Signal & Data Analysis in Neuroscience 2020

Part 3: Poisson processes

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Outline

- Spike train statistics
- The Poisson process
- Beyond Poisson

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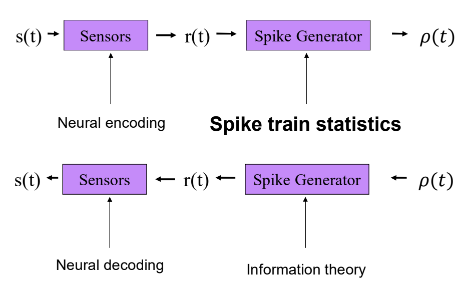
The neuronal transformation



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The problem

- So, we got a spike train…
  - What does it encode?
  - Is it surprising?
  - How does it compare to other spike trains?
- To answer such questions we need a statistical model for the spike train…

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Spike-train statistics

- The relationship between spike and stimulus is stochastic. In an interval Δt: $P(t)=p(t)\cdot\Delta t$
- A series of spikes described as stochastic events: $P(t_1,t_2,\ldots,t_n) = p(t_1,t_2,\ldots,t_n)\cdot(\Delta t)^n$
- **General process**: the probability of a spike can depend on the whole history: $P(t_n|t_1,\ldots,t_{n-1})$
- **Renewal process**: depends on the time of the last spike, $P(t_n|t_1,\ldots,t_{n-1}) = P(t_n|t_{n-1})$
- **Poisson Process**: independent of the spike history, $P(t_n|t_1,\ldots,t_{n-1}) = P(t_n)$

P → probability
p → probability density function (pdf)

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Outline

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- The Poisson process
- Assessing a Poisson process

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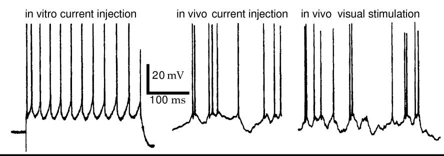
Poisson process

- Generation of each spike depends **only** on a driving signal, r(t) → the generation of each spike is independent of all other spikes → **independent spike hypothesis** leading to a Poisson process.
- Spike generation is highly reliable and deterministic, as has been demonstrated by countless numbers of in-vitro studies.
- The noise in in-vivo neural responses is believed to result from the fact that synapses are very unreliable, not the spike generator!



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Types of Poisson processes

- Homogeneous Poisson process
  - Constant firing rate → r
- Inhomogeneous Poisson process
  - Time dependent firing rate → r(t)

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Homogeneous Poisson process I

• Mean firing rate of a cell is constant i.e. *r(t)* = *r* → Every sequence of *n* spikes over the same, fixed time, interval has an equal probability.

• Thus, the spike train with a probability $P[t_1,t_2,\ldots,t_n]$ can be expressed by a probability function that considers only the number of spikes within a duration T → $P_T[n]$

$$P[t_1, t_2, \ldots, t_n] = n!\, P_T[n] (\frac{\Delta t}{T})^n$$

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Homogeneous Poisson process II

Assessing $P_T[n]$

- Divide the time *T* into *M* bins of size $\Delta t = T/M$
- We assume that Δt is small enough such that we never get two spikes within any one bin.
- $P_T[n]$ depends on the following factors:
  1. The probability of generating n spikes within *M* bins
  2. The probability of not generating spikes in the remaining bins
  3. Combinatorial factor equal to the number of ways of putting *n* spikes into *M* bins

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Homogeneous Poisson process III

1. The probability of a single spike occurring in a specific bin is $r\Delta t$ → The probability of *n* spikes appearing in *n* specific bins is $(r\Delta t)^n$
2. The probability of not having a spike in a given bin is $1-r\Delta t$ → The probability of having the remaining *M-n* bins without any spikes in them is $(1-r\Delta t)^{M-n}$

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Homogeneous Poisson process IV

3. The number of ways of putting *n* spikes into *M* bins is given by the binomial coefficient

$$\binom{M}{n} = \frac{M!}{(M-n)!\,n!}$$

As a result we get

$$P_T[n] = \lim_{\Delta t \to 0} \frac{M!}{(M-n)!\,n!} (r\Delta t)^n (1-r\Delta t)^{M-n}$$

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Homogeneous Poisson process V

For $\Delta t \to 0$ *M* grows without bound $(M = T/\Delta t)$

Thus, we can approximate $M - n \approx M$

$$\lim_{\Delta t \to 0} (1 - r\Delta t)^{M-n} = \lim_{\Delta t \to 0} \left((1 - r\Delta t)^{\frac{1}{\Delta t}} \right)^{T} =$$

$$\lim_{\Delta t \to 0} \left((1 - r\Delta t)^{\frac{1}{-r\Delta t}} \right)^{-rT} = \lim_{\varepsilon \to 0} \left((1 + \varepsilon)^{\frac{1}{\varepsilon}} \right)^{-rT} = e^{-rT}$$

$\varepsilon = -r\Delta t$

$lim_{\varepsilon \to 0}\left((1+\varepsilon)^{\frac{1}{\varepsilon}}\right) = e$

