MSc in Artificial Intelligence and Robotics
MSc in Control Engineering
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Neuroengineering

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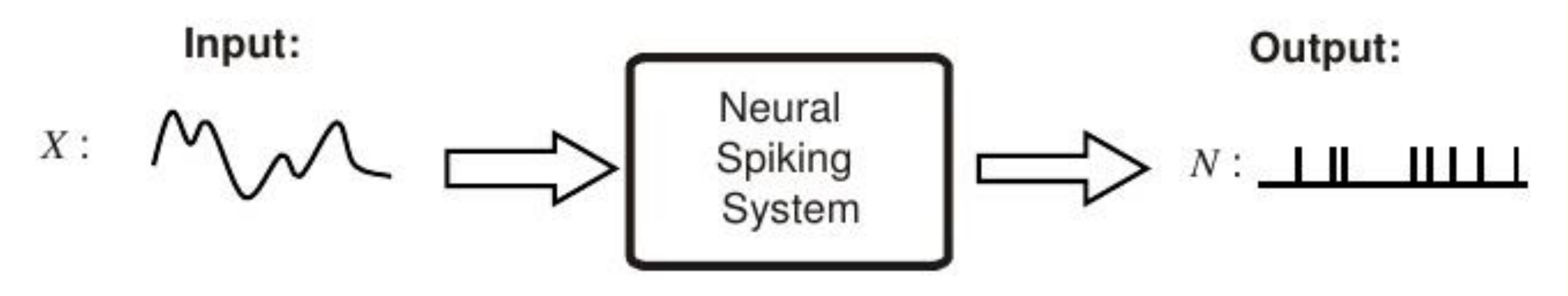
5.1- NEURAL ENCODING

Learning objectives of the lesson

1. Understand the definition of neural encoding and decoding
2. Describe the rate-coding hypothesis
3. Define the neural response function and the spike-count firing rate
4. Illustrate the experimental procedure used to build a tuning curve
5. Interpret a given a tuning curve, and specifically:
   a. Describe the neuron behavior as a response to stimulus properties
   b. Compare the neural response to specific values of the stimulus s

Introduction

Neural (En/De)coding: measuring and characterizing how an external (physical, e.g., light or sound intensity) or internal (e.g. the direction of a planned movement) input received by a neuron is translated into a sequence of action potentials (output):

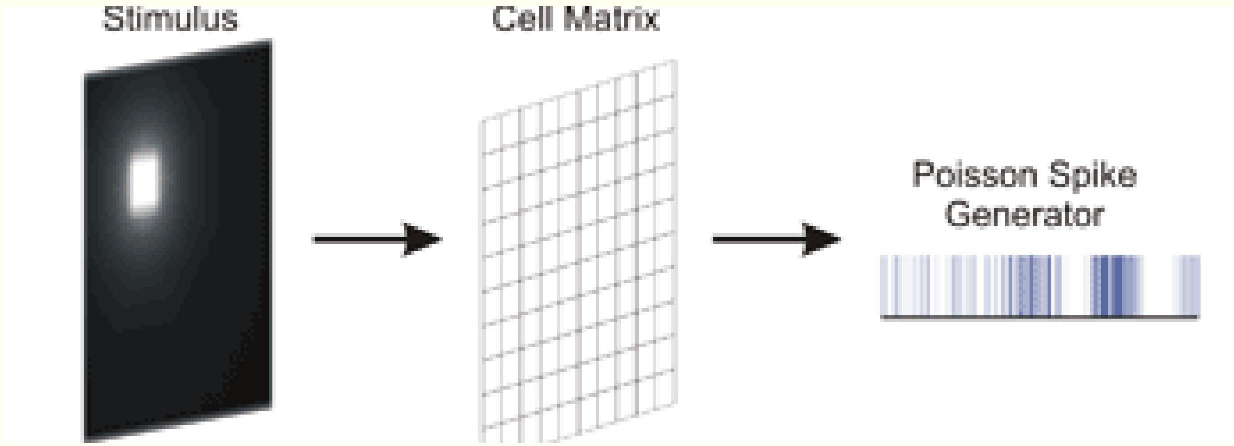


Neural encoding

From stimulus to response

Neural response = f(stimulus)

- *Aim:* describing how neurons react to different stimuli and trying to **predict their response to a new one**

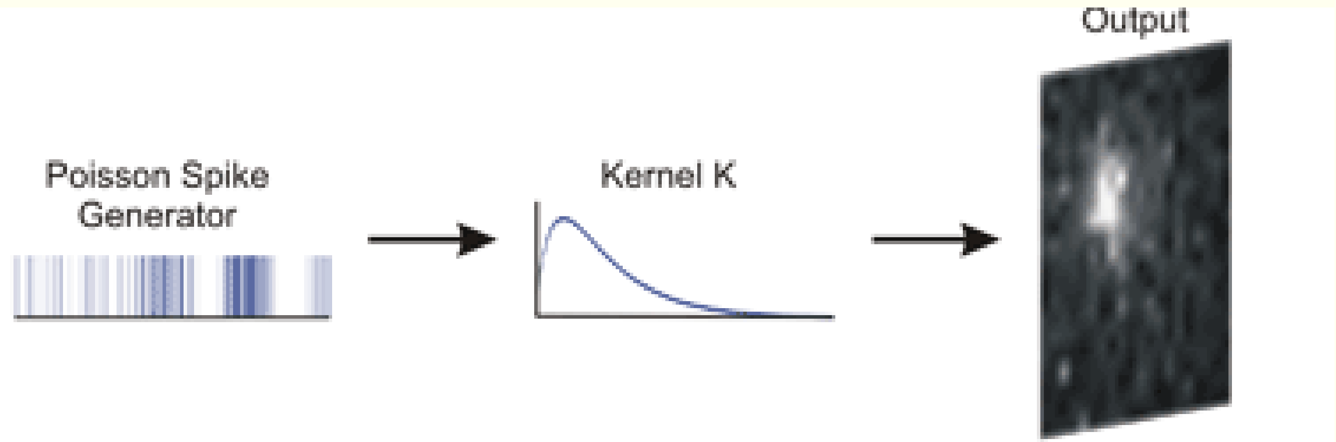


Neural decoding

From neural response to the stimulus that induced it

Stimulus = f^{-1}(neural response)

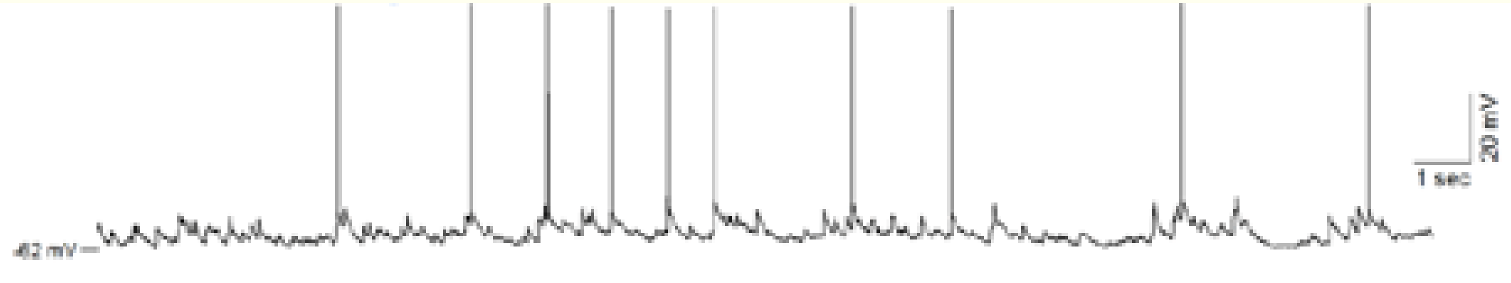
- *Aim:* **recognize the stimulus** (or its properties) that induced the spike train response



Rate-coding hypothesis

- The rate-coding hypothesis suggests that spike frequency (or rate) is the fundamental mechanism of coding information
- e.g.: the number of action potentials from cutaneous nerve fibers in the leg of a cat was proportional to the pressure applied to the footpad (Adrian and Zotterman, 1926)

