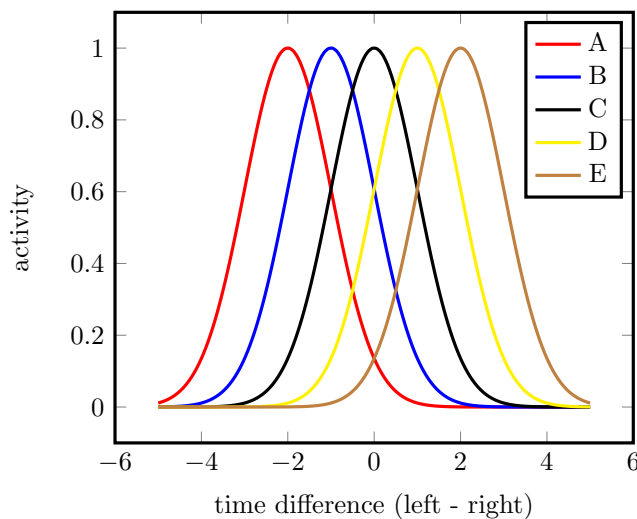


## Solution 8.1: Interaural time differences

The neural network model in this exercise was proposed by Jeffress in 1948. Its main features are temporally coded input signals, delay lines, and coincidence detectors. It is an example of a theoretically postulated network for which experimental evidence has been found later on (about half a century later in the barn owl). In contrast to this, grid cells had never been theoretically postulated before their discovery.

1. It is a temporal code, since the difference in timing between the left and right spikes determines which neuron A-E gets excited the most.
2. The tuning curves which describe the dependence on the interaural time difference of the neurons A-E are bell-shaped:



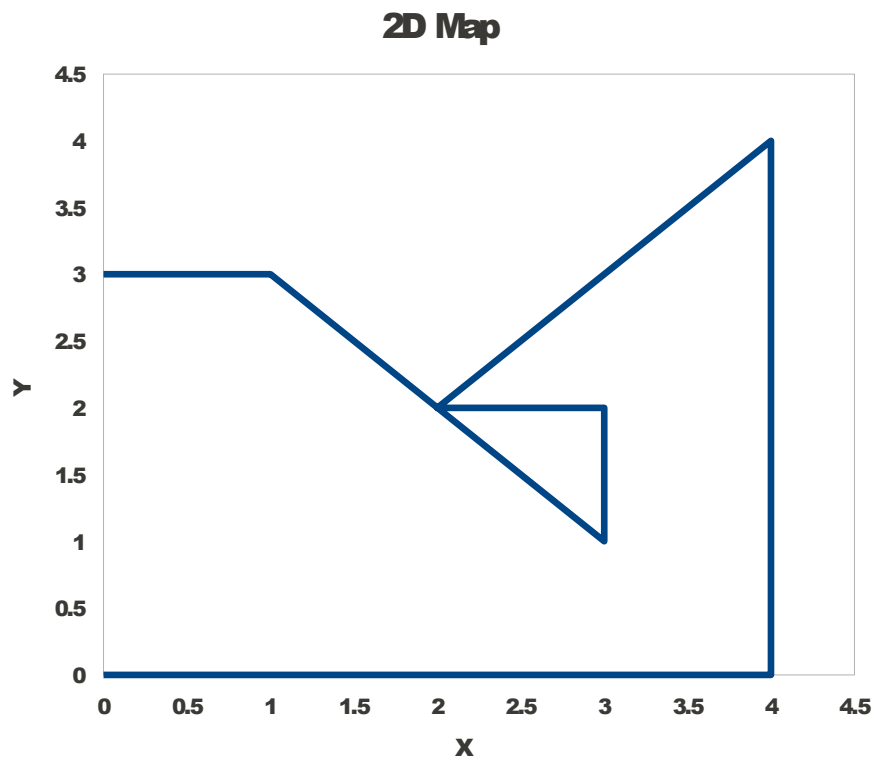
3. The time difference for the signal to arrive at the left and right ear is about half the duration of an action potential:

$$t = \frac{x}{v} = \frac{0.15 \text{ m}}{350 \frac{\text{m}}{\text{s}}} = 0.43 \text{ ms.} \quad (1)$$

4. Points of equal interaural time differences have a constant distance difference to the ears, *i.e.*, the distance to the left ear minus the distance to the right ear is the same for all these points. Therefore, all the points with constant interaural time difference form a hyperbola.

