Poisson Model of Spike Generation

Professor David Heeger

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In the cortex, the timing of successive action potentials is highly irregular. The interpretation of this irregularity has led to two divergent views of cortical organization. On the one hand, the irregularity might arise from stochastic forces. If so, the irregular interspike interval reflects a random process and implies that an instantaneous estimate of the spike rate can be obtained by averaging the pooled responses of many individual neurons. In keeping with this theory, one would expect that the precise timing of individual spikes conveys little information. Alternatively, the irregular ISI may result from precise coincidences of presynaptic events. In this scenario, it is postulated that the timing of spikes, their intervals and patterns can convey information. According to this view, the irregularity of the ISI reflects a rich bandwidth for information transfer.

In this handout, we take the former point of view, that the irregular interspike interval reflects a random process. We assume that the generation of each spike depends only on an underlying continuous/analog driving signal, $r(t)$, that we will refer to as the instantaneous firing rate. It follows that the generation of each spike is independent of all the other spikes, hence we refer to this as the *independent spike hypothesis.*

If the independent spike hypothesis were true, then the spike train would be completely described a particular kind of random process called a *Poisson process.* Note that even though a Poisson spike train is generated by a random process, some stimuli could still evoke spikes very reliably by forcing the instantaneous firing rate to be very large at particular moments in time so that the probability of firing would then be arbitrarily close to 1.

Certain features of neuronal firing, however, violate the independent spike hypothesis. Following the generation of an action potential, there is an interval of time known as the absolute refractory period during which the neuron can not fire another spike. For a longer interval known as the relative refractory period, the likelihood of a spike being fired is much reduced. Bursting is another non-Poisson feature of neuronal spiking. Some neurons fire action potentials is clusters or bursts, and these tend to be poorly described a purely Poisson spike-generation process. Below, I present ways of extending the Poisson model to account for refractoriness and bursting.

Probability and Random Processes

A *random variable* is a number assigned to every outcome of an experiment. This could be the outcome of the roll of a die, or the number of action potentials generated by a visual neuron during a 1 sec stimulus presentation. The probability of getting each possible outcome is characterized by a *probability density function*. For a fair die, there is a 1/6 probability of getting each possible outcome. The familiar bell-shaped curve of the normal distribution is another example of a probability density function.

The integral of a probability density function is called the *cumulative distribution function*. Cumulative distributions characterize the probability of getting an outcome less than or equal to some specified value. For example, there is a 1/2 probability of getting a roll less than or equal to 3 on a fair die.

A random process is a rule for assigning a function $x(t)$ to every outcome of an experiment. For example, the voltage trace recorded from an intracellular electrode during a 1 sec stimulus presentation might be considered a random process.

Instantaneous Firing Rate

Define $\rho(t)$, the *neural response function*, to be a bunch of impulses, one for each action potential:

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

where k is the total number of spikes in the spike train, and t_i are the times that each spike occurred. The unit impulse signal is defined as:

$$\delta(t) = \begin{cases} 1 & \text{if} \quad t = 0 \\ 0 & \text{otherwise} \end{cases},$$

such that the integral of $\delta(t)$ is one:

$$\int_{-\infty}^{\infty} \delta(t) = 1.$$

We would like to think of the neural response function as a random process. The neural response function is completely equivalent to a list of the spike times in the spike train. Nevertheless, it is useful for re-expressing sums over spikes as integrals over time. For example, we can write the *spike count*, the number of spikes fired between times t_1 and t_2 as the integral:

$$n = \int_{t_1}^{t_2} \rho(t)dt,$$

because each spike contributes 1 to the integral.

