

Poisson Processes for Neuroscientists

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This note is an introduction to the key properties of Poisson processes, which are extensively used to simulate spike trains. For being mathematical idealizations, Poisson processes rely on some simplifying assumptions that limit their scope of application. The best way to understand these limitations is perhaps by constructing the Poisson process gradually starting from the intuitively clear situation of independent spiking in a finite number of time bins. After following this approach to define Poisson processes, we conclude by discussing various methods to simulate Poisson processes numerically.

1 Independent spiking in time bins

We partition the time interval $[0, T]$ into n identical time bins B_i , $1 \leq i \leq n$. We use this partition to represent spike trains as binary sequences X_i , encoding the presence ($X_i = 1$) or the absence of a spike ($X_i = 0$) in a time bin B_i . Such a representation implicitly assumes that the bins duration $\Delta t = T/n$ is short enough to ensure that at most one spike may occur in a given time bin. We are going to model the spike generation in these bins as a random process with the least possible structure. Specifically, we are going to assume that a (single) spike may be generated independently in each bin with the same probability q , $0 \leq q \leq 1$. Simulating such a binary vector X in Matlab is easily achieved by using the command `x = double(rand(1, n) < q)`, where `double` is utilized to convert logical values into numerical values. In this section, we introduce two natural spike trains' statistics and their corresponding distributions: 1) the spike counts over a finite time windows, which follows a binomial distribution and 2) the inter-spike intervals (ISI) for infinite overall duration ($T \rightarrow \infty$), which follows a geometric distribution.

1.1 Binomial distribution

The number of spikes occurring in n bins is a random integer K satisfying $0 \leq K = \sum_{i=1}^n X_i \leq n$. By independence of the Bernoulli variables X_i , the probability of observing k spikes in n bins is given by the binomial distribution

$$\mathbb{P}(K = k) = p(k) = \binom{n}{k} q^k (1 - q)^{n-k},$$

where the binomial coefficients $\binom{n}{k}$ are counting the number of combinations of k spikes in n bins. Observe that the binomial distribution is indeed a probability distribution as we have

$$\sum_{k=0}^n p(k) = \sum_{k=0}^n \binom{n}{k} q^k (1 - q)^{n-k} = (q + 1 - q)^n = 1.$$

The binomial probability distribution function is available in Matlab via the command `binopdf(k, n, q)`. You can check that the following code produces an histogram that closely matches the binomial distribution:

```
nsample=1000;  
n=100;  
q=0.02;  
k=zeros(1,nsample);  
for i=1:nsample  
    k(i)=sum(double(rand(1,n)<q));  
end  
h=hist(k,0:n)/nsample;  
figure()  
bar(h);  
hold on  
plot(binopdf(0:n,n,q))  
hold off
```

Matlab can directly generate binomial samples using the command `binornd(n, q)`. The mean and the variance of the binomial distribution are obtained from the mean and the variance of the independent Bernoulli variables X_i

$$\begin{aligned}\mathbb{E}(K) &= \mathbb{E}\left(\sum_{i=1}^n X_i\right) = \sum_{i=1}^n \mathbb{E}(X_i) = nq, \\ \mathbb{V}(K) &= \mathbb{V}\left(\sum_{i=1}^n X_i\right) = \sum_{i=1}^n \mathbb{V}(X_i) = nq(1 - q).\end{aligned}$$

These formula are intuitively clear: the expected number of spikes increases linearly with the duration of the time window, while the variability of the spike counts is maximum when it is equally likely to spike or not. Moreover, if $q = 0$ or $q = 1$, there is no randomness since we only get 0 or 1 and the variance vanishes.

1.2 Geometric distribution

The number of bins separating two consecutive spikes is a measure of the ISI length L , which is a positive random integer number. However, by contrast with spike counts K , the length L is not well-defined in a finite time interval $[0, T]$. For this reason, we are now considering an infinite time window ($T = \infty$). Then by independence of the the Bernoulli variables X_i , the probability to observe $l - 1$ consecutive bins with no spikes before observing a spike in the l -th bin is

$$\mathbb{P}(L = l) = p(l) = (1 - q)^{l-1}q,$$

which is the same as the geometric probability function of parameter q . This probability function is given in Matlab by the command `geopdf(1, q)`. You can check that the following code produces an histogram that closely matches the geometric distribution:

```
n=100000;
q=0.02;
spikes=double(rand(1,n)<q);
ISI=diff(spikes(find(spikes==1)));
M=max(ISI);
N=length(ISI);
h=hist(k,0:M)/L;
figure()
bar(h);
hold on
plot(geopdf(0:M,q))
hold off
```