Spike trains and firing rate



- Each spike is like a Dirac δ function
- For n spikes, t_i is the time in which the i[th] spike occurred:

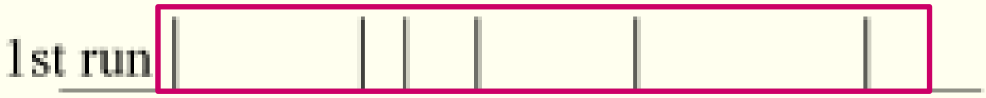
  $i=1,2,\ldots,n$ and $0 \le t_i \le T$ (T= trial duration)
- The spike train can be thus written as:

$$\rho(t) = \sum_{i=1}^{n} \delta(t - t_i)$$

$\rho(t)$ is the neural response function

Spike-count firing rate

$$r = \frac{n}{T} = \frac{1}{T}\int_0^T \rho(\tau)\, d\tau$$



$\int_0^T \rho(\tau)\, d\tau$=n

$/T$

The spike-count firing rate is the time average of the neural response function over the duration of the trial.

n/T= Hz

e.g.: T= 1 s n= 6

r = 6 Hz

Stimulus-response link

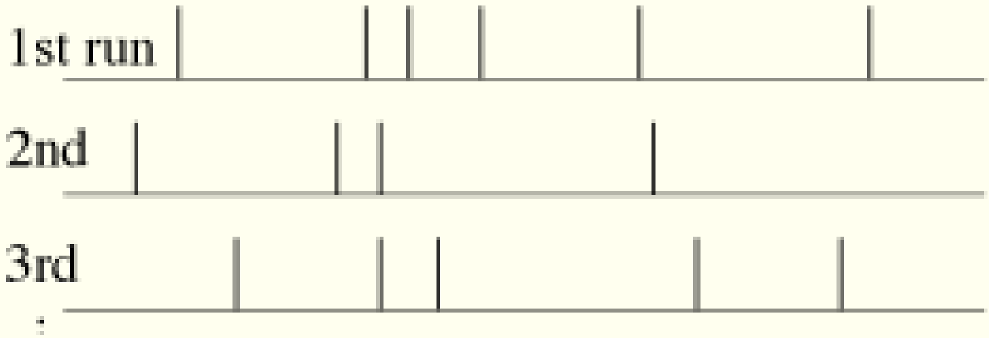
- Spike sequences reflect both the intrinsic dynamics of the neuron and the temporal characteristics of the stimulus
- We can use the spike-count firing rate when the stimulus is stationary (otherwise we need a time-resolved definition for the spike rate)
- Many neurons respond to the same given stimulus → we should examine the relationships of these firing patterns to each other across the population of responding cells (neural networks)

Stimulus-response link

- Neural responses can vary across repetitions (trials) even when the same stimulus is presented repeatedly → We cannot describe the timing of each spike deterministically → we use a probabilistic approach (average firing rate **<r>** across trials)

$$\langle r \rangle = \frac{\langle n \rangle}{T} = \frac{1}{T}\int_0^T r(t)dt$$

e.g.:



r_1= 6 Hz

r_2= 4 Hz

r_3= 5 Hz

<r>= 5 Hz

Tuning curves

A stimulus is characterized by many properties (e.g.: shape, orientation, contrast, movement, …)

We focus on a single property *s* and we assume it's stationary along each trial (repetition of the stimulation)

Stimulus property *s* → f(s) → <average> firing rate <r>

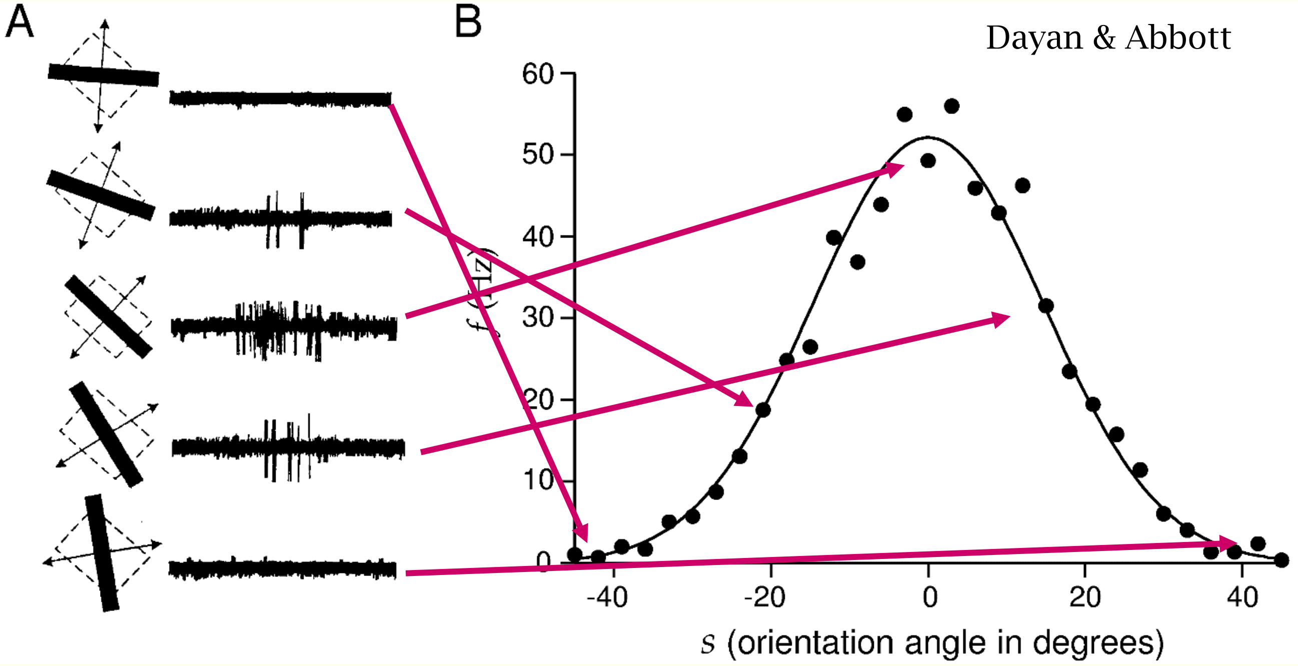
Stimulus → Neuron → Spike train

$$\langle r \rangle = f(s)$$

Tuning curve of the neuronal response

Examples of tuning curves - 1

- Primary visual cortex in an animal subject (monkey)
- Visual stimulation (bar with different orientations)
- s = orientation angle of the bar (degrees)

