

Exercise 8.1: Interaural time differences

The interaural time difference is the difference in arrival time of a sound between two ears. It is important in the localisation of sounds, because it provides a cue to the direction or angle of the sound source from the head. In this exercise you should assume that the axonal delay between two neurons increases with the length of the physical connection between them. Furthermore assume that a single spike will cause an EPSP that is too small to cause the neuron to fire; only if a second spike arrives within some $\Delta t_{\text{coincidence}}$ the membrane potential will cross its threshold causing the neuron to fire.

1. Look at Figure 1. Describe the nature of the spike input from the left and right side of the auditory system in order to process inter-aural time differences. Is it a temporal or a rate code? Explain.
2. The neurons (A-E) serve as coincidence detectors and fire maximally when they receive the left and right sided input simultaneously. Nevertheless, the output of the neurons (A-E) has different tuning curves, due to the different lengths of the axons from the left and right sided input neurons. Describe the tuning properties of the output neurons (A-E) qualitatively.
3. Given that the speed of sound in the air is ≈ 350 m/s and the distance between the left and right ear is ≈ 15 cm (in humans), how big is the time delay between the left and right ear for a sound coming directly from the side? How does that relate to the duration of an action potential?
4. (optional) What geometrical figure is described by points of equal interaural time differences?

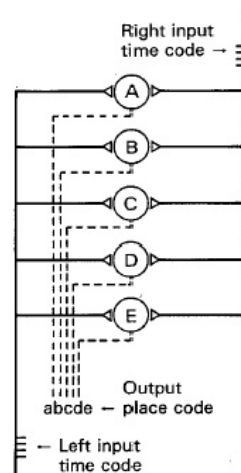


Figure 1: Coincidence detectors for sound localization.

Exercise 8.2: Interpreting multi-unit spike recordings

When recording spike activity from rodent brains during navigation tasks, it has been found that some cells respond preferentially to spatial features, such as location, or orientation within the environment. In this artificially generated data set we assume that some creature follows a fixed trajectory in 2D space over 20 identical trials (shown in Figure 2, top). At the same time we record the activity of 11 neurons, and plot the aligned raster plots for all neurons and all trials (Figure 2, bottom). Your task is to interpret the neural activity, and find out what features the individual neurons encode.

1. Sketch the trajectory of the creature on a 2D map.
2. Describe the spiking activity individually for all 11 neurons (A-K). What feature is encoded by each cell? Explain how you arrived at these conclusions.

3. Identify groups of neurons that encode the same type of feature, and explain in which aspects the individual neurons differ.
4. Now assume that we keep on measuring from the same neurons as before, while the creature follows a new trajectory. From the raster plots in Figure 3 (again over 20 identical trials), can you reconstruct the trajectory that the creature followed?

If you find that there is more than one consistent interpretation for the function of a neuron, it is sufficient if you describe one of them. All neurons encode at least one behaviourally relevant feature, and their function can be seen from the trajectory alone. This is an idealized dataset, in which the neurons show no spontaneous activity, only trial-to-trial variability.

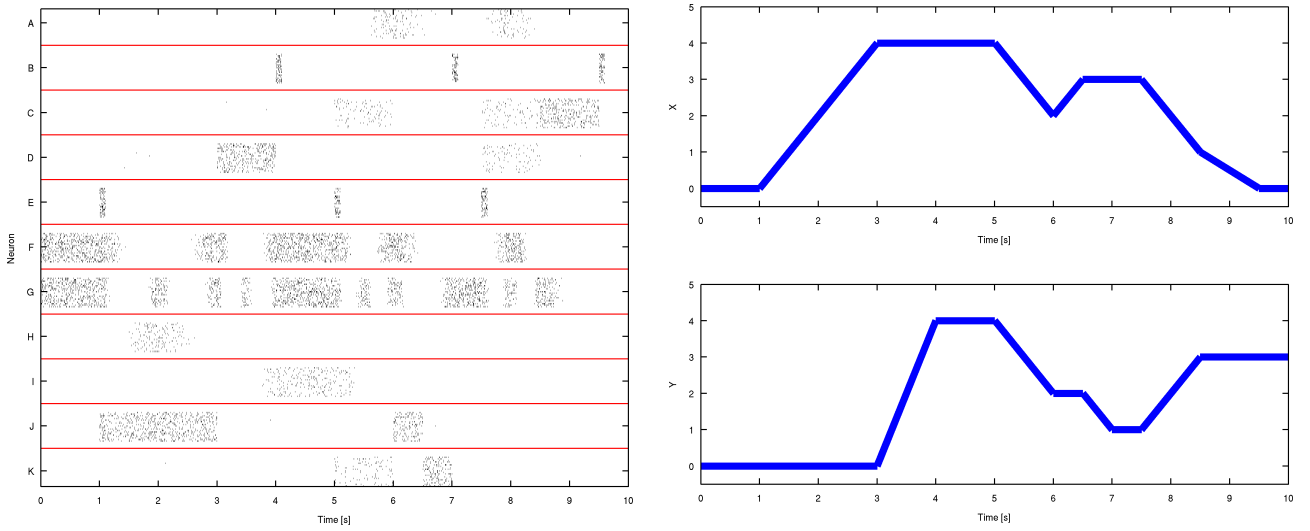


Figure 2: Trajectory in X- and Y-dimension of the artificial creature (right), and raster-plot of the spike-response of 11 neurons (A-K) in 20 trials.

