Computational Neuroscience
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Lecture – 22

Lecture 22 : Spike train statistics and response measure

Welcome. So with a very brief introduction on random variables and random processes to do with our course, we will be now going into the statistics of spike trends and what we call response measures that we will be using throughout the course. So as discussed now we are going into the cases where we have basically over time a series of spike trends or spikes which will be occurring at different time points t in parallel with some phenomena that is going on and we want to understand what the neuron that is producing this particular spike trend has to do with this phenomena that is what is being encoded in that phenomena that is going on in terms of these neurons responses. In order to do that we first need to define what is the response measure that we will be talking about. So when we talk about response measure since the spikes are as we have discussed all or non-events they can simply be represented by points on time that is there are events occurring at these particular time points. So this spike is an event each of these spikes are events in time.

This representation is called what we call is a dot raster representation of spike trends. Now we generally consider the response as a function of time but of different resolutions in time that is r as a function of some delta times i that is delta is the resolution in time that we are looking at resolution in time that is at what interval we are discretizing the time window and r and i is basically the index that is it is starting from 1 to i and so on and there may be let us say capital M intervals or the bins that we are looking at and r represents the rate or the number of spikes by delta that occur in that window i delta to i plus or i minus 1 delta to i delta. So in this case so basically for i equals 1 it is from 0 to delta times 0 to delta and this is 2 delta 3 delta and so on. So our delta the choice of delta is what essentially defines how we are going to treat the response or define our response measure.

The delta may be so large that there is only one bin or it is equal to M delta whatever or M times delta is such that M is essentially 1. So in that case we are essentially looking at the spike count or the overall rate in a large time window. Now as you think as you can imagine that if we keep on reducing delta to smaller values we will ultimately go to a stage where only one spike can occur at most one spike can occur in a delta window or even when we are close to that value we can have only very few possibilities of the number of spikes occurring in a delta window. So in that case given the stochasticity of spike trends we generally estimate this R delta i from a number of repetitions of the experiment that we are doing. That is whatever phenomena is going on which may be a stimulus in our control and if it is being determined experimentally this is this part is in our control the hash part the phenomena that we are wanting to study.

So we repeat that same thing over and over again and that is what we mean by each realization. So we are repeating the experiment over and over again and we get different spike trends every time and depending on how variable things are we decide on number of repetitions required and then get an estimate of this R delta i. It also is heavily depend on the choice of delta the larger the delta the fewer repetitions we may need and the smaller the delta the more number of repetitions we need in order to reliably estimate the R delta i or the spike rate in a specific window of size delta at the ith position and so on. So what we are then left with is essentially representation of the rate as a function of time which let us say is time and let us say this is 0 this is our capital T which is equal to M delta and for each delta we there is this is rate in spikes or the number of spikes occurring per second within that delta window and that representation is what we call is a very stimulus time histogram when it is associated with a stimulus occurring within that time window or that phenomena that we have been talking about. So this very stimulus time histogram essentially represents the R delta i that is the rate or the number of spikes per unit time over the different window sizes.

Now this R delta i is variable can be variable over time or in general can be constant over time that is R delta i is independent of i and in that case we have only a single R value and it does not have to be indexed with time and that is the simply the rate or we can also represent or replace it by simply the spike count over the entire window that we are considering. So in this in general when we think of the rate as a fixed size over the entire window capital T we also generally think of the random variable spike count as something that follows a Poisson distribution. So here is how we can consider that is that let us say there is a window time window capital T that we are analyzing 0 to capital T and there are let us say N spikes that have to occur in 0 to capital T or that occur in 0 to capital T. Let us say we say that probability of N spikes in the window or probability of capital the probability of N spikes in the window capital T as $P_T[N]$ and this probability can be computed by making this assumption in the case assumption that there is a fixed rate as we were saying that the fixed rate R of probability of spikes in that window 0 to capital T. Now that is R and we will consider the time bins as delta T and let us say there are capital M time bins equal to that is M times delta is equal to capital T.