The instantaneous firing rate (e.g., of a sensory neuron) can now be formally defined to be the expectation of the neural response function, averaged over an infinite number of repeats (e.g., of

the same stimulus presentation):

$$r(t) = \langle \rho(t) \rangle.$$

In practice, of course, you can not run an infinite number of trials. The function you get by averaging over a finite number of trials, is an estimate of the instantaneous firing rate:

$$r_M(t) = \tfrac{1}{M} \sum_{j=1}^{M} \rho_j(t),$$

where M is the number of trials and $\rho_j(t)$ is the neural response function for each trial. This, of course, is not a continuous function because it is just a sum of δ functions. You get a smooth function only in the formal limit with an infinite number of trials. Typically, when working with real data, you would blur r_M to make it smooth. We do not have to worry about that in this class because the theoretical/computational neuroscientist has the luxury of being able to just make up a continuous function, $r(t)$.

The average spike count can then be defined from the instantaneous firing rate:

$$\langle n \rangle = \int_{t_1}^{t_2} r(t)dt. \tag{1}$$

This is equivalent, of course, to counting the spikes n_j in each of a very large (i.e., infinite) number of repeated trials, and then averaging those spike counts across the trials.

For sufficiently small intervals, when $t_2 = t + \delta t/2$ and $t_1 = t - \delta t/2$, the average spike count can be approximated by $\langle n \rangle = r(t)\delta t$. Furthermore, δt can be reduced until the probability that more than one spike could appear in this interval is small enough to be ignored. In this case, the average spike count is equal to the probability of firing a single spike. That is, the probability of a spike occurring during a given brief time interval is equal to the value of the instantaneous firing rate during that time interval times the length of the interval:

$$P\{1 \text{ spike during the interval } (t - \delta t, t + \delta t)\} = r(t)\,\delta t. \tag{2}$$

Unlike the neural response function which provides a complete description of the neural response, the instantaneous firing rate is a highly reduced description. It is constructed by averaging the neural response function over many repeated trials, to identify the "systematic component" of the response that is common to all trials. Other averages of the neural response function could be constructed, for example, the response correlation function $\langle \rho(t)\rho(t') \rangle$. The question is whether or not it is worth the effort to keep track of anything other than the instantaneous firing rate.

Poisson Processes

Poisson processes are important in a variety of problems involving rare, random events in time or space, e.g., radioactive emissions, traffic accidents, and action potentials.

Homogeneous Poisson Process

We will begin by assuming that the underlying instantaneous firing rate r is constant over time. This is called a homogeneous Poisson process. Later we will treat the inhomogeneous case in which $r(t)$ varies over time. Imagine that we are given a long interval $(0, T)$ and we place a single spike in that interval at random. Then we pick a sub-interval (t_1, t_2) of length $\Delta t = t_2 - t_1$. The probability that the spike occurred during the sub-interval equals $\Delta t / T$.

Now let's place k spikes in the $(0, T)$ interval and find the probability that n of them fall in the (t_1, t_2) sub-interval. The answer is given by the binomial formula:

$$P\{n \text{ spikes during } \Delta t\} = \frac{k!}{(k-n)!\, n!} p^n q^{k-n},$$

where $p = \Delta t / T$ and $q = 1 - p$. If you have never seen this binomial formula before, look in any undergraduate level probability or statistics book. The binomial formula is what you use to calculate the probability of n events of a certain type out of k trials, for example, the probability of getting 10 sixes out of 100 rolls of a fair die.

Next we increase k and T keeping the ratio $r = k/T$ constant. Since k is the total number of spikes and T is the total time, $r = k/T$ is the mean firing rate, the average number of spikes per second. It can be shown that as $k \to \infty$, the probability that n spikes will be in an interval of length Δt equals:

$$P\{n \text{ spikes during } \Delta t\} = e^{-r\Delta t} \frac{(r\Delta t)^n}{n!}. \tag{3}$$

This is the formula for the Poisson probability density function. Given the mean firing rate r, the formula tells you the probability of having n spikes during a time interval of length Δt. The formula is only correct when the spikes are completely independent of one another, i.e., that they are placed randomly throughout the full $(0, T)$ time interval.