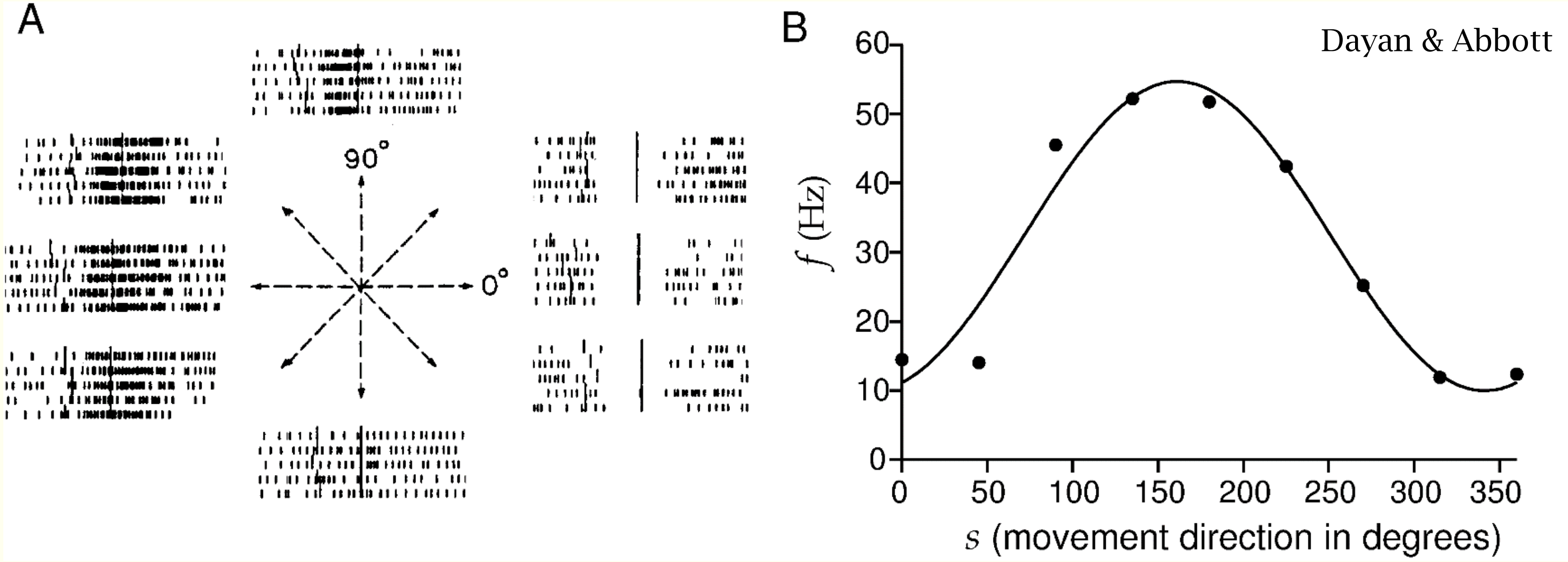


$$f(s) = r_{max} e^{-\frac{1}{2}\left(\frac{s - s_{max}}{\sigma_f}\right)^2}$$

s_{max}=angle evoking the maximum response r_{max}

σ_f=amplitude of the tuning curve

Examples of tuning curves - 2

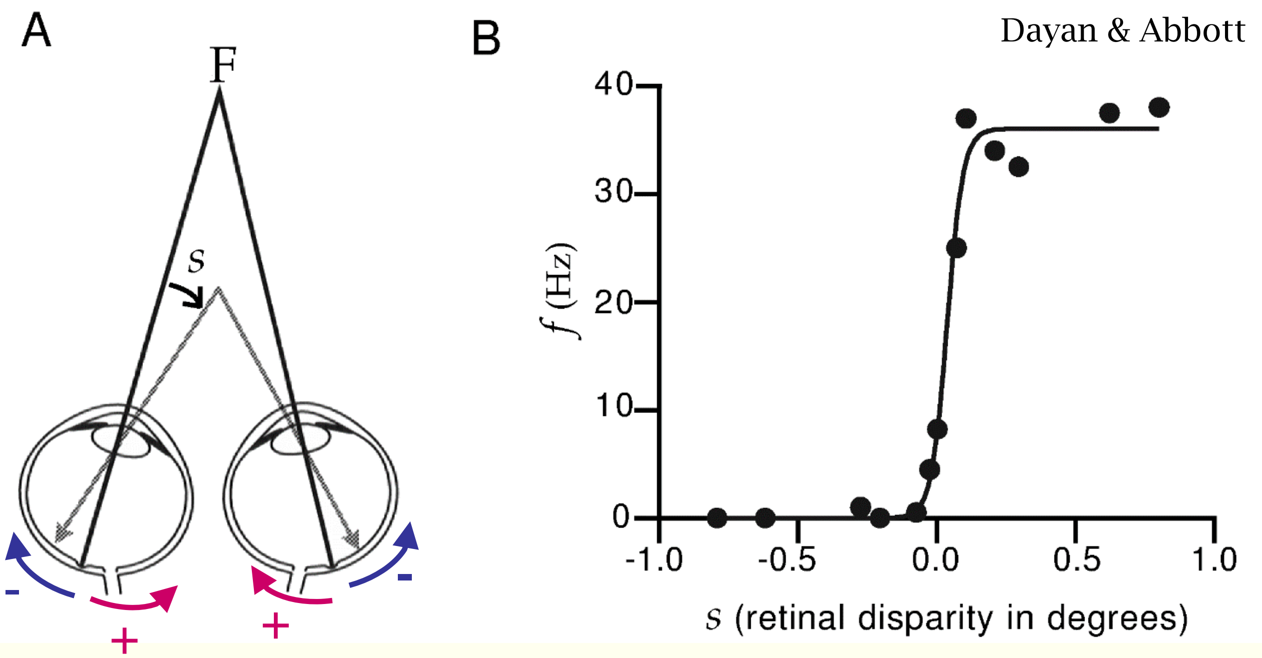


- A neuron in the primary motor cortex of a monkey trained to reach in different directions
- The firing rate of the cell is correlated with the direction of arm movement s (in degrees)

$$\boxed{f(s) = r_0 + (r_{max} - r_0)\cos(s\text{-}s_{max})}$$

s=movement direction (degrees)
s_{max}=angle evoking the max response r_{max}
r_0=offset (to avoid negative firing rate)

Examples of tuning curves - 3



- Primary visual cortex neuron (cat) reacting to retinal disparity (a difference in the retinal location of an image between the two eyes)
- F: fixation point
- The neuron responds only to positive s → far objects (far-tuned neuron)

$$f(s) = \frac{r_{max}}{1 + exp\left[\left(s_{1/2} - s\right)/\Delta_s\right]}$$

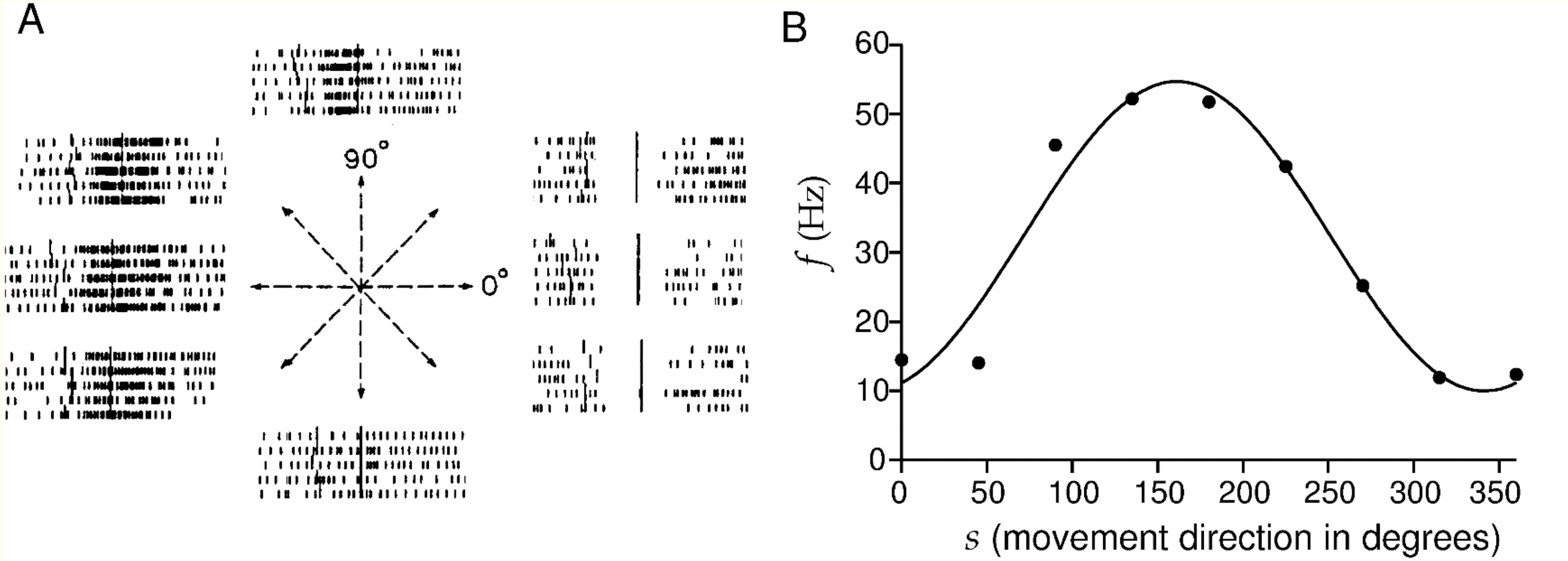
s=binocular retinal disparity (degrees)
$S_{1/2}$=disparity inducing a response equal to ½ of the maximum r_{max}
Δ_s=controls how quickly the firing rate increases as a function of s

References

- Dayan & Abbott:
  - Chapter 1.1 (From Stimulus to Response)
  - Chapter 1.2 (Spike Trains and Firing Rates, Tuning Curves)

Self-evaluation

Given the following tuning curve:



- Is the neural response for a movement direction of 90 degrees greater than for 180 degrees?
- Will I build a different tuning curve for each trial?
- Which firing rate can I expect when the movement direction is 250 degrees?
- If the measured firing rate is 55Hz, can I «guess» which was the movement direction that produced that response?