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Homogeneous Poisson process VI

For large *M*:

$$\frac{M!}{(M-n)!} \approx M^n = (T/\Delta t)^n$$

As a result, the original formula:

$$P_T[n] = \lim_{\Delta t \to 0} \frac{M!}{(M-n)!\,n!} (r\Delta t)^n (1 - r\Delta t)^{M-n}$$

may be presented as the Poisson distribution

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

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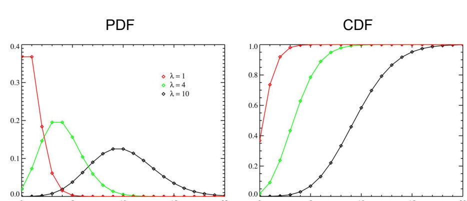
The Poisson distribution

$$\lambda = r \cdot T \qquad P(n) = \frac{\lambda^n}{n!} e^{-\lambda}$$



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Properties of the Poisson process

Mean spike count: $\mu_n = rT$

Variance of spike count: $\sigma_n^2 = rT$

Thus, the ratio of the variance and the mean is constant: $\frac{\sigma_n^2}{\mu_n} = 1$

The proportion between the variance and mean is also called **Fano factor**.

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Homogeneous Poisson process Interspike interval distribution I

Suppose a spike occurs at time t_i , the probability of a HPP generating the next spike in the interval

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

for small Δ*t*, is the probability that no spike is fired for a time *t*, times the probability of generating a spike within the following small interval Δ*t* *(r*Δ*t)*.

$$P_\tau[0] = \frac{(r\tau)^0}{0!} e^{-r} \ = e^{-r}$$

$$P[\tau \leq t_{i+1} - t_i < \tau + \Delta t] = r\Delta t P_\tau[0] = r\Delta t e^{-r\tau}$$

$$p.d.f. \to p[\tau \leq t_{i+1} - t_i < \tau + \Delta t] = re^{-r\tau} \to Exp.dist.$$

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Homogeneous Poisson process Interspike interval distribution II

Mean interspike interval: $\langle \tau \rangle = \int_0^\infty \tau r e^{-r\tau} d\tau = \frac{1}{r}$

Variance of interspike intervals:

$$\sigma_\tau^2 = \int_0^\infty \tau^2 r e^{-r\tau} d\tau - \langle \tau \rangle^2 = \frac{1}{r^2}$$

Coefficient of variation: $C_V = \frac{\sigma_\tau}{\langle \tau \rangle} = 1$

In renewal processes, for large samples the Fano factor of the spike count in equal to C_V^2 of the interspike interval.

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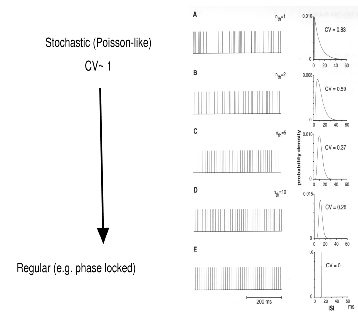
Coefficient of variation



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Inhomogeneous Poisson Process I

• Firing rate depends on time → different sequences of *n* spikes occur with different probabilities → $p(t_1,t_2,\ldots,t_n)$ depends on the spike times.

• Spikes are still generated independently by an inhomogeneous Poisson process → their times enter into $p(t_1,t_2,\ldots,t_n)$ only through the time-dependent firing rate $r(t)$

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Inhomogeneous Poisson Process II

Divide the interval $[t_i,t_{i+1}]$ in M segments of length Δ t.
The probability of no spikes in $[t_i,t_{i+1}]$ is

$$
\begin{aligned}
P[\text{nospikes}] &= \prod_{m=1}^{M} \{1 - r(t_i + m\Delta t)\Delta t\} \\
\ln P[\text{nospikes}] &= \sum_{m=1}^{M} \ln\{1 - r(t_i + m\Delta t)\Delta t\} \\
&\approx -\sum_{m=1}^{M} r(t_i + m\Delta t)\Delta t \\
&\approx -\int_{t_i}^{t_{i+1}} dt r(t)
\end{aligned}
$$

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Inhomogeneous Poisson Process III

The probability of spikes at times $t_1,\ldots,t_n$ is:

$$\begin{aligned} P[t_1,t_2,\ldots,t_n] &= \exp\left(-\int_0^{t_1} dt r(t)\right) r(t_1) \exp\left(-\int_{t_1}^{t_2} dt r(t)\right) \\ & \quad r(t_2)\ldots r(t_n) \exp\left(-\int_{t_n}^{T} dt r(t)\right) \\ &= \exp\left(-\int_0^{T} dt r(t)\right) \prod_i r(t_i) \end{aligned}$$

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Renewal process

- **Poisson Process**: independent of the spike history, $P(t_n|t_1,\ldots,t_{n-1})=P(t_n)$
- **Renewal process**: depends on the time of the last spike, $P(t_n|t_1,\ldots,t_{n-1})=P(t_n|t_{n-1})$
- Dependence is only upon the last spike.
- Each spike resets the system.

