

# Assignment 3

## Systems & Theoretical Neuroscience [Gatsby]

Due: Mon, 13th November

Note: Red text contains clarifications since the assignment was first published.

1. In many animals, the current eye position appears to be encoded by a cartesian distributed scalar code in which the tuning curves are linear ramp functions of either the horizontal or vertical eye-position; while the intended target of a saccadic eye movement is more often represented with radial bump-shaped tuning curves distributed in 2D. Suggest why this might be so.

(you may consider reading the SWC assignment question for some hints)

2. A scalar stimulus that is uniformly distributed in a fixed range (say  $[0,1]$ ) is encoded in the firing rate of a neuron. Sketch a (pathological) tuning curve for which the average Fisher information conveyed by the firing rate is very large, but the average mutual information is low. Is the reverse possible: can the mutual information be high, whilst the Fisher information is very low? Justify both your answers.

### 3. Fisher information for a Gaussian distribution

Consider a conditional response distribution of the form

$$p(\mathbf{r}|x) = \frac{e^{-(\mathbf{r}-\mathbf{f}(x)) \cdot \boldsymbol{\Sigma}^{-1}(x) \cdot (\mathbf{r}-\mathbf{f}(x))/2}}{\text{Det}(2\pi\boldsymbol{\Sigma}(x))^{1/2}}.$$

Compute the Fisher information,

$$I(x) = \left\langle -\frac{\partial^2 \log p(\mathbf{r}|x)}{\partial x^2} \right\rangle,$$

where the average is with respect to  $p(\mathbf{r}|x)$ . Note that the covariance matrix depends on  $x$ ; this complicates the expression.

### 4. Bias in a locally optimal linear estimator

Consider a population of neurons whose firing activity is given by the usual tuning curve plus noise model,

$$\mathbf{r} = \mathbf{f}(x) + \boldsymbol{\xi}. \tag{1}$$

The noise is zero mean and has covariance matrix  $\boldsymbol{\Sigma}$ ,

$$\langle \boldsymbol{\xi}\boldsymbol{\xi} \rangle = \boldsymbol{\Sigma}.$$

Consider a linear estimator,  $\mathbf{w}$ ,

$$\hat{x} - x_0 = \mathbf{w} \cdot (\mathbf{r} - \mathbf{f}(x_0)).$$

Show that if  $\Sigma$  is independent of  $x$ ,  $\mathbf{w}$  is chosen to be a optimal (in the sense of minimum variance) and unbiased at  $x = x_0$ , and  $x$  is close to  $x_0$ , then the gradient of the bias at  $x_0$  is given, to lowest order in  $x - x_0$ , by

$$\left. \frac{\partial b(x)}{\partial x} \right|_{x=x_0} = \frac{1}{2} \frac{\partial \log I(x_0)}{\partial x_0} (x - x_0)$$

where the bias is defined to be:

$$b(x) = \langle \hat{x} \rangle - x,$$

and  $I$  is the inverse of the variance of the locally optimal linear estimator at  $x = x_0$  (AKA the linear Fisher information).

## 5. Differential correlations

For this question it may be helpful to read *Information-limiting correlations*. by Moreno-Bote, Ruben, et al., *Nature neuroscience* 17.10 (2014): 1410-1417.

Consider a covariance matrix,  $\Sigma_0$ , perturbed by a rank one matrix,

$$\Sigma = \Sigma_0 + \epsilon \mathbf{u}(x) \mathbf{u}(x).$$

Assume a tuning curve plus noise model, as in Eq. (1). Show that the linear fisher information can be written as:

$$I_{LINEAR}(x) = I_0(x) \sin^2 \theta + \frac{I_0(x) \cos^2(\theta)}{1 + \epsilon I_u(x)}$$

where

$$\begin{aligned} I_0(x) &= \mathbf{f}'(x) \cdot \Sigma_0^{-1} \cdot \mathbf{f}'(x) \\ I_u(x) &= \mathbf{u}(x) \cdot \Sigma_0^{-1} \cdot \mathbf{u}(x) \\ \cos^2 \theta &= \frac{[\mathbf{f}'(x) \cdot \Sigma_0^{-1} \cdot \mathbf{u}(x)]^2}{\mathbf{f}'(x) \cdot \Sigma_0^{-1} \cdot \mathbf{f}'(x) \mathbf{u}(x) \cdot \Sigma_0^{-1} \cdot \mathbf{u}(x)}. \end{aligned}$$

If both  $I_0(x)$  and  $I_u(x)$  are  $\mathcal{O}(n)$ , where  $n$  is the number of neurons, then the only way to have  $\mathcal{O}(1)$  information is to have  $\theta = 0$ , for which  $\mathbf{u}(x) = \mathbf{f}'(x)$ .