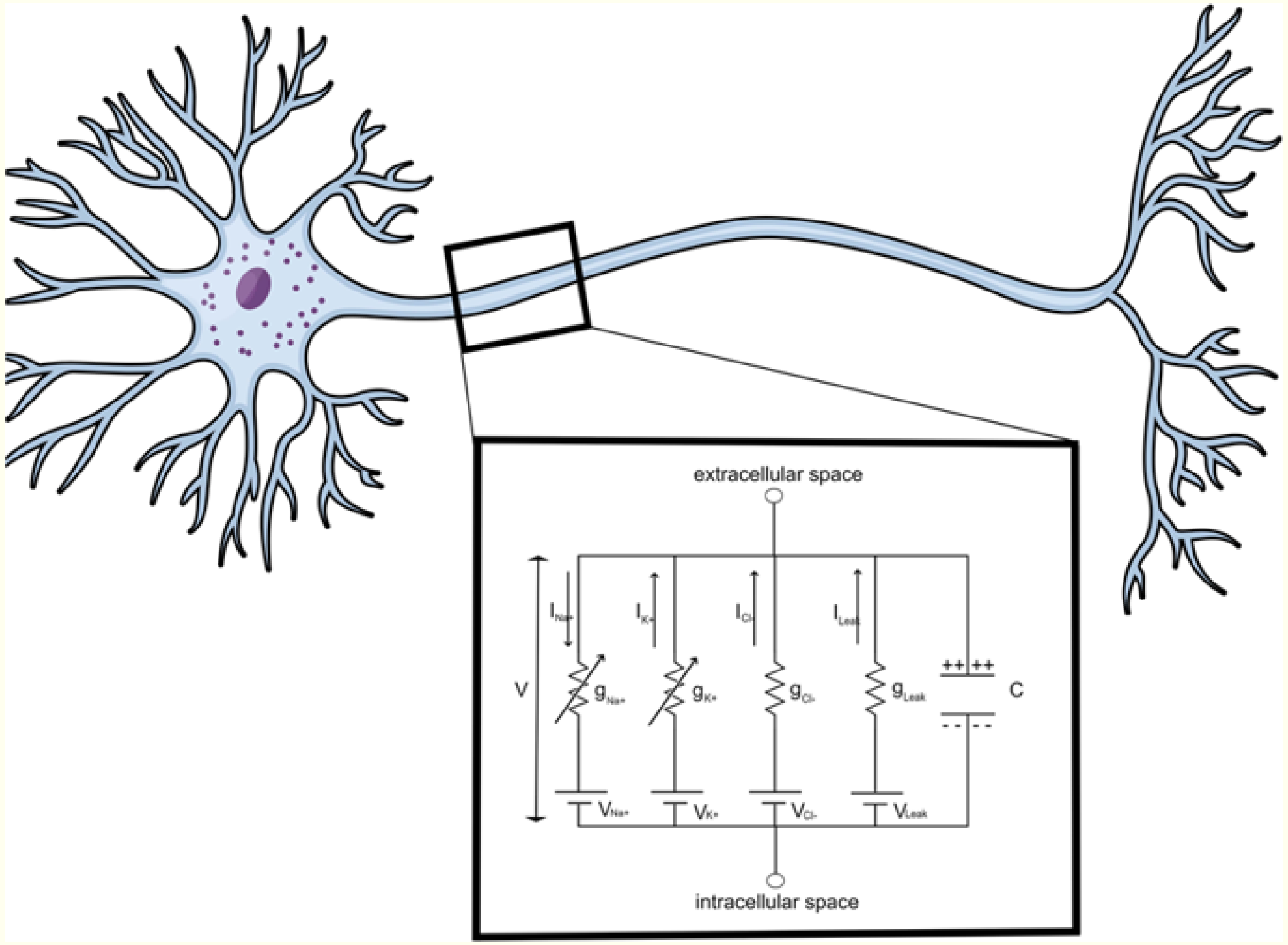
5.2- THE POISSON SPIKE GENERATOR

Learning objectives of the lesson

1. Understand the statistical properties of the spike train generated by a neuron when the firing rate is *r*
2. Identify a stochastic process able to simulate the neuronal behavior in terms of input/output relation *(f)*
3. Describe the homogeneous Poisson distribution and the inter-spike interval distribution
4. List the steps to build a Poisson spike generator
5. Compare the real data with the simulates spike trains and
   a. Understand why there are such differences
   b. Explain how to mitigate such differences

we are able to model the neuron in deterministic way

Why a stochastic model of the neuronal response?



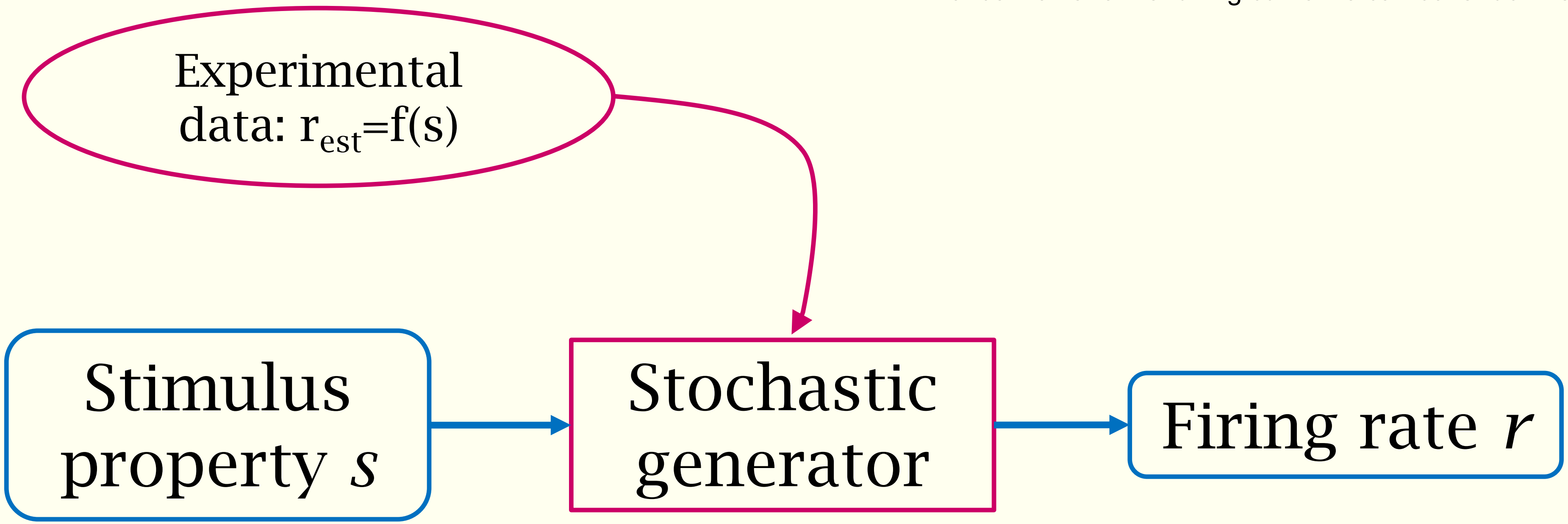
Mind the Graph, https://mindthegraph.com

The relation between a given stimulus property *s* and the generation of a single action potential is very complex to be modeled (we would need a complete electrical model of the entire membrane of each individual neuron) which captures the main properties of the neural behaviour in a statistical way allowing to build much simpler model that can mimic not the specific behaviour that a neuron has in a specific moment but the average behaviour.