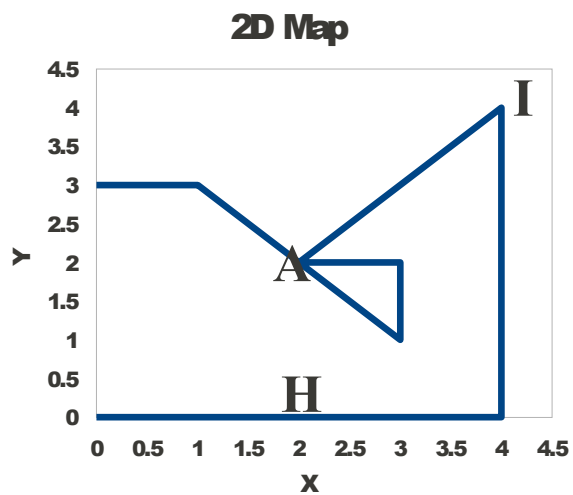
## Solution 8.2: Interpreting multi-unit spike recordings

1. The trajectory:

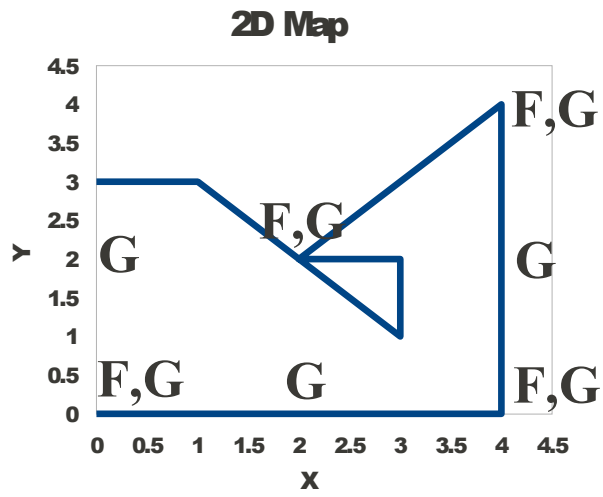


2.-3. We can identify four different types of neurons:

(a) Place neurons fire at a certain location:

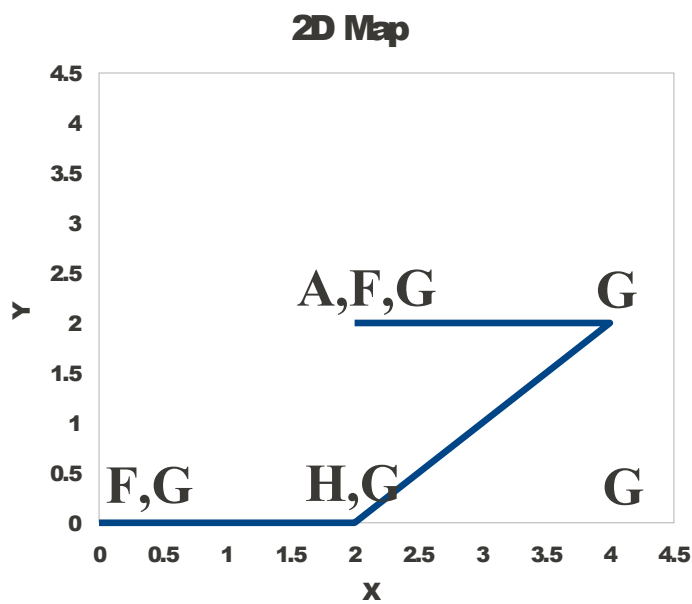
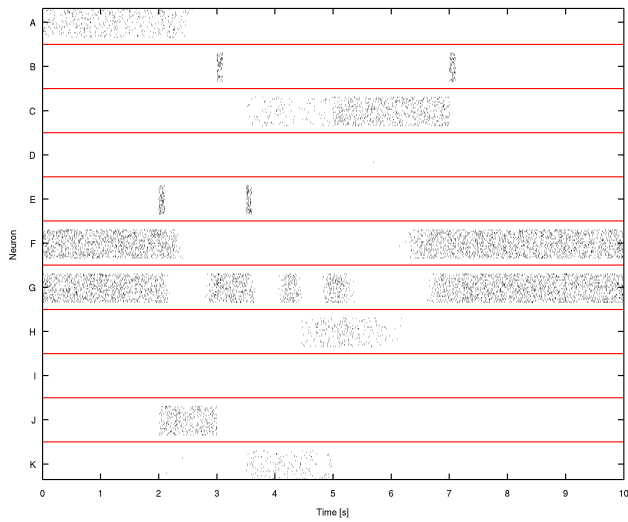
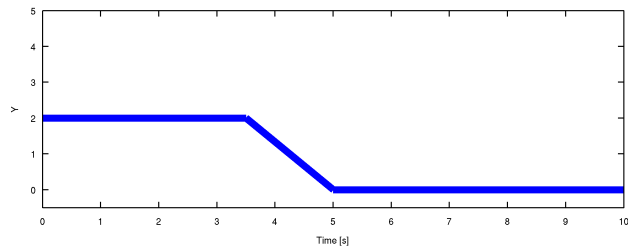
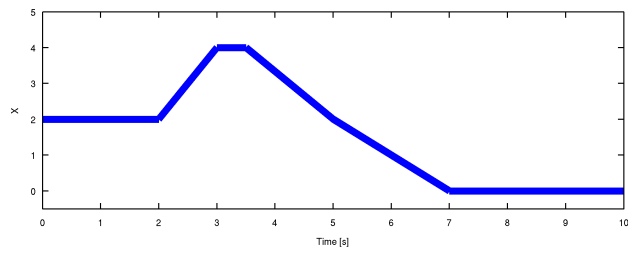