Matlab can directly generates geometric samples using the command `geornd(q)`. Note that this distribution is defined over the range of all integers to allow for the possibility of very long ISI. Still, the distribution is normalized to one as expected for a probability function:

$$\sum_{l=0}^{\infty} p(l) = \sum_{l=1}^{\infty} (1 - q)^{l-1}q = \frac{q}{1 - (1 - q)} = 1.$$

The mean and the variance of the geometric distribution of parameter q can be computed via many different routes. Perhaps the most direct route is the following

$$\begin{aligned}
\mathbb{E}(L) &= \sum_{l=1}^{\infty} l(1-q)^{l-1}q, \\
&= -p \sum_{l=1}^{\infty} \frac{d}{dp} \left((1-q)^l \right), \\
&= -p \frac{d}{dq} \left(\sum_{l=1}^{\infty} (1-q)^l \right), \\
&= -p \frac{d}{dq} \left(\frac{1}{q} \right), \\
&= \frac{1}{q},
\end{aligned}$$

where we use the fact that we can interpret the mean ISI as the derivative of a simple function with respect to the parameter q . A similar calculation yields the variance:

$$\mathbb{V}(L) = \frac{1-q}{q^2}.$$

The key aspect of the above formulae is that the expected ISI is inversely proportional to the spiking probability, which is in keeping with our intuition. The less probable spiking events are, the longer silent time periods in between these events and the mean and the variance actually diverge when $q \rightarrow 0$.

2 Limit of infinitely small bins

Simulating spike trains as binary sequences of Bernoulli variables X_i has led us to consider two related statistics: spike counts and ISIs. In the previous section, we have shown that these statistics obey simple probability distributions that crucially depends on the bin spiking probability q . The spiking probability q can be seen as the rate of spiking events per bin. In the following, we make use of this observation to make our model independent of the binning size by considering the limit of infinitely short binning intervals $\Delta t \rightarrow 0$. Taking the binomial distribution and the geometric distribution through that limit will lead us to introduce two important probability distributions: the Poisson distribution defined for positive integers (counts) and the exponential distribution defined for all positive numbers (time).

2.1 Poisson distribution

We want to establish the distribution of spike counts occurring in a finite time window $[0, T]$ and in the limit of small bins $\Delta t \rightarrow 0$. Interpreting q as the rate of spiking event per bin suggests to introduce r , the rate of spikes per unit of time which satisfies $q = r\Delta t = rT/n$. For finite bin sizes, the spike-count probability is given by the binomial distribution

$$\mathbb{P}(K = k) = p(k) = \binom{n}{k} \left(\frac{rT}{n}\right)^k \left(1 - \frac{rT}{n}\right)^{n-k},$$

and considering the limit of small bins is equivalent to take the limit $n \rightarrow \infty$ in the above formula. To evaluate this limit, we first rearrange the terms to get

$$\begin{aligned} p(k) &= \frac{n!}{k!(n-k)!} \left(\frac{rT}{n}\right)^k e^{(n-k)\ln(1-\frac{rT}{n})}, \\ &= \frac{n!}{(n-k)!n^k} \frac{(rT)^k}{k!} e^{(n-k)\ln(1-\frac{rT}{n})}, \\ &= \frac{n}{n} \frac{n-1}{n} \dots \frac{n-k+1}{n} \frac{(rT)^k}{k!} e^{(n-k)\ln(1-\frac{rT}{n})}. \end{aligned}$$

For fixed k , we have the limits

$$\begin{aligned} (n-k)\ln\left(1 - \frac{rT}{n}\right) &\xrightarrow{n \rightarrow \infty} -rT, \\ \frac{n}{n} \frac{n-1}{n} \dots \frac{n-k+1}{n} &\xrightarrow{n \rightarrow \infty} 1, \end{aligned}$$

so that the limit probability to count k spikes in a time window $[0, T]$ is given by

$$p(k) = \frac{(rT)^k}{k!} e^{-rT},$$

which is that of a Poisson distribution of parameter rT . This parameter is in fact the mean number of spikes in a time window of duration T with spiking rate r :

$$\mathbb{E}(K) = \lim_{n \rightarrow \infty} \mathbb{E}\left(\sum_{i=1}^n X_i\right) = \lim_{n \rightarrow \infty} \sum_{i=1}^n \mathbb{E}(X_i) = \lim_{n \rightarrow \infty} n \frac{rT}{n} = rT.$$