Why a stochastic model of the neuronal response?

We need a statistical model that allows us to estimate the probability of an arbitrary spike sequence occurring, based on our knowledge of the responses actually recorded

once we have the tuning curve we can construct the stochastic model



The Poisson process-1

If the probability of generating an action potential is independent of the presence or timing of other spikes the firing rate r is all we need to compute the probabilities for all possible action potential sequences.

An extremely useful approximation of stochastic neuronal firing is provided by the Poisson process:

- homogeneous, when the firing rate r is constant over time

if the firing rate changes during the time

- inhomogeneous, for a time-dependent firing rate $r(t)$

We will focus on the homogeneous Poisson process (r constant in time)

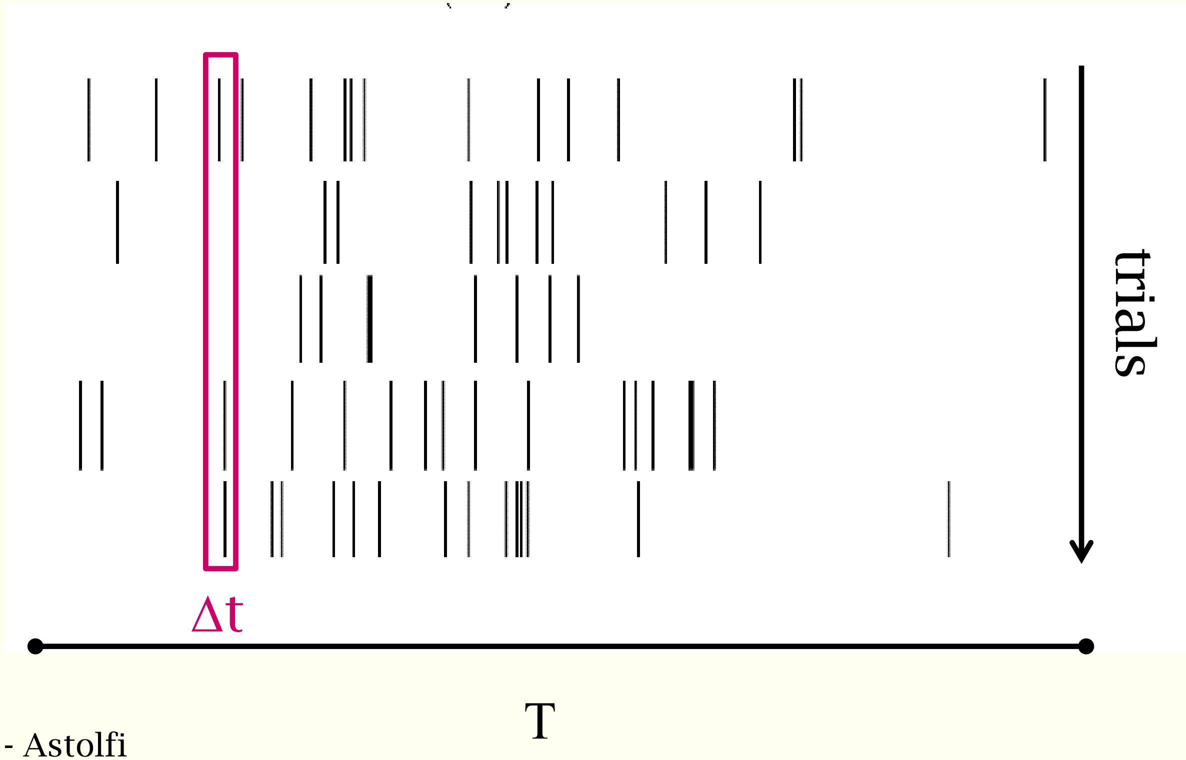
The Poisson process-2

A Poisson stochastic process produces an integer, nonnegative number of statistically independent discrete events

For the neuron:

the spike is virtually instantaneous

- Each action potential is an event
- By dividing the trial duration T in very small time intervals Δt ($\rightarrow 0$) we have:
  1. No more than a single spike for each interval
  2. Independent events (spikes) at each interval



The Poisson process-3

We will focus on:

probability of having an action potential in a trial. Different stimulations have different number of spikes

1) The probability of n spikes in a trial of duration T

2) The inter-spike interval distribution

probability of have a specific time distance between two spikes.

