Lecture 2.1 Exercises: Statistical models of neuronal activity and neural coding

1.1 Poisson neuron with dead time

A simplified way to incorporate a refractory period is to use a Poisson process with a dead time. In such a process, the interspike interval T is simply the sum of an exponentially distributed random variable t ($P(t) = \lambda \exp(-\lambda t)$), and a fixed refractory period τ_{arp}.

1. Write down the probability density function of inter-spike intervals $P(T)$ for such a process.

2. Compute the mean interspike interval, and the firing rate r, as a function of λ and τ_{arp}. Sketch r as a function of λ.

3. Compute the variance of the ISIs, and the CV. Sketch the CV as a function of λ. What is the effect of the refractory period on the CV? What is the range of allowed values of the CV in this model?

1.2 Bursty neuron

We consider a simple point process model for a bursty neuron. At each spike, the next interspike interval is drawn randomly in the following way: with probability p, the next interspike interval is equal to the refractory period τ_{arp}; with probability $1 - p$, it is drawn from the Poisson model with dead time of the previous exercise (sum of an exponentially distributed random variable t, $P(t) = \lambda \exp(-\lambda t)$, and a refractory period τ_{arp}).

1. Write down the probability density function of inter-spike intervals $P(T)$ for such a process.

2. Compute the mean interspike interval, and the firing rate r, as a function of λ, τ_{arp} and p. Sketch r as a function of λ for different values of p.

3. Compute the variance of the ISIs, and the CV. Sketch the CV as a function of λ for different values of p. What is the effect of p on the CV? Can the CV become larger than 1 in this model? Plot a few (CV=constant) lines in the $p - \lambda\tau_{arp}$ plane (e.g. CV=0, 0.5, 1, 2). Is there a limit in which the CV diverges?

1.3 Information transmitted by a Poisson neuron in the short and long time limits

We consider a single Poisson neuron that responds with a firing rate $r(s)$ to a stimulus $s \in [0, 1]$. The stimulus is randomly drawn from a distribution $\rho(s)$. The mean firing rate, averaged over all possible stimuli, is denoted as $\bar{r}$:

$$\bar{r} = \int ds\, \rho(s) r(s)$$

The maximal firing rate is r_{max} .

1. What is the probability $p(k|s)$ that the neuron emits k spikes in an interval $[0, t]$ when stimulus s is presented?

2. A standard measure to quantify the information carried by a neuron about an external stimulus is Shannon's mutual information, in bits. Shannon's mutual information quantifies how much the uncertainty about the stimulus is reduced by observing neuronal activity. One bit of information corresponds to a reduction of uncertainty by a factor two (for instance, if there are only two possible stimuli, A and B, and a neuron always fire in response to A but never in response to B, then the neuronal response carries one bit of information about the stimulus). Here, we consider the information i $I(k|s)$carried by the number of spikes in an interval $[0, t]$ about the stimulus s. $I(k|s)$ is given by

$$I(k|s) = \sum_{k=0}^{\infty} \int_0^1 ds\, \rho(s) p(k|s) \log_2 \frac{p(k|s)}{\int_0^1 ds\, \rho(s) p(k|s)}$$

   Write down $I(k|s)$ as a function of $r(s)$, $\rho(s)$, and t.

3. Short time limit
   a. If t is small ($t \ll 1/r_{max}$), we can make the approximation that the number of spikes in the time window $[0, t]$ is either 0 or 1. What are the probabilities that the neuron emits 0 and 1 spikes when stimulus s is presented, up to first order in t?

   b. Compute the mutual information $I(k|s)$ in the limit $t \to 0$ up to first order in t. How does it depend on t? Check that when the firing rate is independent of s, $r(s) = \bar{r}$, the mutual information vanishes.

c. We consider a neuron that responds to the stimulus with a binary tuning curve: $r(s) = r_{max}$ if $s > u$, $r(s) = 0$ otherwise. The stimulus is uniformly distributed, $\rho(s) = 1$ for all s.
   i. Compute $\bar{r}$ as a function of r max and u.
   ii. Compute the mutual information between k and s for this neuron, as a function of t (in the small time limit), r_{max} and u.
   iii. Plot how the mutual information depends on u in the range $u \in [0, 1]$. What is the value of the threshold u that optimizes the mutual information in the short time limit? What is the value of the mutual information at this optimum? What is the optimal information per spike?

d. We now consider a neuron that responds with a linear tuning curve, $r(s) = r_{max}s$ for $s \in [0, 1]$. The stimulus is again uniformly distributed, $\rho(s) = 1$ for all s.
   i. Compute the mutual information in that case.
   ii. Compare the two types of tuning curves. What is the best strategy in the short time limit, binary or linear?

4. Long time limit.
   a. We consider again the case $r(s) = r_{max}$ if $s > u$, $r(s) = 0$ otherwise, and uniformly distributed stimulus, but arbitrary t.
      i. Compute $P(k)$, the probability that k spikes are observed, averaged over stimuli (distinguish the two cases $k = 0$ and $k > 0$).
      ii. Compute the mutual information $I(k|s)$ in terms of t, r_{max} and
      $$p_0 = u + (1 - u)e^{-r_{max}t}$$
      (be careful again to separate the terms corresponding to k=0 and k>0)
      iii. Check that as $t \rightarrow 0$ you recover the information computed in the short t limit.
      iv. Compute the information in the large t limit. Plot again how the mutual information depends on u in the range $u \in [0, 1]$. What is the value of the threshold u that optimizes the mutual information in this limit? What is the value of the mutual information at this optimum? Explain why this result was to be expected.

   b. We move again to the linear tuning curve scenario. Without doing any calculation, explain what is the limit of the mutual information in the large t limit.

i. Compare again the two types of tuning curves. What is now the best strategy in the long time limit?