A similar calculation shows that the variance of the Poisson distribution is equal to its mean:

$$\mathbb{V}(K) = \lim_{n \rightarrow \infty} \mathbb{V}\left(\sum_{i=1}^n X_i\right) = \lim_{n \rightarrow \infty} \sum_{i=1}^n \mathbb{V}(X_i) = \lim_{n \rightarrow \infty} n \frac{rT}{n} \left(1 - \frac{rT}{n}\right) = rT.$$

The fact that $\mathbb{E}(K) = \mathbb{V}(K)$ is an important property of the Poisson distribution that can easily be checked on time series data. Matlab can directly generate Poisson-distributed samples using the command `poissrnd(q)`, where q is the mean count.

Another important property of Poisson variables is that the sum of two independent Poisson variables K_1 and K_2 , say with parameters r_1T and r_2T , is still a Poisson variable but of parameter $(r_1 + r_2)T$. To see why, we first have to realize that the probability distribution of the sum of two independent variables K_1 and K_2 can be computed as a convolution of their individual probability distributions p_1 and p_2 . Indeed, we have:

$$\mathbb{P}(K_1 + K_2 = k) = p(k) = \sum_{k_1=1}^k p_1(k_1)p_2(k - k_1) = (p_1 \star p_2)(k)$$

From there, we can use the formula for Poisson distributions together with the binomial law to show that

$$\begin{aligned} (p_1 \star p_2)(k) &= \sum_{k_1=1}^k \frac{(r_1T)^{k_1}}{k_1!} e^{-r_1T} \frac{(r_2T)^{(k-k_1)}}{(k-k_1)!} e^{-r_2T} \\ &= \sum_{k_1=1}^k \frac{1}{k_1!(k-k_1)!} (r_1T)^{k_1} (r_2T)^{(k-k_1)} e^{-(r_1+r_2)T}, \\ &= \frac{e^{-(r_1+r_2)T}}{k!} \sum_{k_1=1}^k \binom{k}{k_1} (r_1T)^{k_1} (r_2T)^{(k-k_1)}, \\ &= \frac{((r_1 + r_2)T)^k}{k!} e^{-(r_1+r_2)T}. \end{aligned}$$

2.2 Exponential distribution

We want to establish the distribution of ISIs over an infinite length time window and in the limit of small bins $\Delta t \rightarrow 0$. For finite bin size, measuring ISIs in unit of bins leads to considering geometrically distributed random integers L . In the limit of small bins $\Delta t \rightarrow 0$, ISIs take increasingly larger values and working directly on the distribution of L is not well posed when considering the limit $\Delta t \rightarrow 0$. The variable that is suited to our investigation is τ , the duration of the ISI measured in time unit, which satisfies $\tau = LT/n$. Although this variable is defined as a multiple of the bin size T/n for finite n , we expect τ to be defined on the set of all positive real numbers in the limit $n \rightarrow \infty$. This observation suggests to take a slightly different approach than for the Poisson distribution by working on the

cumulative function rather than on the probability function. For finite bin size, the ISI obeys the geometric cumulative probability function given by:

$$\mathbb{P}[L \leq \lambda] = \sum_{l=0}^{\lambda} p(l) = \sum_{l=1}^{\lambda} (1-q)^{l-1} q = \frac{1 - (1-q)^{\lambda}}{1 - (1-q)} = \frac{1 - (1-q)^{\lambda}}{q}.$$

Just as for the Poisson distribution, we can express in the above expression the bin spiking probability q in terms of the rate of spiking per unit of time r via $q = rT/n$. Correspondingly, λ , the ISI length in bin size can also be written in terms of the ISI length in unit of time t via $\lambda = nt/T$. Thus, we can write the cumulative probability distribution for the ISI measured in unit of time and take the limit of small bins $\Delta t \rightarrow 0$ to obtain:

$$\mathbb{P}[\tau \leq t] = \mathbb{P}[L \leq \lambda] = 1 - (1-q)^{\lambda} = 1 - \left(1 - \frac{rT}{n}\right)^{\frac{nt}{T}} \xrightarrow{n \rightarrow \infty} 1 - e^{-rt}. \quad (1)$$