Probability of n spikes in a trial of duration T- 1

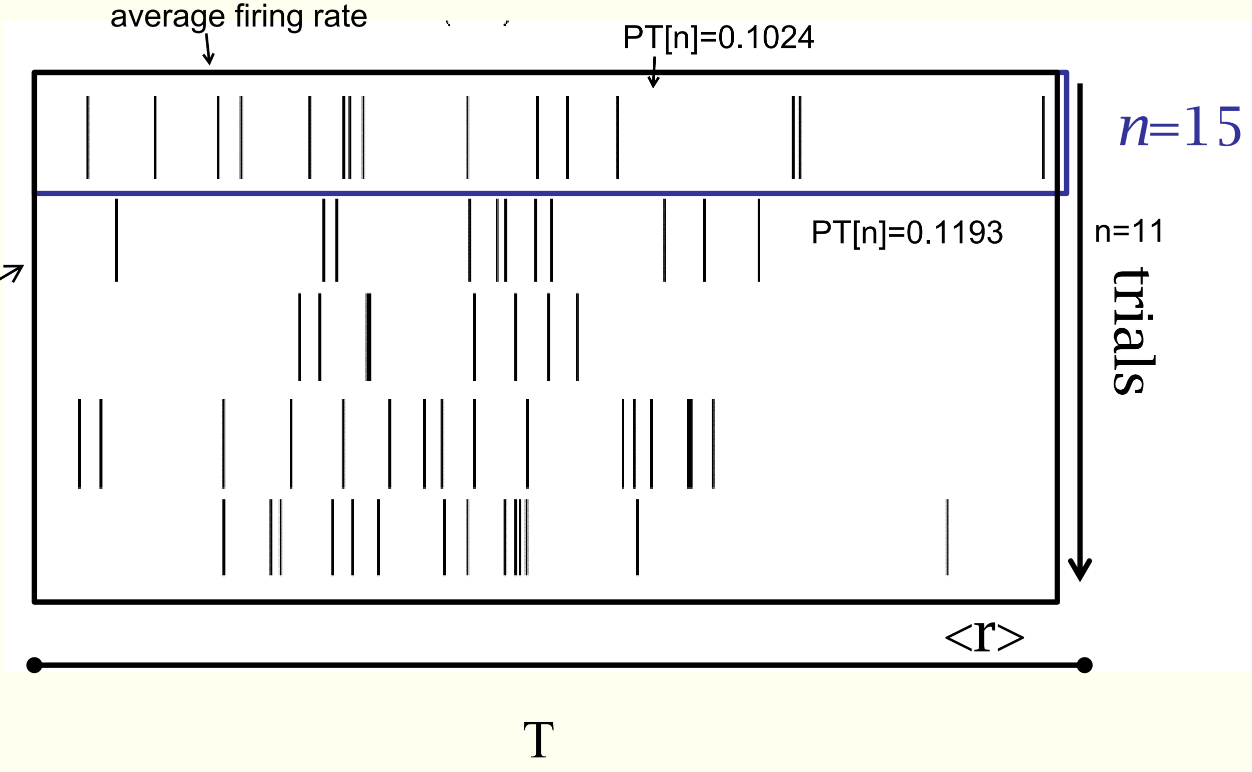
trial duration

$$P_T[n] = \frac{(rT)^n}{n!} e^{(-rT)}$$

derived from Poisson distribution

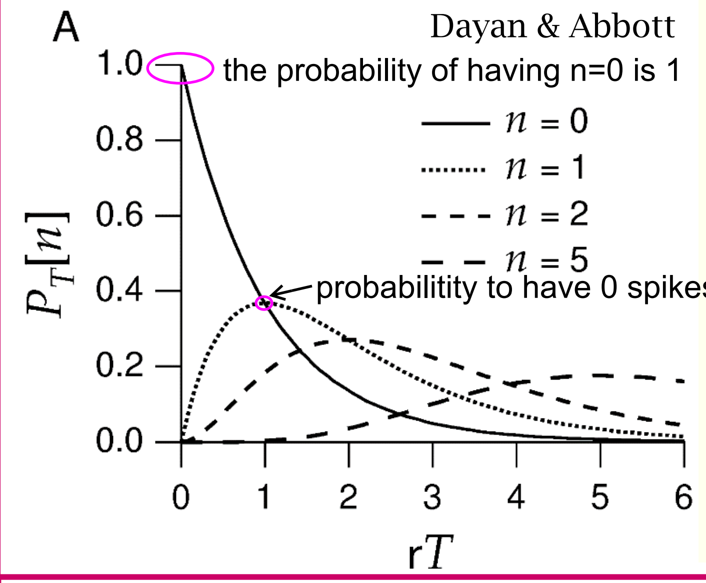
- $P_T[n]$ is the probability of n spikes occurring during a trial of length T
- r is the firing rate (usually the average across trials <r>)
- rT is the average (across trials) number of spikes in T

5 trials



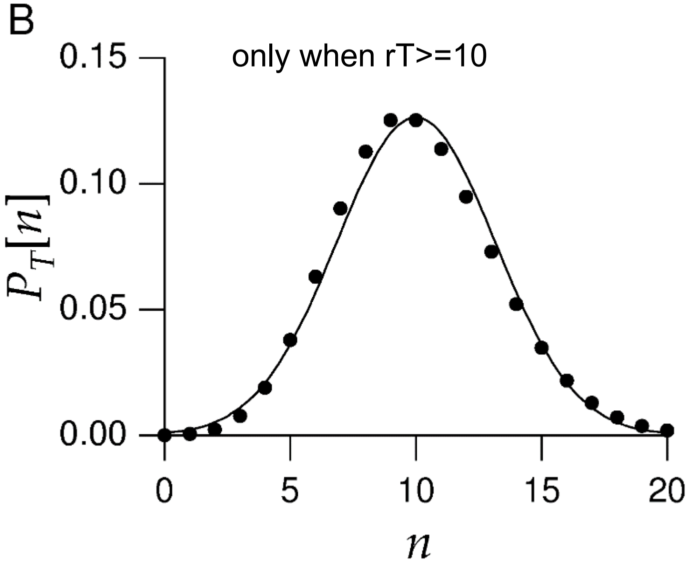
Probability of n spikes in a trial of duration T- 2

distribution for different values of n



A: probability of different n as a function of rT

- for a given n, the maximum $P_T[n]$ corresponds to $rT = n$ the max of each curve corresponds to rT=n
- When T increases, higher values of n are more likely Poisson distribution becomes a Gaussian with the expected value equal to the variance and both equal to rT
- The same applies when r increases



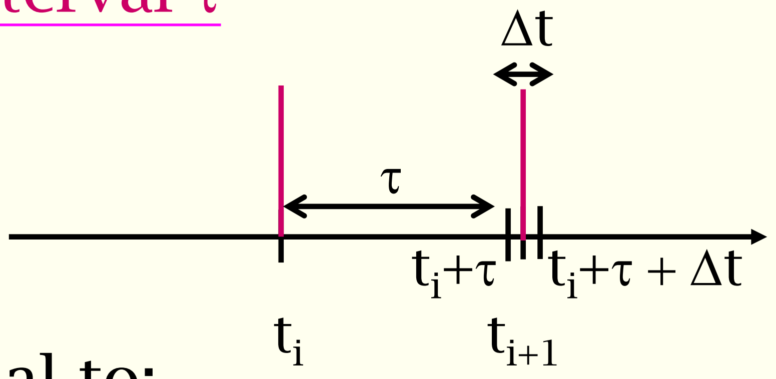
B: Probability of different n when $\boldsymbol{rT}$**=10**

- n=10 ~~N=10~~ is the most likely
- When $rT \geq 10$, the distribution becomes a Gaussian with expected value and variance both equal to rT

distance between 2 subsequent action potentials

The inter-spike interval distribution - 1

Given a spike at t_i, the probability of the following spike to be produced in the interval τ



$$t_i + \tau \le t_{i+1} \le t_i + \tau + \Delta t$$

is equal to:

$$\boxed{\text{probability of no spike for a time } \tau \text{ * probability of a spike in } \Delta t}$$

- Probability of no spike in τ → $n = 0$ and $T = \tau$ in the Poisson distribution:

$$P_T[n] = \frac{(rT)^n}{n!} e^{(-rT)} \rightarrow P_\tau[0] = \frac{(r\tau)^0}{0!} e^{(-r\tau)} = \boxed{e^{(-r\tau)}}$$

comes from the previous case formula

the probability of having zero spikes decreases exponentaily with tau according to r.

- Probability of a spike in $\Delta t = \boxed{r\Delta t}$

The inter-spike interval distribution - 2

Finally:

$$P[\tau] = P[t_i + \tau \leq t_{i+1} \leq \ t_i + \tau + \Delta t] = r\Delta t e^{(-r\tau)}$$

(inter-spike interval distribution)

it tells us that the most inter spikes interval are the short ones

give a fixed r, it's more probable that we have short interval between spikes. If we change r also the velocity changes

- The most likely inter-spike intervals are short ones, and long intervals have a probability that falls exponentially as a function of their duration.

For a homogeneous Poisson process (r constant):

- the mean of the inter-spike interval $\langle\tau\rangle = 1/\mathrm{r}$
- the variance of the inter-spike interval $\sigma_\tau^2 = 1/\mathrm{r}^2$

The ratio of the standard deviation to the mean $\frac{\sigma_\tau}{\langle\tau\rangle}$ is called the coefficient of variation (Cv) and it's =1 for a homogeneous Poisson process

Now lets go to the practical part. We need r to describe the behaviour of our neuron.

The Poisson spike generator

stochastic generator

the Gaussian is not good for all neuron behaviour. If you have a condition in which the neuron do fire a very few spikes, the gaussian is not good

A stochastic model of the neural response to a stimulus property s

we start from the tuning curve

It produces a spike train with the same r of the neuron

- 1° step: experimental estimation of the firing rate r_{est} (tuning curve)
- 2° step: build a spike generator based on a Poisson distribution with $r = r_{est}$

the same threshold for ex 0.5 can produce a spike or not according to the firing rate because if we have a low firing rate, the probability of generating a spike is 0.2, we will not have a spike in that time interval. While if the firing rate is higher and the threshold is always 0.5 we will have spike

The Poisson spike generator

<u>A simple algorithm that a computer can run:</u>

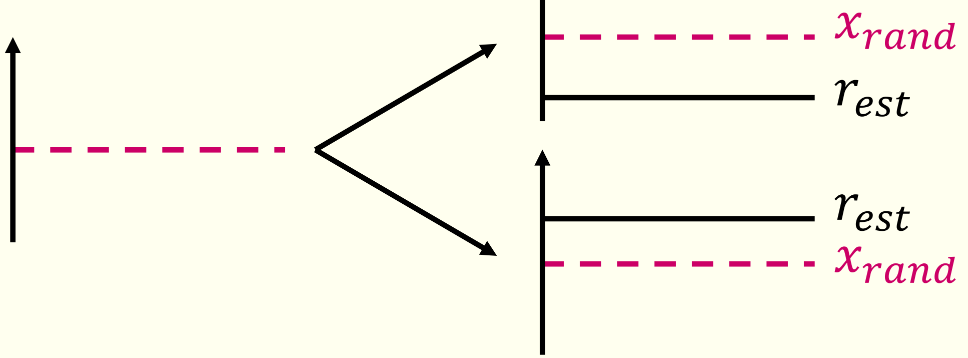
r estimated from the data is the starting point