The spike count for a homogeneous Poisson process, dropping the time-dependence from Eq. 1, is given by:

$$\langle n \rangle = \int_{t_1}^{t_2} r\, dt = r\Delta t, \tag{4}$$

for any interval of length $\Delta t = t_2 - t_1$. As expected, the average spike count equals the mean firing rate times the duration. The variance of the spike count is a bit harder to derive but it turns out that the result is the same, i.e.,

$$\sigma_n^2 = r\Delta t.$$

The ratio of the variance to the mean spike count is called the *Fano factor*,

$$F = \frac{\sigma_n^2}{\langle n \rangle} = 1. \tag{5}$$

The Fano factor characterizes the variability in the spike count. The fact that the spike count mean and variance are equal is a distinguishing characteristic of a Poisson process.

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Waiting Time Between Spikes

Given any time t_0, what is the waiting time for the next spike to occur? This can be computed if we know the probability for no spike to occur within the interval $(t_0, t_0 + \tau)$. Plugging $n = 0$ into Eq. 3,

$$P\{\text{next spike occurs after } \tau\} = e^{-r\tau}$$

The probability that a spike has already occurred is 1 minus this result, i.e.,

$$P\{\text{next spike occurs before } \tau\} = 1 - e^{-r\tau}. \tag{6}$$

This is a cumulative distribution function for the probability of a spike occurring within the interval $(t_0, t_0 + \tau)$. It is zero for $\tau = 0$ and increases monotonically to 1. The longer one waits, the more likely a spike is to occur.

The probability density function for the waiting time until the next spike is the derivative of the above cumulative distribution:

$$p(\tau) = \tfrac{d}{dt}\left(1 - e^{-r\tau}\right) = r\, e^{-r\tau}. \tag{7}$$

Thus, the *interspike interval density* for a homogeneous Poisson spike train is an exponential function. The most likely interspike intervals are short ones and long intervals have a probability that falls exponentially as a function of their duration. Interspike interval histograms can be extracted from data by counting the number of interspike intervals falling in various time bins.

The mean duration between events is:

$$\langle \tau \rangle = \int_0^\infty \tau\, p(\tau)\, d\tau = \tfrac{1}{r},$$

consistent with our interpretation of r as the mean rate. The variance of the interspike intervals is:

$$\sigma_\tau^2 = \int_0^\infty \tau^2\, p(\tau)\, d\tau - \langle \tau \rangle^2 = \tfrac{1}{r^2}.$$

The ratio of the standard deviation to the mean interspike interval is called the *coefficient of variation*,

$$C_V = \tfrac{\sigma_\tau}{\langle \tau \rangle} = 1. \tag{8}$$

The coefficient of variation characterizes the variability in the interspike intervals. The fact that the coefficient of variation is one is another distinguishing characteristic of a homogeneous Poisson process.

Notice that our choice of the starting time t_0 does not affect any of these results. The waiting time until the next spike does not depend on whether or not a spike has occurred recently.

Generating Poisson Spike Trains

There are two commonly used procedures for numerically generating Poisson spike trains. The first approach is based on the approximation in Eq. 2 for the probability of a spike occurring

during a short time interval. For the homogeneous Poisson process, this expression can be rewritten (removing the time dependence) as

$$P\{1 \text{ spike during } \delta t\} \approx r\delta t$$

This equation can be used to generate a Poisson spike train by first subdividing time into a bunch of short intervals, each of duration δt. Then generate a sequence of random numbers $x[i]$, uniformly distributed between 0 and 1. For each interval, if $x[i] \leq r\delta t$, generate a spike. Otherwise, no spike is generated. This procedure is appropriate only when δt is very small, i.e, only when $r\delta t \ll 1$. Typically, $\delta t = 1$ msec should suffice. The problem with this approach is that each spike is assigned a discrete time bin, not a continuous time value.

