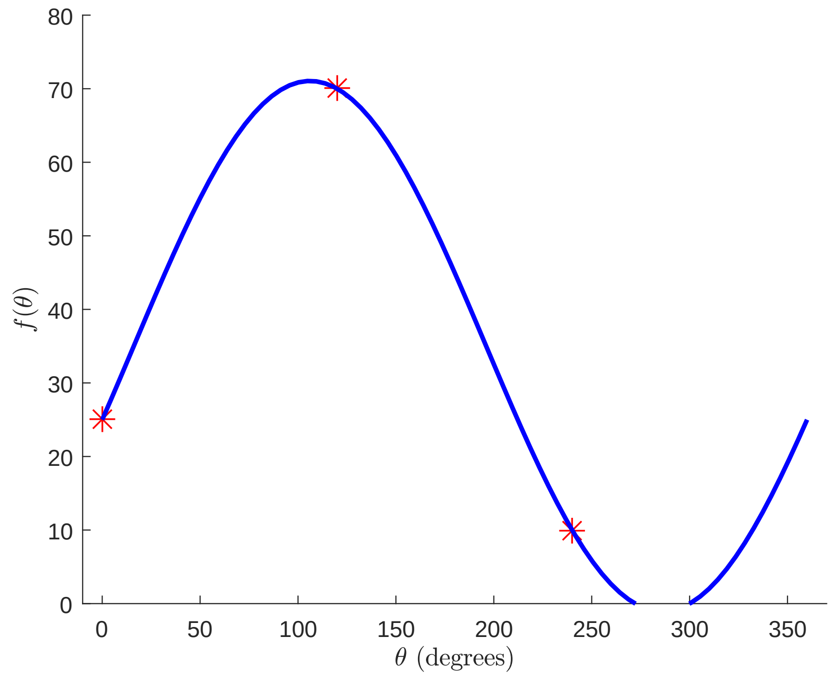


Figure 1: Tuning curve from question 2.

mean-square error between the tuning curve and the observed data i.e

$$\hat{W} = \arg\min_{W} \sum_{\theta_i}^{6} \left(y_{\theta_i} - f(\theta_i)\right)^2$$

If we stack $Y = [y_0, \ldots, y_{300}]^T$ as a vector and $F = [f_0, \ldots, f_{300}]^T$ as a matrix where each row $f_{\theta_i} = [1, sin(\theta_i), cos(\theta_i)]$, we can simplify the above expression as

$$\hat{W} = \arg\min_{W} ||Y - FW||_2^2$$

This is the familiar ordinary least squares problem and $\hat{W}$ is given as

$$\hat{W} = \left(F^T F\right)^{-1} F^T Y$$

Applying to the observed data, we can find $\hat{W} = [k_0, k_1, k_2]^T = [31.67, 24.54, -5.83]^T$. Solving for c_0, c_1 and θ_0, we get $c_0 = 31.67$, $c_1 = 25.22$ and $\theta_0 = 103.37$.

3. (5 points) Refractory periods

   (a) (2 points) In class, we introduced the exponential distribution to model inter-spike intervals (ISI). Does the exponential distribution incorporate the concept of refractory periods? Please explain.

   Solution: No. The exponential distribution has much of its mass near zero rather than centered around a mean value.

$\lambda = 50$

(b) (3 points) If a model neuron spikes at 50 spikes per second according to a homogeneous Poisson process, what percentage of spikes would violate a 1 ms refractory period?

Solution: We have $T \sim \exp(\lambda = 50)$. Thus,

$$\begin{aligned} P(T < 0.001) &= 1 - \exp(-50 \cdot 0.001) \\ &= 1 - \exp(-0.05) \end{aligned}$$

4. (34 points) A neuron spikes according to a homogeneous Poisson process with rate λ.

(a) (2 points) What is the mean ISI of this neuron?

Solution: The mean ISI of the neuron is $\mathbb{E}[T]$. Hence, the mean ISI is $\mathbb{E}[T] = 1/\lambda$.