## 6. Fisher information and refractory firing

Consider a hypothetical cell, which responds to the presentation of a stimulus with a continuous feature  $s$  by firing at a homogeneous rate  $f(s)$  in a (fixed) interval  $[0, T]$ . Assume that the firing rate is 0 outside this interval. We will be interested in the contributions made to the Fisher information by spike-timing, with and without a refractory period.

First, assume that the firing is Poisson.

- What is the probability of observing spikes at times  $\{t_1 \dots t_n\} \subset [0, T]$ ?
- What is the Fisher information  $J_{t, \text{Poiiss}}(s)$  associated with this probability density function, assuming that the relevant interval  $[0, T]$  is known? How does it compare to the Fisher information  $J_{n, \text{Poiiss}}$  associated with the distribution of spike counts  $P(n|s)$ ?

Now consider refractory firing. Recall that one way to model a refractory period is to use a gamma-interval renewal process in place of a Poisson process. Thus, now assume that the cell's firing follows a gamma-interval process with the same mean rate  $f(s)$  and with integral gamma order  $\gamma$ .

- (c) What is the probability of observing spikes at times  $\{t_1 \dots t_n\} \subset [0, T]$  from this process?
- (d) What is the Fisher information  $J_{t, \text{Gamma}}(s)$  associated with the new probability density function? You may assume that  $T$  is long enough to neglect contributions due to the first spike, and due to the silence after the last spike.

Finally, we wish to see how much of this information gain is available in the spike count.

- (e) Which signal (count or spike-timing) do you expect to carry more information for this process? Why?
- (f) Find an expression for the the distribution of spike counts  $P(n|s)$  under the gamma-interval model.
- (g) Write down the expression for the corresponding Fisher information  $J_{n, \text{Gamma}}$ , and thus for  $J_{n, \text{Gamma}} - J_{t, \text{Gamma}}$ . You need not necessarily evaluate the expectation. Identify the term(s) responsible for the difference between  $J_{n, \text{Gamma}}$  and  $J_{t, \text{Gamma}}$ .

## 7. Estimation Theory

- (a) We derived the Fisher information  $J(\theta)$  as the expected value of the second derivate (curvature) of the log-likelihood in the lecture.
  - i. Repeat the derivation for a *vector* parameter (or stimulus in our setting)  $\theta$ , showing that the Fisher information in this case is given by a matrix.

As mentioned in the lecture, there is an alternate definition in terms of the first derivative. For vector parameters this is:

$$J(\theta_0) = \text{Cov}_{\theta_0} \left( \nabla \log p(n|\theta) \Big|_{\theta_0} \right).$$

where  $\text{Cov}_{\theta_0}$  means the covariance evaluated under  $p(n|\theta_0)$ .

- ii. Demonstrate that these two definitions are the same (or more precisely, give conditions under which these two definitions are the same).
- (b) Consider an LNP model:

$$p(n|\mathbf{x}) = \text{Pois}(g(\mathbf{w} \cdot \mathbf{x}))$$

- i. What is  $J(\mathbf{x})$  (the Fisher Information about the stimulus value available to the rest of the brain)? How does it depend on  $\mathbf{w}$ ? Working in two dimensions (recall the picture from lecture) show how  $J(\mathbf{x})$  varies around the vector linear projection vector  $\mathbf{w}$ .
- ii. What is  $J(\mathbf{w})$  (the Fisher Information about the weight vector available to an experimenter — consider the case of multiple measurements  $n_i$ , each in response to a different stimulus  $\mathbf{x}_i$ )? How does it depend on the distribution of  $\mathbf{x}$ ? What would be a good distribution with which to probe the cell if we knew (say) the orthant of stimulus space in which  $\mathbf{w}$  lay?