The second approach for generating a homogeneous Poisson spike train, that circumvents this problem, is simply to choose interspike intervals randomly from the exponential distribution. Each successive spike time is given by the previous spike time plus the randomly drawn interspike interval[1]. Now each spike is assigned a continuous time value instead of a discrete time bin. However, to do anything with the simulated spike train (e.g., use it to provide synaptic input to another simulated neuron), it is usually much more convenient to discretely sample the spike train (e.g., in 1 msec bins), which makes this approach for generating the spike times equivalent to the first approach described above.

Figure 1A shows a snippet of a spike train that was generated using the first of these two methods. The instantaneous firing rate was chosen to be $r = 100$ spikes/second, and the time binsize was chosen to be $\delta t = 1$ msec. In fact, I generated many different spike trains, each of 1 sec duration (1000 time samples). Then I counted the number of spikes in each of these repeats. Figure 1B shows a histogram of the spike counts, superimposed with the theoretical (Poisson) spike count density given by Eq. 3. As expected, both the mean and the variance of the spike count histogram are 100 spikes/sec, so the Fano factor is one. Finally, Fig. 1C plots the interspike intervals calculated from the simulation (of course, these intervals are accurate only to 1 msec because the spikes were spaced by integer multiples of the time binsize), superimposed with the theoretical (exponential) interspike interval density given by Eq. 7. As expected, both the mean and the standard deviation of the interspike interval histogram is 10 msec, so the coefficient of variation is 1.

Inhomogeneous Poisson Process

The Poisson model, for time-varying firing rates is basically the same. We simply replace the constant r with a rate function $r(t)$ that varies with time.

For an inhomogeneous Poisson process, the probability of observing exactly n spikes in a particular interval (t_1, t_2) is given by:

$$P\{n \text{ spikes during } (t_1, t_2)\} = e^{\langle n \rangle} \frac{(\langle n \rangle)^n}{n!},$$