(b) (4 points) What is the probability that a given ISI is greater than the mean ISI?

Solution: Here, we need to calculate $P(T > 1/\lambda)$. This is given by:

$$\begin{aligned} P(T > 1/\lambda) &= 1 - P(T \leq 1/\lambda) \\ &= 1 - (1 - \exp(-\lambda \cdot 1/\lambda)) \\ &= 1/e \end{aligned}$$

convert > to <

(c) (7 points) What is the expected ISI *given* that it is larger than the mean ISI?

Solution: Here, we need to calculate $\mathbb{E}[T|T > 1/\lambda]$. This is given by:

$$\begin{aligned} \mathbb{E}[T|T > 1/\lambda] &= \int_0^\infty tP(T = t|T > 1/\lambda)dt \\ &= \int_0^\infty t\frac{P(T = t, T > 1/\lambda)}{P(T > 1/\lambda)}dt \\ &= \int_0^\infty t\frac{P(T = t)P(T > 1/\lambda|T = t)}{P(T > 1/\lambda)}dt \\ &= \int_{1/\lambda}^\infty t\frac{\lambda\exp(-\lambda t)}{e^{-1}}dt \\ &= e\int_{1/\lambda}^\infty \lambda t\exp(-\lambda t)dt \\ &= e\left[-t\exp(-\lambda t)|_{1/\lambda}^\infty + \int_{1/\lambda}^\infty \exp(-\lambda t)dt\right] \\ &= e\left[0 - \left[-\frac{1}{\lambda e}\right] - \frac{1}{\lambda}\exp(-\lambda t)\bigg|_{1/\lambda}^\infty\right] \\ &= e\left[\frac{1}{\lambda e} + \frac{1}{\lambda e}\right] \\ &= \frac{2}{\lambda} \end{aligned}$$

Please note that on the 4th equality we used the fact that $P(T > 1/\lambda|T = t)$ is 1 if $t > 1/\lambda$ and 0 otherwise.

(d) (7 points) What is the expected ISI *given* that it is smaller than the mean ISI?

Solution: Note for this question, we will use that $P(T < 1/\lambda) = 1 - P(T > 1/\lambda) = 1 - 1/e = (e-1)/e$. Following this, we want to solve for $\mathbb{E}[T|T < 1/\lambda]$. Thus, we have:

$$
\begin{aligned}
\mathbb{E}[T|T > 1/\lambda] &= \int_0^\infty tP(T = t|T < 1/\lambda)dt \\
&= \int_0^\infty t\frac{P(T = t, T < 1/\lambda)}{P(T < 1/\lambda)}dt \\
&= \int_0^\infty t\frac{P(T = t)P(T < 1/\lambda|T = t)}{P(T < 1/\lambda)}dt \\
&= \int_0^{1/\lambda} t\frac{\lambda\exp(-\lambda t)}{1 - 1/e}dt \\
&= \frac{e}{e-1}\int_0^{1/\lambda} \lambda t\exp(-\lambda t)dt \\
&= \frac{e}{e-1}\left[-t\exp(-\lambda t)|_0^{1/\lambda} + \int_0^{1/\lambda}\exp(-\lambda t)dt\right] \\
&= \frac{e}{e-1}\left[-\frac{1}{\lambda e} - \frac{1}{\lambda}\exp(-\lambda t)\Big|_0^{1/\lambda}\right] \\
&= \frac{e}{e-1}\left[\frac{1}{\lambda e} - \frac{1}{\lambda e} + \frac{1}{\lambda}\right] \\
&= \frac{e}{e-1}\left[\frac{e-2}{\lambda e}\right] \\
&= \frac{e-2}{\lambda(e-1)}
\end{aligned}
$$

(e) (7 points) What is the expected number of spikes that will be fired before one sees an ISI greater than the mean ISI?