Hp: the probability to generate a spike during Δt is $r_{est}\Delta t$ time step

1. the program progresses through time in small steps of size Δt
2. it generates, at each time step, a random number x_{rand} chosen uniformly in the range [0,1] (threshold, independent from r)
   threshold is between 0 and 1 because we need to combine it with the probability
   probability of spike firing in deltat
3. for each Δt, if $\boxed{r_{est}\Delta t} > x_{rand}$ at that time step, a spike is fired, otherwise it is not
   from this product returns the probability of having a spike in that time interval

this value is dependent from the firing rate and it is compared with the threshold

Same threshold x_{rand}



Low r_{est} → lower probability to fire

High r_{est} → higher probability to fire the firing rate is not computed but it is extracted from the data

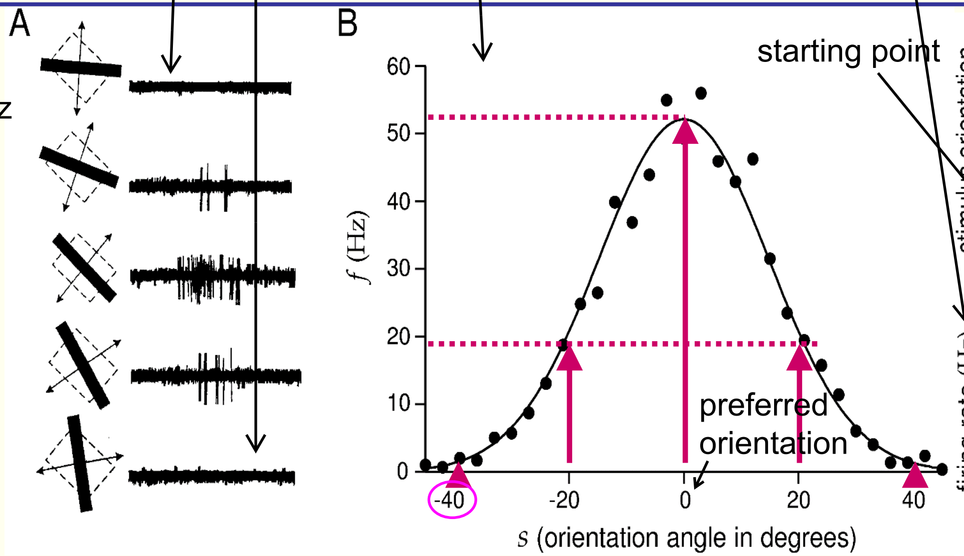
Example

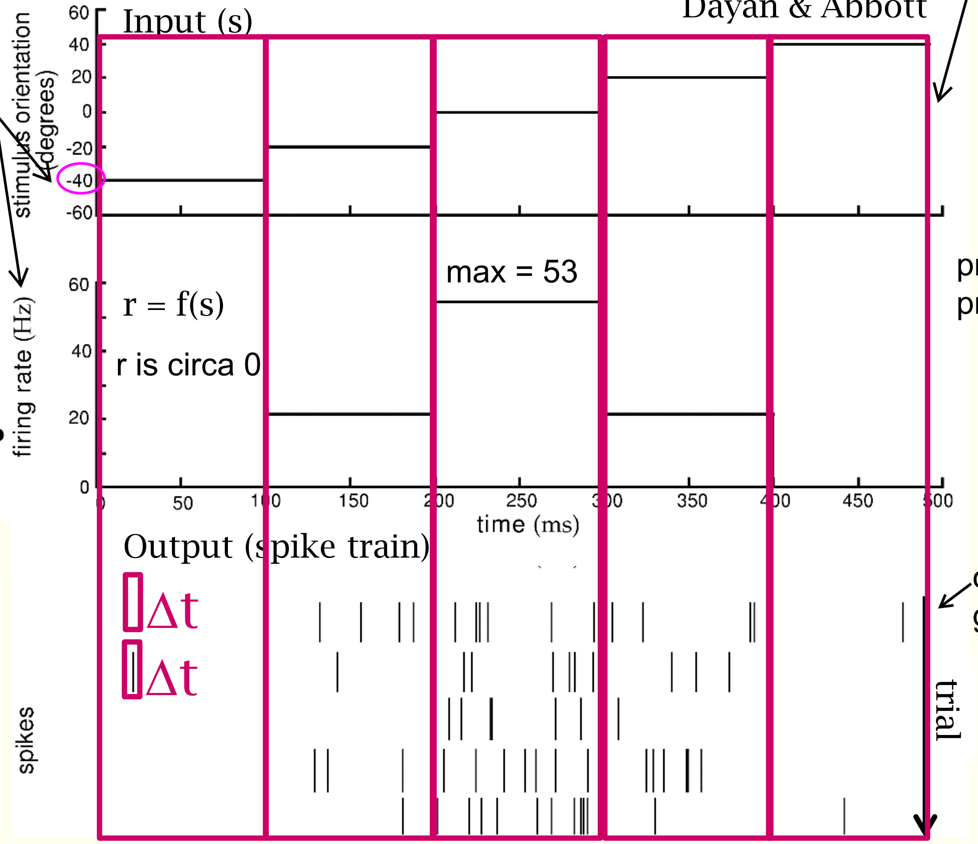
in the first graph we have the stimulus variations that we want to simulate

rmax = 52.14 Hz
smax = 0°
sigmaf = 14.73°

almost no spikes

Tuning curve in Hz





probability of proucing a spike

output of the poisson generator

$$f(s) = r_{max} e^{-\frac{1}{2}\left(\frac{s - s_{max}}{\sigma_f}\right)^2}$$

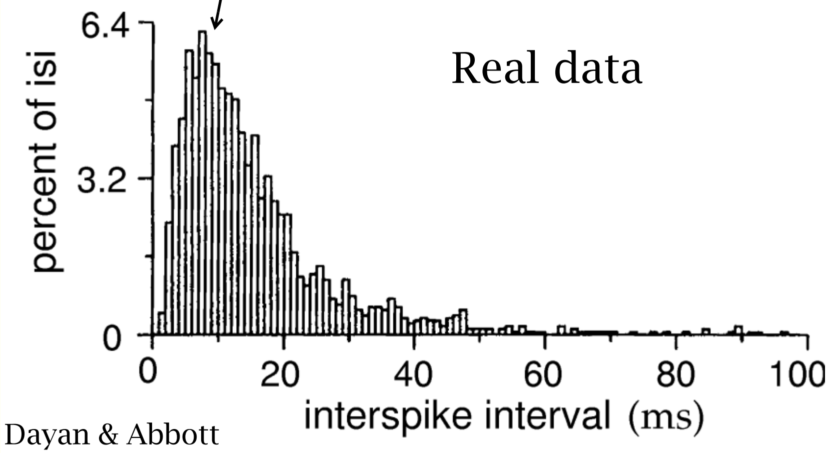
1. Select *s* values: -40, -20, 0, 20, 40
2. Get the corresponding *r(t)* from *f(s):* 0, 20, 53, 20, 0
3. The Poisson generator produces spike trains with the desired *r(t)*

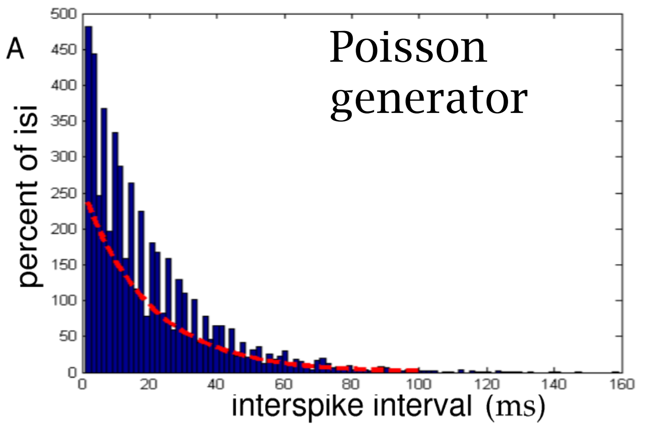
if you increase the number of trials the value is much more close to 20

Limitations of the Poisson generator - 1

Inter-spike interval histogram (comparison with real data):

distribution of how many times we have that result in our data, so it's empirical