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[1]At the risk of confusing you, remember that even though you are choosing each spike time based on an interspike interval, the spike times are truly independent of one another because exponentially distributed interspike intervals correspond to a Poisson (independent spike) process.
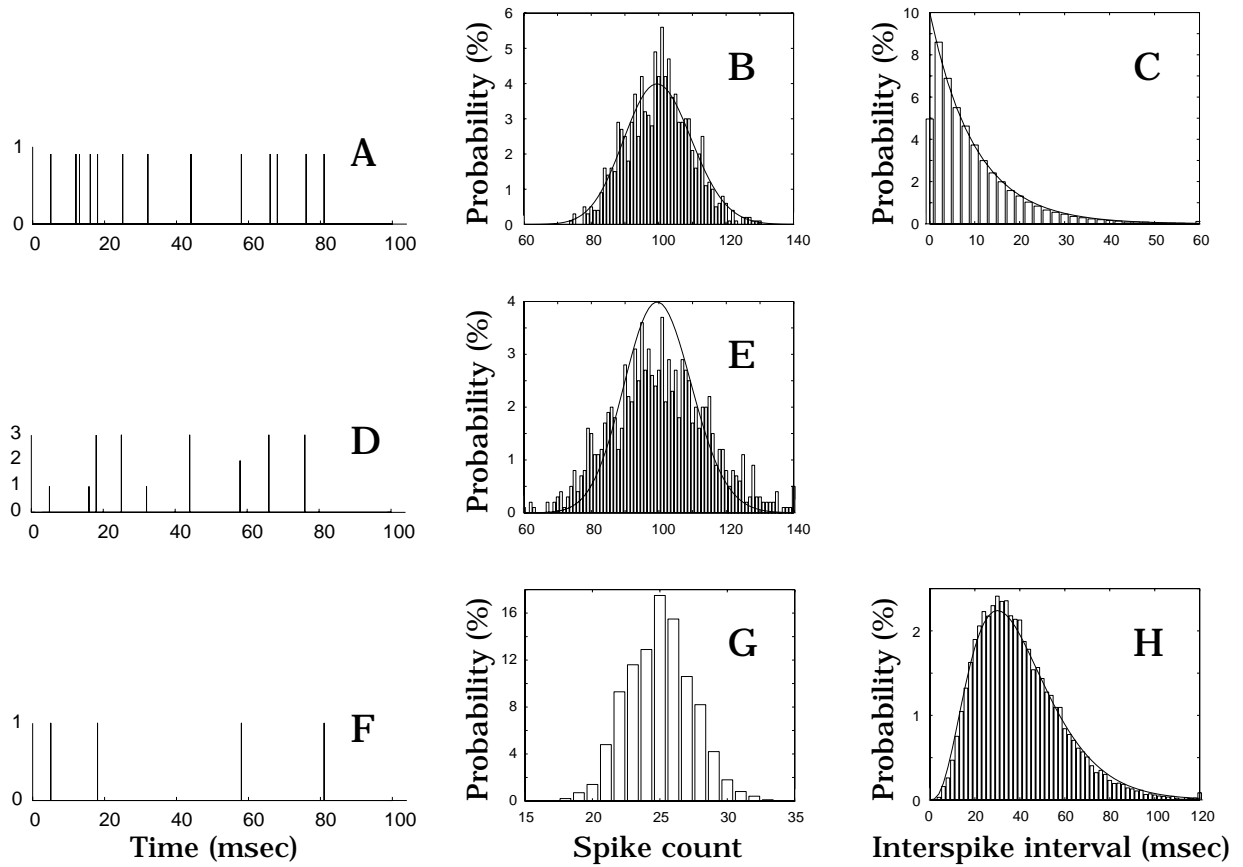
Figure 1: **A.** Snippet of a Poisson spike train with $r = 100$ and $\delta t = 1$ msec. **B.** Spike count histogram calculated from many Poisson spike trains, each of 1 sec duration with $r = 100$, superimposed with the theoretical (Poisson) spike count density. **C.** Interspike interval histogram calculated from the simulated Poisson spike trains superimposed with the theoretical (exponential) interspike interval density. **D.** Snippet bursty spike train generated by replacing each spike in **A** with a "burst" of zero, one, or more spikes. The height of each impulse represents the number of spikes in that time bin. The number of spikes per burst was Poisson distributed with a mean of $\langle n_b \rangle = 1$ spike/burst. **E.** Spike count histogram calculated from many bursty spike trains like that in **D**, superimposed with the Poisson spike count density. The bursty spike trains have the same mean spike count, but the variance of the bursty spike count histogram is twice that of the Poisson. **F.** Renewal process spike train generated from **A** by removing all but every fourth spike. **G.** Spike count histogram calculated from many renewal spike trains like that in **F**. The mean spike count is 1/4 that of the Poisson, as expected. **H.** Interspike interval histogram calculated from the renewal process spike trains superimposed with the theoretical (gamma) interspike interval density. The mean interspike interval is 40 msec, four times longer than that in **C**, as expected because we have removed 3/4 of the spikes. The standard deviation of the interspike intervals is 20 msec so the coefficient of variation is 1/2.

where $\langle n \rangle$ is the average spike count given by Eq. 1. This reduces to the homogeneous case (Eq. 3) by noting that for a homogeneous Poisson process $\langle n \rangle = r\Delta t$ (see Eq. 4). It turns out that the variance of the spike count is still equal to the mean spike count,

$$\sigma_n^2 = \langle n \rangle,$$

so that the Fano factor is still equal to one. I find this to be quite remarkable; regardless of how the instantaneous firing rate varies over time and no matter what time interval you consider, the variance in the spike count always equals the mean spike count (for a derivation, see Appendix A.5 of Rieke *et al.*, 1997).