So this is delta delta and this is our M delta 2 delta and so on. So the probability of observing N spikes in this window capital T can be obtained in this manner that we have a fixed rate capital R and the events or spikes occurring in each of these time windows are independent of each other that is whether there is a spike in the previous or side by time windows it does not influence the spiking in the other windows in that particular window or in other windows. So essentially that means that there are independent events that are occurring over time. So this probability can be such that so essentially we have N spikes that need to occur in this capital T window and if we assume that our delta T is this delta T is so small that there is only at most one spike possible in that time window. Now from our previous section we know that this there is such a delta T given the absolute refractory of a spike that is we know that after the neuron crosses threshold when the neuron gets inactivated the or sorry the sodium channels get inactivated there is no possibility of producing an action potential within that time window and so that naturally creates that delta T that will allow only one spike in that delta T which is about a millisecond or so.

So in also I mean in theoretically also we can think of delta T going to a very small value not necessarily limited to one millisecond. So since N since the spikes are events in time all are non-events in time and they do not have any size or any extent over time. So that means we need to put in these N spikes in the capital M delta T time windows. So the way in which we can put in the N spikes is by choosing those N bins and the probability of observing N spikes after we have chosen those N bins the probability of observing spikes in those N bins is simply $R \times \delta T$ to the power N because they are independent. So let us say we chose one this bin and up to this bin N bins we have chosen and those each of those windows are such that all the windows are such that delta T is very small that is only one spike can occur and we know that the probability of spike is simply R times delta T the rate of spiking the number of spikes that are occurring over time times delta T and since they are independent then all those probabilities get multiplied and that is $R\delta T$ to the power N.

Similarly the other M minus N bins cannot have spikes and the probability of that is $1 - R\delta T$ to the power M minus N and the way we can choose those N spikes or N bins is simply our M choose N which is nothing but $M!$ divided by $(M - N)! \times N!$. So we can write our $P(T, N)$ as simply $M!$ divided by $(M - N)! \times N!$ $R\delta T$ to the power N $(1 - R\delta T)$ to the power $M - N$. This is our probability of observing N spikes in that capital in that capital T time window where the probability of spike is fixed in that capital T time window and that or there is a fixed rate of spikes occurring that is R. So now if we consider the case where delta T goes to 0 in fact this $P(T, N)$ is when we have this limit δT goes to 0. So when we have delta T going to 0 there are a few observations that we need to take into account that is we have delta this goes to 0 δT into M is our capital T.

Now as delta T goes to 0 our since our capital T is fixed and N is fixed this capital M is going towards infinity it grows unbounded and since if we take this $M - N$ here and so basically N is fixed and M is growing unbounded so that can be replaced simply by M. Now our delta T is also equal to capital T by M and if we replace our delta T by or if we replace M by T by epsilon or minus M by T by epsilon then what we have is if we consider this term only the second part we have $1 - R\delta T$ is M/T and actually we need to put the sorry into $-R\delta T$ is replaced by epsilon then what we have is $-R$ into T/M is replaced by epsilon then $1-R\delta T$ is replaced by $1+\epsilon$ and our capital M. So our M is replaced by $-RT/\epsilon$. So the term $(1 - R\delta T)^{M-N}$ can now be replaced by as above is equal to $(1 + \epsilon)$ to the power approximately to the power M where M can be replaced by $-RT/\epsilon$ that is that is equal to $(1 + \epsilon)^{-RT/\epsilon}$ which is $(1 + \epsilon)^{-1/\epsilon}$ this whole to the power R minus R T. So now as we have limit δT goes to 0 then $-R\delta T$ also goes to 0 that is epsilon goes to 0 and we know that limit ϵ goes to 0 $(1 + \epsilon)^{1/\epsilon}$ this is equal to e.

