## Computational Neuroscience

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## Exercise Sheet 2 — 9 April 2025

## Please submit your solution in the next class with Joao (5 May 2025)

1. Covariance and Correlation. Assume that we have recorded two neurons in the twoalternative-forced choice task discussed in class. We denote the firing rate of neuron 1 in trial i as  $r_{1,i}$  and the firing rate of neuron 2 as  $r_{2,i}$ . We furthermore denote the averaged firing rate of neuron 1 as  $\bar{r}_1$  and of neuron 2 as  $\bar{r}_2$ . Let us "center" the data by defining two data vectors

$$\mathbf{x} = \begin{pmatrix} r_{1,1} - \bar{r}_1 \\ r_{1,2} - \bar{r}_1 \\ r_{1,3} - \bar{r}_1 \\ \vdots \\ r_{1,N} - \bar{r}_1 \end{pmatrix}, \qquad \mathbf{y} = \begin{pmatrix} r_{2,1} - \bar{r}_2 \\ r_{2,2} - \bar{r}_2 \\ r_{2,3} - \bar{r}_2 \\ \vdots \\ r_{2,N} - \bar{r}_2 \end{pmatrix}.$$

(a) Show that the variance of the firing rates of the first neuron is

$$\operatorname{Var}(r_1) = \frac{1}{N-1} \|\mathbf{x}\|^2.$$

- (b) Compute the cosine of the angle between  $\mathbf{x}$  and  $\mathbf{y}$ . What do you get?
- (c) What are the maximum and minimum values that the correlation coefficient between  $r_1$  and  $r_2$  can take? Why?
- (d) What do you think the term "centered" refers to?

## 2. Ridge Regression – Closed-Form Solution

In class we discuss how to quantify overfitting by using cross-validation. In order to avoid overfitting, you should penalize complex models. This is called regularization. Here's a linear regression model with L2 regularization (ridge regression):

$$E(w) = ||y - Xw||^2 + \lambda ||w||^2$$

where:

- $X \in \mathbb{R}^{n \times d}$  is your data.
- $y \in \mathbb{R}^n$  is the target vector.

- $w \in \mathbb{R}^d$  is the weight vector (i.e. the parameters of the model you are trying to fit).
- $\lambda \in \mathbb{R}^+$  is the regularization coefficient
- (a) Why is the extra term  $\lambda ||w||^2$  penalizing complex models?
- (b) Start by assuming  $\lambda=0$  (i.e. regression without regularization) and solve for the optimal weight vector w. Hint: as we did for encoding models, start by expanding the error function E(w) and find its minimum. The solution should make use of the pseudo-inverse.
- (c) Now make  $\lambda > 0$  and solve using the same approach.
- (d) If you found the right solution, you will add  $\lambda I$  to  $X^TX$ . What problem does this solve? Hint: think about the rank of  $\lambda I$ .
- (e) What is the optimal value for  $\lambda$ ?
- 3. **Bayes' theorem**. The theorem of Bayes summarizes all the knowledge we have about about the stimulus by observing the responses of a set of neurons, *independently* of the specific decoding rule. To get a better intuition about this theorem, we will look at the motion discrimination task again and compute the probability that the stimulus moved to the left  $(\leftarrow)$  or right  $(\rightarrow)$ . For a stimulus  $s = \{\leftarrow, \rightarrow\}$ , and a firing rate response r of a single neuron, Bayes' theorem reads

$$p(s|r) = \frac{p(r|s)p(s)}{p(r)} \quad .$$

Here, p(r|s) is the probability that the firing rate is r if the stimulus was s. The respective distribution can be measured and we assume that it follows a Gaussian probability density with mean  $\mu_s$  and standard deviation  $\sigma$ ,

$$p(r|s) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(r-\mu_s)^2}{2\sigma^2}\right)$$

The relative frequency with which the stimuli (leftward or rightward motion,  $\leftarrow$  or  $\rightarrow$ ) appear is denoted by p(s), often called the *prior probability* or, for short, the *prior*. The distribution p(r) denotes the probability of observing a response r, independent of any knowledge about the stimulus.

- (a) How can you calculate p(r)? What shape does it have?
- (b) The distribution p(s|r) is often called the *posterior* probability or, for short, the *posterior*. Calculate the posterior for  $s = \leftarrow$  and sketch it as a function of r, assuming a prior  $p(\leftarrow) = p(\rightarrow) = 1/2$ . Draw the posterior  $p(\rightarrow |r)$  into the same plot.
- (c) What happens if you change the prior? Investigate how the posterior changes if  $p(\leftarrow)$  becomes much larger than  $p(\rightarrow)$  and vice versa. Make a sketch similar to (b).
- (d) Let us assume that we decide for leftward motion whenever  $r > \frac{1}{2}(\mu_{\leftarrow} + \mu_{\rightarrow})$ . Interpret this decision rule in the plots above. How well does this rule do depending on the prior? What do you lose when you move from the full posterior to a simple decision (decoding) rule?

4. **Linear discriminant analysis (advanced):** Let us redo the calculations for the case of *N* neurons. If we denote by **r** the vector of firing rates, Bayes' theorem reads:

$$p(s|\mathbf{r}) = \frac{p(\mathbf{r}|s)p(s)}{p(\mathbf{r})}$$
.

We assume that the distribution of firing rates again follows a Gaussian so that

$$p(\mathbf{r}|s) = \frac{1}{(2\pi)^{N/2} \sqrt{\det \mathbf{C}}} \exp\left(-\frac{1}{2} (\mathbf{r} - \boldsymbol{\mu}_s)^T \mathbf{C}^{-1} (\mathbf{r} - \boldsymbol{\mu}_s)\right)$$

where  $\mu_s$  denotes the mean of the density for stimulus  $s = \{\leftarrow, \rightarrow\}$ , and **C** is the covariance matrix, assumed identical for both stimuli.

(a) Compute the log-likelihood ratio

$$l(\mathbf{r}) = \log \frac{p(\mathbf{r} \mid \leftarrow)}{p(\mathbf{r} \mid \rightarrow)}$$
.

- (b) Assume that  $l(\mathbf{r}) = 0$  is the decision boundary, so that any firing rate vector  $\mathbf{r}$  giving a log-likelihood ratio larger than zero is classified as coming from the stimulus  $\leftarrow$ . Compute a formula for the decision boundary. What shape does this boundary have?
- (c) Assume that  $p(\leftarrow) = p(\rightarrow) = 1/2$ . Assume we are analyzing two neurons with uncorrelated activities, so that the covariance matrix is

$$\mathbf{C} = \begin{pmatrix} \sigma_1^2 & 0\\ 0 & \sigma_2^2 \end{pmatrix}$$

Sketch the decision boundary for this case.