Dayan & Abbott

For small values of tau(interspike interval) we can see that the result is different in real data and in Poisson generator where we have the maximum value of percent of isi in 0. This means that our model is not good for this situation. We go back to the neuron to understand because it is not good(NEXT SLIDE)

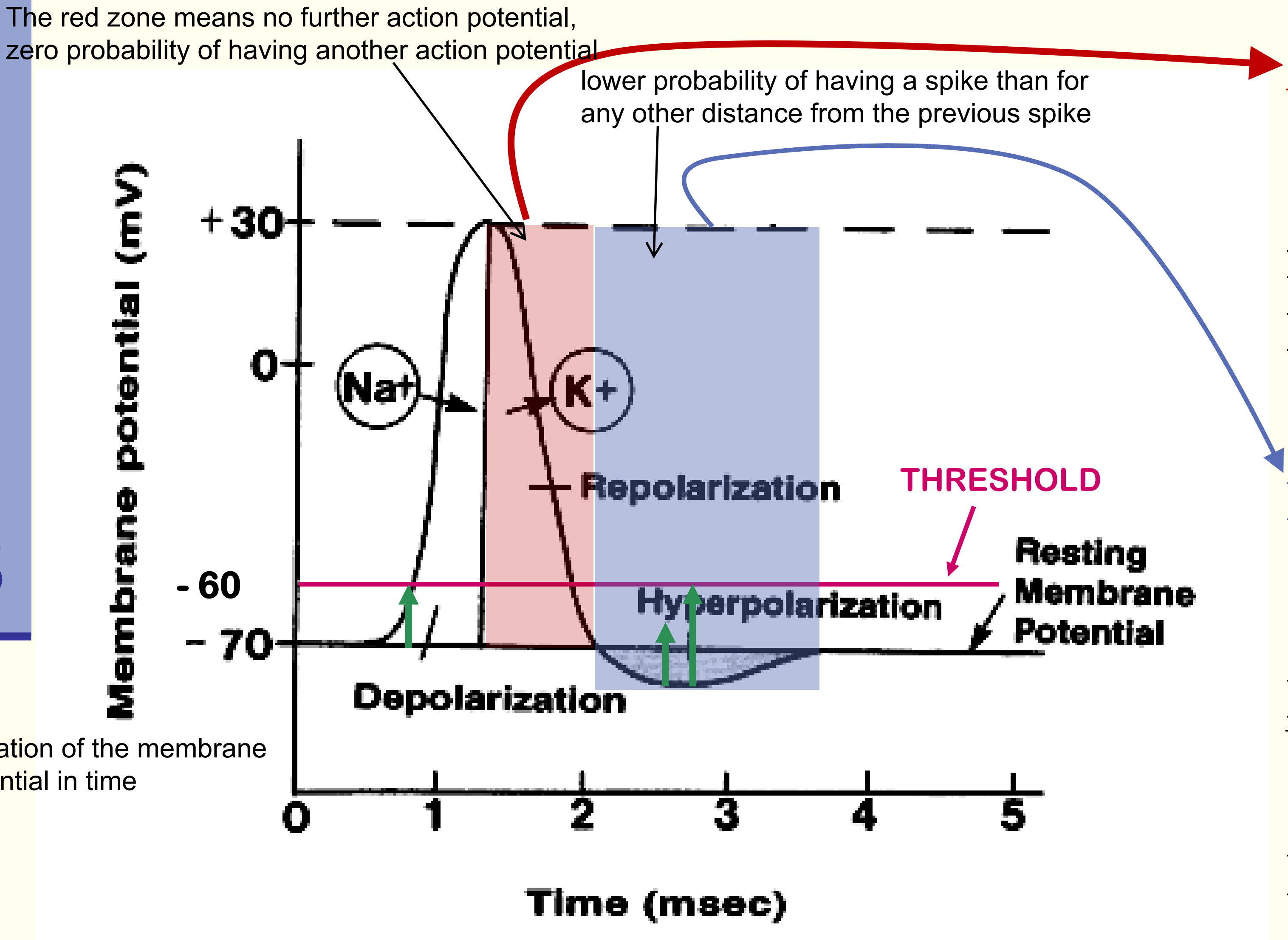
isi (Inter Spike Interval)

Theoretical: $r\Delta t e^{(-r\tau)}$ (exponential)

When *isi* is very low, data don’t align with the exponential rule

Explanation → refractory period

Absolute and relative refractory periods



Variation of the membrane potential in time

Absolute refractory period: due to the Na^+ voltage-gated channels inactivation. No new action potential can be produced (under **any** circumstances)

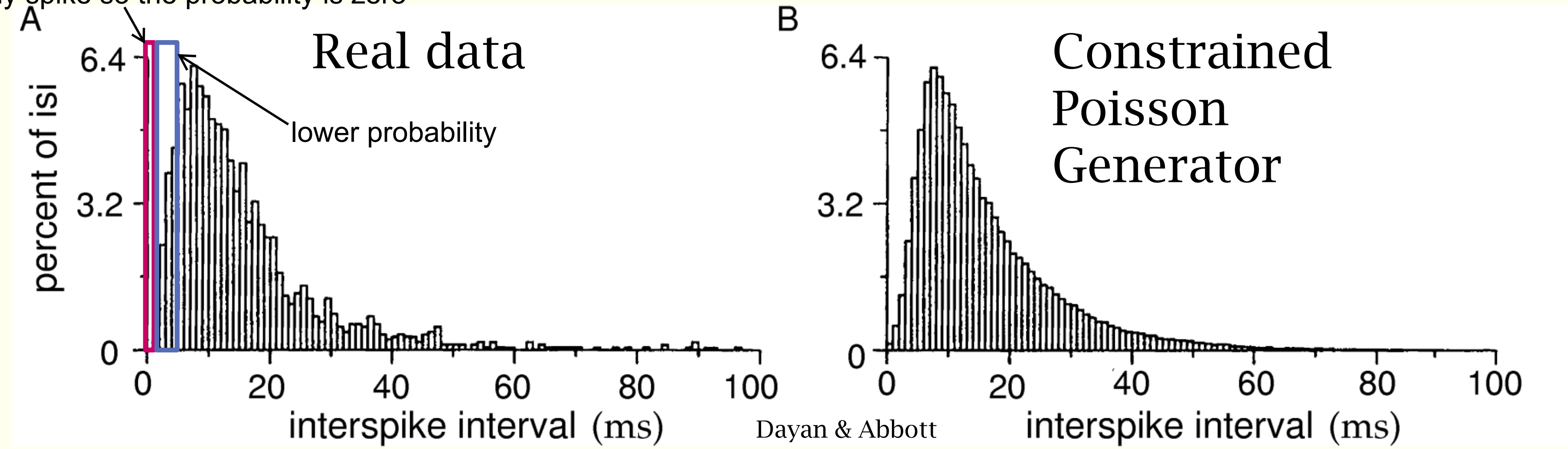
Relative refractory period: due to the K^+ voltage-gated channels. A new action potential can be produced, but it requires a stronger depolarization → it's less likely to occur

Limitations of the Poisson generator - 2

- It does not consider the refractory periods
- In the actual neuron, the minimum inter-spike distance is constrained
- We can build a more complex (and realistic) generator including such constraints:

hard contraint for distances after 1ms, cannot have any spike so the probability is zero

in this case we introduce constraints and so the 2 distributions are more similar



Dayan & Abbott

References

- Dayan & Abbott:
  - Chapter 1.4 (Spike Train Statistics; The Homogeneous Poisson Process, The Poisson Spike Generator, Comparison with Data)

Self-evaluation

1. When the occurrence of each spike is independent from the others, is the firing rate *r* sufficient to compute the probabilities for all possible action potential sequences?
2. In a Poisson process, when *r* increases, higher values of *n* are more or less likely?
3. Long inter-spike intervals (*isi*) have a probability that falls with their duration according to which mathematical law?
4. What are the differences between the distribution of *isi* in real data and in simulated data produced by a Poisson generator? How can we reduce them?