Solution: Here, we can view each draw from the ISI as a Bernoulli r.v., where a success occurs if $T > 1/\lambda$. Then, the number of time steps before we draw an ISI $T > 1/\lambda$ is a geometric random variable with distribution $P(T < 1/\lambda)^{k-1}P(T > 1/\lambda)$. The expected number of time steps is the mean of this distribution, which is the mean of the geometric distribution with parameter $p = P(T > 1/\lambda)$. Thus, the mean is $1/p$ and we have from earlier that $p = 1/e$. Thus the expected number of steps, $\mathbb{E}[N]$ is e.

(f) (7 points) What is the expected waiting time until (and including) an ISI greater than the mean ISI?

Solution:

$$
\begin{aligned}
S &= (\mathbb{E}[N] - 1)\mathbb{E}[T|T \leq 1/\lambda] + \mathbb{E}[T|T > 1/\lambda] \\
&= (e-1)\frac{e-2}{\lambda(e-1)} + \frac{2}{\lambda} \\
&= \frac{e}{\lambda}
\end{aligned}
$$

5. (16 points) You insert a pair of electrodes into the brain. Unbeknownst to you, electrode 1 sits next to a neuron with mean ISI of 20 ms, and electrode 2 sits next to a different neuron with mean ISI of 30 ms. Each neuron spikes independently according to a homogeneous Poisson process. A neuron is "detected" when it fires its first spike.

   (a) (4 points) What is the probability that no neurons are detected (on either electrode) during the first 60 ms?

   Solution: The neurons fire independently, and thus we calculate:

$$\begin{aligned}
\mathbf{Pr}(N_1(t)=0)\mathbf{Pr}(N_2(t)=0) &= \frac{(\lambda_1 t)^0 \exp(-\lambda_1 t)}{0!}\frac{(\lambda_2 t)^0 \exp(-\lambda_2 t)}{0!} \\
&= \exp(-\lambda_1 t)\exp(-\lambda_2 t) \\
&= \exp(-1/20 \cdot 60)\exp(-1/30 \cdot 60) \\
&= \exp(-5)
\end{aligned}$$

   (b) (4 points) Given that no neurons are detected in the first s seconds, what is the probability that no neurons are detected in the first $s+t$ seconds?

   Solution: $\mathbf{Pr}(N(s+t)=0|N(s)=0)$ is equal to $\mathbf{Pr}(N(t)=0)$. Hence, from part (a), we have $\mathbf{Pr}(N(s+t)=0|N(s)=0)=\exp(-(\lambda_1+\lambda_2)t)$.

   (c) (8 points) A single spike comes in, and thus a neuron is detected. What is the probability that a neuron is detected on electrode 1 before electrode 2? (Hint: your answer should not be a function of time.)

   Solution: What we want to find is the probability that $N_1(t)=1$ and $N_2(t)=0$ given that $N(t)=N_1(t)+N_2(t)=1$ (i.e., one spike has happened). Note that we don't simply calculate $\mathbf{Pr}(N_1(t)=1, N_2(t)=0)$. Concretely, this is saying at some time t, neuron 1 is detected and neuron 2 is not. However, we want this to be independent of t, i.e., we want to say given that there has been one spike, what's the probability that it's from neuron 1 and not neuron 2. Hence, we calculate:

$$\begin{aligned}
\mathbf{Pr}(N_1(t)=1, N_2(t)=0|N(t)=1) &= \frac{\mathbf{Pr}(N_1(t)=1, N_2(t)=0, N(t)=1)}{\mathbf{Pr}(N(t)=1)} \\
&= \frac{\mathbf{Pr}(N_1(t)=1)\mathbf{Pr}(N_2(t)=0)}{\mathbf{Pr}(N(t)=1)} \\
&= \frac{\lambda_1 t \exp(-\lambda_1 t)\exp(-\lambda_2 t)}{(\lambda_1+\lambda_2)t\exp(-(\lambda_1+\lambda_2)t)} \\
&= \frac{\lambda_1}{\lambda_1+\lambda_2} \\
&= \frac{1/2}{1/2+1/3} \\
&= \frac{3}{5}
\end{aligned}$$

   In the second equality, we used the fact that $\mathbf{Pr}(N(t)=1|N_1(t)=1, N_2(t)=0)=1$.