As long as $r(t)$ varies slowly with respect the the time interval δt (or equivalently, as long as δt is short enough), we can still use Eq. 2 to generate the spikes. In particular, $r(t)$ must be nearly constant over each interval of length δt. The procedure is as follows. The rate function $r(t)$ is sampled with a sampling interval of δt to produce a discrete-time sequence $r[i]$. Then a sequence of random (uniformly distributed between 0 and 1) numbers $x[i]$ is generated. For each time sample i, a spike is generated when $x[i] \leq r[i]\delta t$. This procedure was used to generate the spike trains for Fig. 4 of the *Synaptic Input* handout.

Refractory Period

One way to add refractory effects to the Poisson spike model is by setting the instantaneous firing rate to zero for a couple milliseconds immediately after a spike is fired. The gradual recovery process during the relative refractory period can then be modeled by letting $r(t)$ return to the its original value at a predetermined rate, for example, with an exponential time course. A better (more theoretically grounded) way to add a refractory period is to replace the Poisson process with a renewal process as discussed below.

Bursting

The simplest way to add burstiness to the Poisson model is to replace each Poisson spike with an *event* that might consist of zero, one, or more spikes. To do this, replace the instantaneous firing rate $r(t)$ with the instantaneous event rate $r_e(t)$, and generate a Poisson train of events using the methods described above. Then specify a probability distribution for the number of spikes per event. A Poisson distribution can be used for this as well, for example, with a mean of 1 spike/burst. For each event, we need to draw (at random) a spike count from this distribution. To do this, choose a random number x uniformly between 0 and 1, and pass it as argument to the inverse of the cumulative Poission distribution. Figure 2, for example, plots the cumulative Poisson distribution with mean 1 spike/burst. When $x = 0.2$ you get 0 spikes in an event, when $x = 0.4$ you get 1 spike in an event, and when $x = 0.8$ you get 2 spikes in an event.

Figure 1D shows a bursty spike train generated by starting with the "event train" in Fig. 1A and replacing each event with a "burst" of zero or more spikes. In fact, I generated many different bursty spike trains this way, each of 1 sec duration, and counted the number of spikes in each
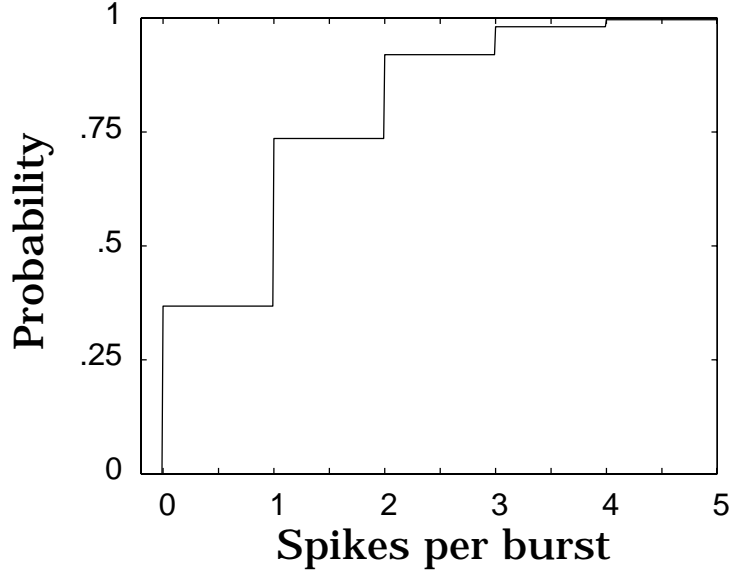
Figure 2: Poisson cumulative distribution function with a mean of 1 spike/burst.

repeat. Figure 1E shows a histogram of the spike counts, superimposed with the Poisson spike count density. The bursty spike trains have the same mean spike count, but the variance of the bursty spike count histogram is twice that of the Poisson. Hence, the Fano factor is 2.