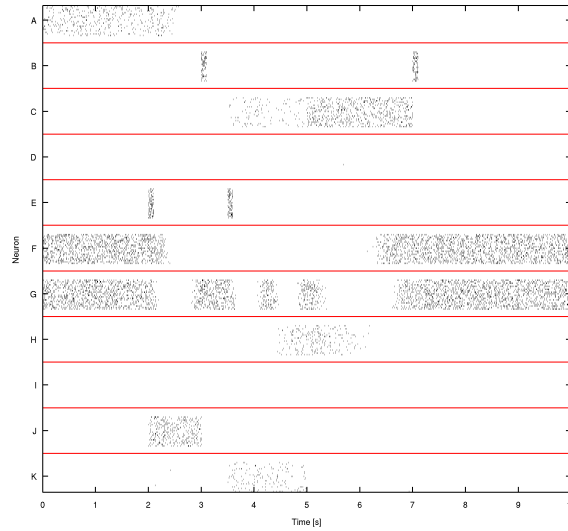


Figure 3: Raster-plot of the spike-response of the same 11 neurons (A-K) as in Figure 2 in 20 trials, where the creature follows another trajectory.

Exercise 8.3: Poisson spike train (optional)

Spike trains are simply a sequence of events and are often represented in a raster plot. Now, a Poisson spike train is a sequence of events (spikes) that happen with particular statistics. You will get to know some of these statistics in this exercise. The exercise is based on the chapter Spike-Train Statistics in Peter Dayan and L. F. Abbott, Theoretical Neuroscience, The MIT Press.

We only need two assumptions about our spike train:

- There is no dependence of the timing of an event/spike on the preceding events/spikes.
- The firing rate r is constant (independent of time); so we expect $r\Delta t$ spikes in a short interval Δt .

Let $t_1, t_2, \dots, t_n$ be the spike times of a sequence of n spikes, $0 \leq t_1 \leq t_2 \leq \dots \leq t_n \leq T$. We divide the time T into M bins of size $\Delta t = T/M$. We can assume Δt sufficiently small that no two spikes are ever in the same bin.

1. For given $T, \Delta t$ (small), n, r compute $P_{T,\Delta t}[n]$, the probability that there are exactly n spikes in the trial of duration T with bin length Δt .
2. If you have computed $P_{T,\Delta t}[n]$ correctly above and if you take the limit $\Delta t \rightarrow 0$ (when taking this limit we can assume that $M!/(M-n)! \approx M^n$ because of Stirling's formula and that $M-n \approx M$ because M grows without bound: $M\Delta t = T$) you get:

$$P_T[n] = \lim_{\Delta t \rightarrow 0} P_{T,\Delta t}[n] = \frac{(rT)^n}{n!} \exp(-rT)$$

This is the Poisson distribution which you already know from the release probabilities of synaptic vesicles at the neuromuscular junction (exercises 17 + 18)!

Using the properties of the Poisson distribution we can confirm:

- The expected number of spikes in the interval T is rT .
- The variance of the spike counts in the interval T is also rT .

The *Fano factor* is defined as the ratio of the variance and mean of the spike count. Which value does it have for the Poisson spike train?

3. The probability density of time intervals between adjacent spikes is called the *interspike interval* (ISI) distribution, and it is a useful statistic for characterizing spike trains.

Suppose that a spike occurs at a time t_i . For small Δt , what is the probability P that the next spike occurs somewhere in the interval $t_i + \tau \leq t_{i+1} < t_i + \tau + \Delta t$? What probability density $p(\tau)$ do you get? Hint: using the Poisson distribution above, calculate the probability that no spikes occur for period τ and that in the subsequent interval Δt a spike is generated.

4. In part 3 you have derived that the ISI distribution for a Poisson spike train is an exponential. The Poisson spike train is an extremely useful approximation of stochastic neuronal firing because it is simple and matches biological data on neural response variability to a certain extent in some recordings (Fano factor, ISI distributions *etc.*). However, what feature of neuronal firing do you know due to which the ISI distribution cannot be an exponential?