(b) Grid neurons fire at multiple places aligned on a grid:



- (c) Movement off- and on-set neurons (B, E) fire when the animal stops or starts moving.
- (d) Head direction neurons (C left, J right, D up, and K down) indicate the orientation.

4. The trajectory can be reconstructed since we already know the features recognized by each neuron:



Note that the Nobel prize for Physiology or Medicine was awarded in 2014 for the discovery of place and grid cells.

### Solution 8.3: Poisson spike train (optional)

1. The probability of a spike occurring in one specific time bin is  $r\Delta t$  and the probability of not having a spike in a given time bin is  $(1 - r\Delta t)$ . Note that we neglect the case that more than one spike are in a time bin because  $\Delta t$  is sufficiently small. With simple combinatorics we get

$$P_{T,\Delta t}[n] = \underbrace{\frac{M!}{(M-n)!n!}}_{\text{number of ways of putting } n \text{ spikes into } M \text{ bins, } = \binom{M}{n}} \cdot \underbrace{(r\Delta t)^n}_{\text{probability of } n \text{ spikes occurring in } n \text{ specific time bins}} \cdot \underbrace{(1 - r\Delta t)^{M-n}}_{\text{probability of having the remaining } M - n \text{ time bins without any spikes}}$$

2. The Fano factor is  $rT/rT = 1$ , independent of the time interval  $T$ . This is one of the characteristic features of Poisson spike trains.
3. The probability is

$$P[\tau \leq t_{i+1} - t_i < \tau + \Delta t] = \underbrace{P_\tau[0]}_{\substack{\text{Probability of} \\ \text{not firing a} \\ \text{spike for period} \\ \tau}} \cdot \underbrace{r\Delta t}_{\substack{\text{probability of} \\ \text{generating a} \\ \text{spike within the} \\ \text{small interval} \\ \Delta t}} = \exp(-r\tau) \cdot r\Delta t$$

Note that  $0! = 1$ . So the probability density is simply

$$p(\tau) = p[\tau \leq t_{i+1} - t_i < \tau + \Delta t] = \frac{P[\tau \leq t_{i+1} - t_i < \tau + \Delta t]}{\Delta t} = r \cdot \exp(-r\tau)$$

This formula is very useful if you have to generate the spike times of a spike train artificially. Also, it helps us to decide whether an observed spike train could have been generated by a Poisson process at all.

4. An exponential ISI distribution is in contradiction with the refractory period because the refractoriness makes short ISI less likely than the Poisson model would predict. Remember that the refractory period is the brief period after the generation of an action potential during which a second action potential is difficult or impossible to elicit. Also, our assumption that the firing rate  $r$  is constant is generally not true. To respect this, modifications need to be made to the simple Poisson spike train.