It turns out that there are simple relationships to predict the mean and variance of the spike count from the mean and variance of the number of events per trial and of the number of spikes per event. Define $\langle n_e \rangle$ to be the mean number of events per trial (100 in our example) and $\langle n_b \rangle$ to be the mean number of spikes per event (1 in our example). Then the mean number of spikes per trial is given by:

$$\langle n \rangle = \langle n_e \rangle \langle n_b \rangle.$$

In our example, $\langle n \rangle = 100$, as expected. Likewise, define σ_e^2 to be the variance of the event count (100 in our example) and σ_b^2 to be the variance in the number of spikes per burst (1 in our example). Then the variance in the spike count is given by:

$$\sigma_n^2 = \sigma_e^2 \left(\langle n_b \rangle^2 + \sigma_b^2 \right).$$

In our example, $\sigma_n^2 = 2$. See Bair *et al.*(1994) for further examples, and for references on how to prove these results.

Connecting up the Poisson Spike Generator

To use the Poisson spike generator in a simulation, we need to hook it up to a model neuron. The simplest way to do this is the choose the Poisson rate to be proportional to membrane potential above some threshold:

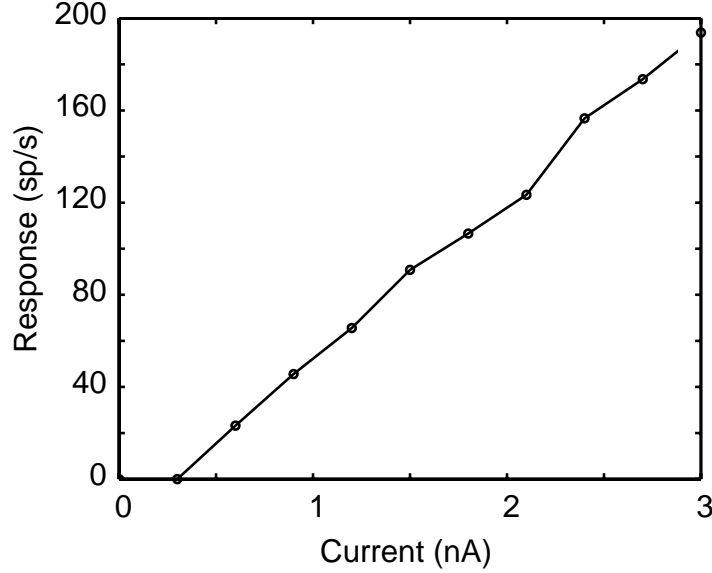$$r(t) = \alpha \left[V(t) - V_{th} \right],$$

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Figure 3: F-I curve a Poisson neuron, that is, firing rate as a function function of injected current for current steps of various amplitudes. Parameters: $C = 0.2$ nF, $g = 0.02$ uS, $V_{th} = 15$ mV, $E = V_{\text{rest}} = 0$ mV.

where α has units of spikes/sec/mV and determines the slope of the F-I curve (firing rate as a function of injected current for current steps of various amplitudes).

The passive membrane response to a step of constant current I, switched on at $t = 0$ and remaining on indefinitely is given by:

$$V(t) = u(t)\,(I/g)\,\left(1 - e^{(-t/\tau)}\right),$$

where $u(t) = 0$ for $t < 0$ is the unit step signal, and we have assumed that $V(0) = V_{\text{rest}} = E = 0$. The steady state membrane potential is proportional to the injected current:

$$V_s = (I/g).$$

So the steady state firing rate is given by:

$$
\begin{aligned}
r(t) &= \alpha\left[V_s - V_{th}\right] \\
&= \alpha\,(I/g) - \alpha\,V_{th}
\end{aligned}
$$

The firing rate is proportional to the injected current once above threshold. An example is shown in Fig. 3. Each data point was computed by simulating 5 secs of a Poisson spike process for each current amplitude, and counting the number of spikes that resulted. The graph is not perfectly linear because the Poisson model is a random process. In the limit, if we were to simulate longer and longer stimulation epochs, the graph would become perfectly linear.