Observe that in the limit of small bins $\Delta t \rightarrow 0$, the resulting cumulative distribution is that of an exponential distribution and is independent of T . The exponential probability distribution

$$p(t) = \frac{d}{dt} \mathbb{P}[\tau \leq t] = \frac{e^{-rt}}{r}, \quad (2)$$

is given by the command `exppdf(t, r)`, while exponential samples are generated by using the command `exprnd(r)`. The mean and the variance of the exponential distribution can be recovered from the mean and the variance of the geometric distribution of parameter q by writing $q = rT/n$ and taking the limit $n \rightarrow \infty$:

$$\begin{aligned} \mathbb{E}[\tau] &= \lim_{n \rightarrow \infty} \mathbb{E}[LT/n] = T \lim_{n \rightarrow \infty} \frac{\mathbb{E}[L]}{n} = T \lim_{n \rightarrow \infty} \frac{1}{nq} = 1/r, \\ \mathbb{V}[\tau] &= \lim_{n \rightarrow \infty} \mathbb{V}[LT/n] = T^2 \lim_{n \rightarrow \infty} \frac{\mathbb{V}[L]}{n^2} = T^2 \lim_{n \rightarrow \infty} \frac{1-q}{n^2 q^2} = 1/r^2. \end{aligned}$$

Perhaps the most important property of the exponential distribution is the so-called “memoryless” property. Informally stated, this property tells us that at any given time, the time one has to wait for the next spike to occur is independent from the time when the last spike took place. More formally, suppose with no loss of generality that at time s , the last spike occurred at time 0. Then the probability that the next spike occurs after a duration t is

$$\mathbb{P}[\tau > t + s | \tau > s] = \frac{\mathbb{P}[\tau > t + s]}{\mathbb{P}[\tau > s]} = \frac{e^{-r(t+s)}}{e^{-rs}} = e^{-rt} = \mathbb{P}[\tau > t],$$

which is independent of s as announced.

By contrast with Poisson variables, the sum of two independent exponential times, say τ_1 and τ_2 with same rate r , is not an exponential variable. To see why, remember that by independence, the probability distribution $p^{(2)}$ of $\tau_1 + \tau_2$ is given by the convolution of an exponential distribution with itself:

$$p^{(2)}(t) = \int_0^t r e^{-rs} r e^{-r(t-s)} ds = r^2 e^{-rt} \int_0^t ds = r^2 t e^{-rt}.$$

The above probability distribution, which represents the time separating two consecutive spikes, is that of a Gamma distribution. Gamma distributions gives the general form of the distribution of times separating n consecutive spikes as:

$$p^{(n)}(t) = \frac{r(rt)^{n-1} e^{-rt}}{(n-1)!}.$$

3 Poisson spiking model

Now that we are equipped with the Poisson distribution and the exponential distribution, we have all the ingredients to define Poisson processes, which are the simplest stochastic point processes amenable to represent spike trains in continuous time. Poisson processes over the time axis are entirely determined by the time-dependent rate of spiking $r(t)$. Although this rate is in general a function of time, we only show elementary properties of Poisson processes for constant rate of firing r , i.e. for homogeneous Poisson processes. However, we will state core formulae for the generic case of an inhomogeneous Poisson process

3.1 Definition via Poisson distributions

Poisson processes are point processes that count the number of spikes in an given time window of the time axis. As such, a Poisson process N maps a time interval, e.g. $(s, t]$, with $s < t$, onto a random positive integer variable denoted $N(s, t]$. The variable $N(s, t]$ represents the number of spikes occurring in $(s, t]$. The defining properties of a Poisson process with unit rate is that the random count $N(s, t]$ follows a Poisson distribution with mean $t - s$ and that for times $s < t < u$, the counts $N(s, t]$ and $N(t, u]$ are independent. These are natural properties if we consider a Poisson process as the limit of independent spiking in time bins of vanishing durations. Indeed, the limit of a binomial distribution is then a Poisson distribution of equal mean and the numbers of spikes happening in disjoint time windows are independent by construction (the presence or absence of a spike is decided by an

independent coin toss). When the time interval starts in 0, the convention is to write $N(0, t] = N_t$ so that we have $N(s, t] = N_t - N_s$.