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Poisson process: deviations

Certain features of neuronal firing violate the independent spike hypothesis.

1. Following the generation of an action potential, there is an interval of time known as the absolute refractory period during which the neuron cannot fire another spike.
2. For a longer interval known as the relative refractory period, the likelihood of a spike being fired is much reduced.
3. Bursting is another non-Poisson feature of neuronal spiking.

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Poisson + Refractory period

- **Absolute refractory period** – reset instantaneous firing rate to 0 for t_r.
- **Relative refractory period** – gradual return to original rate.

$$r(t) = k^{(\tau_r+1-t)} \cdot r \qquad t \le \tau_r$$

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Gamma function

- Gamma function is an extension of the factorial function to complex and non-integer numbers.

$$\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt \qquad if\ \mathrm{Re}(z) > 0$$

- For integers

$$\Gamma(z) = (z-1)!$$

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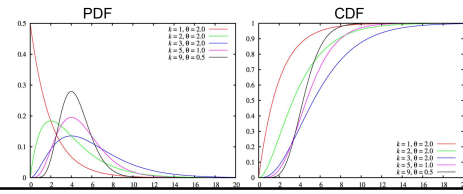
The Gamma distribution

Sum of k exponentially distributed random variables, each of which has mean θ.

$$f(x;k,\theta) = x^{k-1}\frac{e^{-x/\theta}}{\theta^k\,\Gamma(k)} \text{ for } x>0 \text{ and } k,\theta>0.$$

Exp(θ) = Gamma(1,θ) (θ=1/λ)
$\chi^2(\nu)$ = Gamma(ν/2,2)



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Suggested reading

- Theoretical neuroscience, *Dayan P & Abbott LF*, Chapter 1.4
- Neuronal spike trains and stochastic point processes, I. The single spike train, *Perkel DH, Gerstain GL, Moore GP*, Biophysical Journal 1967
- Methods in neuronal modeling, Ed. *Koch C & Segev I*, Chapter 9

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Appendix: Poisson spike generator

1. The probability of firing a spike within a short interval is $r\Delta t$

As long as the rate varies slowly with respect the time interval. The rate function $r(t)$ is sampled with a sampling interval of Δt to produce a discrete-time sequence $r[i]$.

The program can simply progress in time through small time steps Δt and generate, at each time step, a random variable x_{rand} between 0 and 1 and compare this with the probability of firing a spike.

$$r_i\Delta t \begin{cases} > x_{rand} & \text{fire a spike} \\ \le x_{rand} & \text{nothing} \end{cases}$$

2. Using ISI: Choose a series of random numbers q. Set interspike intervals of $-log(q)/r$ works only for constant r (homogeneous process)

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Appendix:
Mean of a Poisson variable

$$P(X = n) = \frac{\lambda^n}{n!} e^{-\lambda}$$

$$E(X) = \sum_{n\geq 0} n \cdot \frac{\lambda^n}{n!} e^{-\lambda} = \lambda \cdot e^{-\lambda} \cdot \sum_{n\geq 1} \frac{\lambda^{n-1}}{(n-1)!}$$

$$= \lambda \cdot e^{-\lambda} \cdot \sum_{k\geq 0} \frac{\lambda^k}{k!} \qquad (k = n-1)$$

$$= \lambda \cdot e^{-\lambda} \cdot e^{\lambda} \qquad (Taylor)$$

$$= \lambda$$

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Appendix:
Variance of a Poisson variable

$$P(X = n) = \frac{\lambda^n}{n!} e^{-\lambda}$$

$$E(X^2) = \sum_{n\geq 0} n^2 \cdot \frac{\lambda^n}{n!} e^{-\lambda} = \lambda \cdot e^{-\lambda} \cdot \sum_{n\geq 1} n \frac{\lambda^{n-1}}{(n-1)!}$$

$$= \lambda \cdot e^{-\lambda} \cdot \left(\sum_{n\geq 1} (n-1) \frac{\lambda^{n-1}}{(n-1)!} + \sum_{n\geq 1} \frac{\lambda^{n-1}}{(n-1)!}\right)$$

$$= \lambda \cdot e^{-\lambda} \cdot \left(\lambda \cdot \sum_{n\geq 2} \frac{\lambda^{n-2}}{(n-2)!} + \sum_{n\geq 1} \frac{\lambda^{n-1}}{(n-1)!}\right)$$

$$= \lambda \cdot e^{-\lambda} \cdot \left(\lambda \cdot \sum_{k\geq 0} \frac{\lambda^k}{k!} + \sum_{k\geq 0} \frac{\lambda^k}{k!}\right)$$

$$= \lambda \cdot e^{-\lambda} \cdot (\lambda \cdot e^{\lambda} + e^{\lambda}) = \lambda^2 + \lambda$$

$$Var(X) = E(X^2) - (E(X))^2 = \lambda^2 + \lambda - \lambda^2 = \lambda$$

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