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Renewal Processes

It is possible to go beyond the Poisson model by allowing the firing probability to depend on both: (1) the instantaneous firing rate, and (2) the time since the most recent previous spike (but not on spike times before the most recent one). This results in a model of spike generation called a renewal process.

A simple way to generate a renewal process spike train is to start with a Poisson spike train and delete all but every κth spike. An example is shown in Fig. 1F. This results in a spike train whose interspike intervals are given by the gamma probability density function:

$$p(\tau) = (\kappa r)^{\kappa} \, \tau^{\kappa-1} \, e^{-\kappa r \tau} \, / (\kappa - 1)!, \tag{9}$$

where κ (an integer) is called the order of the gamma distribution. When κ is one, $p(\tau)$ becomes the exponential; the interval distribution expected of a Poisson process. When κ is infinity, $p(\tau)$ is the distribution of no variance and the spike train is perfectly regular. The mean interspike interval is $\langle \tau \rangle = 1/r$ for the gamma distribution, just as it is for the Poisson distribution. However, the interspike interval standard deviation of the gamma distribution is different,

$$\sigma_\tau = \frac{\langle \tau \rangle}{\sqrt{\kappa}},$$

so that the coefficient of variation of the gamma distribution is given by:

$$C_V = \frac{\sigma_\tau}{\langle \tau \rangle} = \frac{1}{\sqrt{\kappa}}. \tag{10}$$

Empirical Support

There is evidence that the instantaneous firing rate contains most of the information carried by a neuronal spike train, and hence that the independent spike hypothesis is largely correct. However, this issue is currently the subject of heated debate (e.g., Softky and Koch 1993, 1995; Shadlen and Newsome, 1994, 1995).

Neural responses are noisy. Interspike intervals of cortical cells are highly variable; the coefficient of variation is typically near 1 as expected of a Poisson process (Softky and Koch, 1993). Spike counts of cortical cells are also highly variable; the variance in the spike count is typically proportional to the mean spike count with a Fano factor of about 1.5 (e.g., Dean, 1981; Tolhurst *et al.*, 1983; Bradley *et al.*, 1987; Snowden *et al.*, 1992; Britten *et al.*, 1993; Softky and Koch, 1993). Strictly speaking this is a violation of the Poisson model, but it is consistent with a bursty spiking process like that simulated in Figs. 1D-E.

There are a number of studies in which random process models have been successfully applied to model the statistics of spike trains. I will mention only two examples here. Troy and Robson (1992) calculated the interval statistics of spike trains recorded from retinal ganglion cells, and found that they were well modeled as coming from renewal processes with gamma-distributed

intervals. Bair *et al.* (1994), analyzed the spike trains of neurons in visual area MT. They found that the spiking in about a third of the cells was compatible with a Poisson process. Most of the rest of the cells typically responded in bursts, where the bursts were Poisson-distributed, again like the bursty spiking process simulated in Figs. 1D-E.

Caveat: Where's the Noise?

To summarize, I have proposed that we can model a neural response function with an underlying deterministic instantaneous firing rate signal and a random process spike generator. Although this model provides a good description of a large amount of data, especially considering its simplicity, it should not be oversold.

The main problem with all this is that it does not provide the proper mechanistic explanation of neuronal response variability. Spike generation, by itself, is highly reliable and deterministic, as has been demonstrated by countless numbers of *in vitro* studies. Mainen and Sejnowski (1995), for example, recorded from neurons in rat cortex slices while injecting complex time-varying currents. The resulting spike trains were reproducible across repeats to less than 1 msec.

The noise in *in vivo* neural responses is believed to result from the fact that synapses are very unreliable. In fact, greater than half of the arriving presynaptic nerve impulses fail to evoke a postsynaptic response (e.g., Allen and Stevens, 1994). The noise in the synapses, not in the spike generator!

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