Why is a Poisson process different than a Poisson variable? The answer is that a Poisson process N_t is a collection of Poisson variables indexed by time t and organized in a fashion that is consistent with time ordering. To understand this point, consider two time windows $(s, t]$ and $(u, v]$ with $s < t$ and $v < u$. If $t < u$, the time windows are disjoint, i.e. $(s, t] \cap (u, v] = \emptyset$, and spikes happen independently in each time windows. Suppose now that $u < t$, then the time windows are overlapping, i.e. $(s, t] \cap (u, v] \neq \emptyset$, and we expect the counts $N(s, t]$ and $N(u, v]$ to be dependent. Indeed, if many spikes happen in $(s, t]$, we expect that some of these spikes happens in $(s, t] \cap (u, v]$, which means that many spikes are also likely to happen in $(u, v]$. Poisson processes capture this dependence that can be quantified via the covariance between $N(s, t]$ and $N(u, v]$.

To show this, we denote the overlap between time windows as $(s, t] \cap (u, v] = B$ with length b , and from there, we define new time windows $A = (s, t] \setminus B = A$ and $C = (u, v] \setminus B$ with length a and b , respectively. The spike counts in time windows A , B , and C , denoted by N_a , N_b , N_c , are independent Poisson variables of parameters a , b , and c , respectively, and satisfy $N_{s,t} = N_a + N_b$ and $N_{u,v} = N_b + N_c$. Moreover, we have:

$$\begin{aligned}
\mathbb{E}[(N_a + N_b)(N_b + N_c)] &= \mathbb{E}[N_a N_b] + \mathbb{E}[N_a N_c] + \mathbb{E}[N_b^2] + \mathbb{E}[N_b N_c] , \\
&= \mathbb{E}[N_a] \mathbb{E}[N_b] + \mathbb{E}[N_a] [N_c] + \mathbb{E}[N_b^2] + \mathbb{E}[N_b] [N_c] , \\
&= ab + ac + \mathbb{E}[N_b^2] + bc , \\
&= \mathbb{E}[N_b^2] - \mathbb{E}[N_b]^2 + ab + ac + b^2 + bc , \\
&= \mathbb{V}[N_b] + (a + b)(b + c) .
\end{aligned}$$

Thus, the covariance between $N_{s,t}$ and $N_{u,v}$ can be computed as

$$\begin{aligned}
\text{Cov}(N_{s,t}, N_{u,v}) &= \mathbb{E}[N_{s,t} N_{u,v}] - \mathbb{E}[N_{s,t}] \mathbb{E}[N_{u,v}] , \\
&= \mathbb{E}[(N_a + N_b)(N_b + N_c)] - \mathbb{E}[N_a + N_b] \mathbb{E}[N_b + N_c] , \\
&= \mathbb{V}[N_b] + (a + b)(b + c) - (a + b)(b + c) , \\
&= \mathbb{V}[N_b] , \\
&= \min(t, v) - \max(s, u) ,
\end{aligned}$$

showing that the covariance between overlapping time windows is equal to the mean number of spikes occurring in the overlapping portion of both windows.

3.2 Definition via exponential distributions

The above definition of Poisson processes may seem a little bit abstract. In particular, it may not be apparent how one can estimate the probability of a specific spike trains $0 \leq t_1 < t_2 < \dots < t_n \leq T$. This remark leads us to define Poisson processes in a different, albeit entirely equivalent fashion, by specifying the probability distribution of spike trains. From our analysis of ISI statistics, we know that consecutive spikes are separated by independent exponentially distributed (memoryless) times. Thus, denoting $t_0 = 0$, we have

$$\begin{aligned} p(t_1, \dots, t_n) &= \prod_{i=1}^n p(t_i | t_{i-1}) \mathbb{P}(t_{n+1} > T | t_n), \\ &= \prod_{i=1}^n r e^{-r(t_i - t_{i-1})} e^{-r(T - t_n)}, \\ &= r^n e^{-rT}, \end{aligned}$$