So this particular whole term turns out to be simply e^{-RT}. Now if we consider the rest of it rest of the expression that is M choose N and $R\delta T$ to the power M we have $M!$ divided by $(M - N)!$ and $N!$ since $M!$ by $(M - N)!$ can be replaced by M^N because it this whole term together turns out to be M into $M - 1$ like this and there are N terms up to $M - N + 1$. So since N is fixed and small compared to capital M and M is going to growing unbounded towards infinity this the ratio of these two factorials can be replaced by M capital M to the power M and so what we have as $P(T, N)$ is simply M^N divided by $N!$ $R\delta T$ to the power N limit δT tends to 0 and e^{-RT}. Now when we use this M actually M R delta T can be replaced by so by using our delta T into M is equal to capital T M delta T can be replaced by T. So M R delta T becomes R T and so the overall expression turns out to be P T N equals so this whole term now becomes RT^N divided by $N!$ e^{-RT}.

So finally what we have is $PTN = \frac{RT^N}{N!} e^{-RT}$. Now note that RT is nothing but the number of spikes or the average number of spikes occurring in the window capital T or this is the rate or in fact it is the rate times the time window and can be replaced by some spike count in that capital time window and this basically represents the Poisson distribution. So if we say that what is the probability of observing the number of spikes $N = K$ in a particular time window where the rate of spikes is fixed as R over that entire time window then we say that $RT^K e^{-RT}$

by $K!$ that is in this case this is the mean spike count. So we saw that by using the independent assumption over time bins and by considering that the probability of spikes is fixed over the entire window the spiking probability over that time window turns out to be distributed Poisson or the number of spikes occurring in that time window turns out to be distributed Poisson. Well overall we know that those assumptions are not true however based on actual experiments and data we see that there is closeness of the spiking probabilities to be Poisson in a number of regions of the brain where you repeat the stimulus and get the variability of the number of spikes over different trials and they tend to follow Poisson distribution and there are ways in which we can measure and we can conclude that the distribution is Poisson by looking at the mean and variance of the spike counts and also by looking at inter spike intervals.

So for the neuron to be Poisson process like behavior to have it a Poisson process like behavior or a Poisson process behavior because there is independence of spiking in the different intervals within that time window capital T that we are considering and let us say that there is a spike that is occurring at time point Ti and the next spike needs to occur at a time tau after Ti that is in a window small window delta t Ti plus tau and plus delta t plus tau plus Ti. So this is this time point this is this time point. So essentially we need to see so we are trying to find out what is the probability of observing a spike after one particular spike tau later in a small time window Ti. So that means that there should not be any spikes in this window tau the probability of that can be found from above for a Poisson like distribution then with n equals 0 and capital T equals tau we have if the rate is r we have $r\tau^0 e^{-r\tau}$ divided by $0!$ which is 1 and that turns out to be simply $e^{-r\tau}$ this is 1. So the probability of not observing a spike here is $e^{-r\tau}$ and the probability of observing a spike in this delta time window we already know is $r\delta t$.

So the overall probability of observing the spike is $r\delta t$ into $e^{-r\tau}$. So now since the inter spike interval is a continuous random variable we will have a PDF and if this is the probability of observing tau sized inter spike interval or tau to tau plus delta sized interval then the density will simply drop this delta t this probability is obtained by multiplying it with delta t assuming that delta t is very small and the probability is fixed in that time window then the density turns out to be that is the probability of tau inter spike interval is going to be $re^{-r\tau}$ and that is an exponential distribution. So we also see that by looking at inter spike intervals they follow nature generally in exponential distribution and so if we think of inter spike interval and in this case this is the $p\tau$ the density tau then it should be exponentially distributed that is it should go down like this exponentially. However because of refractory that we have studied and relative refractory we cannot get any spikes at this short interval which is the same as the absolute refractory period about a millisecond or so and similarly beyond that period there is a relative refractory period over which the probability of spikes occurring would be less than what we expect from no dependence case and so the inter spike interval distribution finally follows something akin to this which is exponential with this dead time period the dead delta t of absolute refractory and recovery period for due to relative refractory and then it follows the exponential kind of distribution. So the cyan curve is the generally observed inter spike interval distribution which is often approximated to be exponential and we go ahead with the idea that the spikes occur as a Poisson with Poisson distribution that is the number of spikes occur as a Poisson distribution and the spikes occur in time as a Poisson process.

So we will be talking about the Poisson process a little more in later lectures in a little more detail when it comes up and so from here.