which is independent of the spike timing and only depends on the spike count n . What this result tells us is that if one assumes a given spike count n , spiking times are uniformly distributed in the considered time window. At this point, it is important to remember that we have assume a specific time ordering $0 \leq t_1 < t_2 < \dots < t_n \leq T$, which implies that the probability for the spike train to have n spikes is

$$\begin{aligned} &\int_0^T dt_1 \int_{t_1}^T dt_2 \dots \int_{t_n}^T dt_{n-1} p(t_1, \dots, t_n) \\ &= \left(\int_0^T dt_1 \int_{t_1}^T dt_2 \dots \int_{t_n}^T dt_{n-1} \right) r^n e^{-rT}, \\ &= \frac{r^n}{n!} e^{-rT}, \end{aligned}$$

which is the probability of observing n spikes from a Poisson distribution with parameter rT .

3.3 Inhomogeneous Poisson processes

The construction of homogeneous Poisson processes directly carries out to the case of a time-dependent rate function r . To understand why, one just has to realize that all the arguments developed in this note are valid if one has considered a bin-dependent spiking probability q_i in defining independent spiking in time bins. From there, the time-dependent spiking rate can be recovered via

$r(t) = \lim_{n \rightarrow \infty} q_{nt/T}(n/T)$. For inhomogeneous Poisson processes, the mean and covariance formulae reads

$$\mathbb{E}[N_{s,t}] = \int_s^t r(u) du, \quad \text{and} \quad \text{Cov}(N_{s,t}, N_{u,v}) = \int_{\min(t,v)}^{\max(s,u)} r(w) dw,$$

and the probability to observe a spike train $0 \leq t_1 < t_2 < \dots < t_n \leq T$ is

$$p(t_1, \dots, t_n) = \prod_{i=1}^n r(t_i) e^{-\int_0^T r(s) ds}.$$

3.4 Simulation of Poisson processes

Homogeneous Poisson processes are easily simulated by generating successive exponential ISIs. For instance, given a time window $[0, T]$, the following code generate a spike train with firing rate r :

```
T=1000;
t=0;
time=[];
while (t<T)
    isi=exprnd(r);
    t=t+isi;
    if (t<T)
        time=[time,t];
    end
end
```

Another method is to simulate first the number of spiking events n taking place in the time window $[0, T]$ and then to sample uniformly points within that time window:

```
T=1000;
n=poissrnd(rT)
time=zeros(n);
for i=1:n
    time(i)=rand()*T;
end
```

Scaling all the time by a scalar value $1/a$ transform the original spike train N_t defined over $[0, T]$ into a spike train $N_{t/a}$ defined on $[0, T/a]$ but with rate ar . Thus, one can produce homogeneous Poisson processes of any rates by simple

time scaling of Poisson processes with unit rate. This idea can be extended to generate inhomogeneous Poisson processes with fluctuating rate $r(t)$ at the cost of considering nonlinear time scaling. This is done by considering the function $R(t) = \int_0^t r(s) ds$, which represents the mean number of spikes in the time window $(0, T]$ and defines a well-posed change of time if the rate function remains positive finite. Then, R is a one-to-one function with inverse function R^{-1} . One can check that if N_t is a Poisson process with unit rate, the rescaled process $N_{R^{-1}(t)}$ is an inhomogeneous Poisson process with rate $r(t)$. For instance, if $r(t) = a$, we have $R(t) = at$ and $N_{R^{-1}(t)} = N_{t/a}$ as expected.

Another method that is extensively used to generate inhomogeneous Poisson process is called “thinning”. It assumes that the rate function r admits an upper bound over the considered time window: $M \geq r(t)$, $0 \leq t \leq T$. Then, one can always simulate an homogeneous Poisson process with rate M over $[0, T]$. Such a process has too many events as for generic time t , we have $M > r(t)$. The idea of thinning is to find a rule to eliminate some of the spiking events of the homogenous Poisson process with rate M so that the remaining events form the realization of our target Poisson process with rate $r(t)$. This is handily done by observing the following rule: keep spiking events occurring at time t with probability $r(t)/M$ and independently of anything else:

```
T=1000;
n=poissrnd(M)
time=[];
for i=1:n
    t=rand()*T;
    if (rand()<r(t)/M)
        time=[time,t];
    end
end
```