Computational Neuroscience
Dr. Sharba Bandyopadhyay
Department of Electronics and Electrical Communication Engineering
Indian Institute of Technology Kharagpur
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Lecture 25 : Stimulus to Response mapping(Coding) - II

Welcome. We have been discussing how we can use linear time invariant systems to model properties of neurons or the stimulus to response transformation of neurons. We came up with a model or a series of steps which we describe as the model for the neuron or in fact from the stimulus to the spike trains which involves linear time invariant system followed by few other blocks. And so to remind ourselves we have the stimulus as $x(t)$. Then we said that we have an LTI here which is as you know completely represented by its impulse response $h(t)$ that is if we have the system if $x(t)$ is $\delta(t)$ then the output of the system so $x(t)$ and output of the system is $y(t)$. In case of $x(t)$ is equal to $\delta(t)$ $y(t)$ is $h(t)$ that is the impulse response of the system and we said that $h(t)$ is all we need to know about the LTI system in order to be able to model the behavior or the output for any given input.

And followed by this so if this is $y(t)$ we said that $y(t)$ is akin to the membrane potential and so it passes through a static nonlinearity which can be of any type but at least the most common type being that we have a threshold and then some saturation which is usually modeled with a sigmoid like an activation function. And we have said that this can be any arbitrary nonlinearity which we will see that in the process of our determining $h(t)$ it does not matter what kind of nonlinearity this is. That is producing the instantaneous firing rate $\lambda(t)$ which is the driving function for the inhomogeneous Poisson process and what we are observing are basically a point process being driven by the $\lambda(t)$ and that is our $P(t)$ which is a series of impulses that is our $P(t)$ is described as summation of $\delta(t - t_i)$ where i varies from 1 to capital N_t where T is the period over which we are observing the spikes and that is the period over which more or less we have the stimulus $X(t)$. And we need to understand the behavior of this system and we said that all we need to do is find out this $h(t)$ and then we will be done once we have estimated the $h(t)$ if it is good we will be easily able to predict or find out what this nonlinear function is and hence be able to model the system.

And so in order to do that let us think of simply a linear time invariant system let us forget about the other two blocks here and let us say we consider only the first part of it where we have simply an LTI whose impulse response is $h(t)$ we have an input $X(t)$ which is a random process and it is producing a output $Y(t)$ which is also a random process and we will assume the wide sense stationarity and ergodicity in these processes to make things simpler. And I mean they are not bad assumptions because given the kind of results we know that exist by using this kind of modeling we find them to be very good in many cases as we have discussed especially in the peripheral regions and slightly above but it gets difficult to use these models as we go higher up in the hierarchy as we have discussed. So we introduced the idea of the cross correlation function that is $R_{YX}(\tau)$ we are saying τ because we are assuming wide sense stationarity and we if we want to find out what $R_{YX}(\tau)$ is we essentially need to calculate the expectation of our $Y(t+\tau)$ and $X(t)$ this product. The expectation of this is the cross correlation function where Y and X the points that we are considering at every instant are τ apart and from here from this being an LTI linear time invariant system we also know that our $Y(t)$ can be written as the convolution of $X(t)$ and $h(t)$ or in other words we have an integral over minus infinity to infinity our $X(t-u)h(u)du$. So we have simply replaced the dummy variable tau in this case by u if you recollect our definition of the convolution we had instead of u we had τ now we have a different τ here and so we have to introduce a different variable name here which we have taken to be u.

So we can use this $y(t)$ based on the $x(t)$ and $h(t)$ and we can plug it in into this $y(t+\tau)$ and so what is our $y(t+\tau)$ so if we can if we write it here our $y(t+\tau)$ will turn out to be integral minus infinity to infinity we replace t by $t+\tau$ $X(t+\tau)-u$ and $h(u)du$. So in a sense the cross correlation function R_{YX} becomes the expectation of we let us say we write the $x(t)$ first and then the integral $X(t+\tau)-u$ again $X(t+\tau)-u$ $h(u)$ and du. So we can interchange the expectation and the integration because the integration is over u so and it does not matter if we take the $x(t)$ in and the expectation in it can be since the expectation is a linear operator we have the integral let us say integral is over u so let us write the differential first du we have $h(u)$ which is not part of the expectation and then we have the expectation because $h(u)$ is a constant in that sense expectation of $X(t+\tau)-u$ into $X(t)$ so we have simply interchange the expectation and the integral and we have taken $h(u)$ out of the expectation because it is constant function and so it is not a random variable and so if we now look at this expectation it looks very familiar function where if you look at this representation of $R_{YX}(\tau)$ with expectation of $Y(t+\tau)$ $X(t)$ if we take $X(t)$ in the if we take $X(t+\tau)-u$ instead of τ here and this is $X(t)$ this simply becomes $R_{XX}(\tau-u)$ that is the auto correlation function of X and the variable index is the argument is $\tau-u$ so this becomes integral $duh(u)$

and $R_{XX}(\tau - u)$ so now if you look at it again $duh(u)R_{XX}(\tau - u)$ and compare this with the convolution definition convolution equation we have again that $h(u)$ and $X(t - u)$ instead of $X(t - u)$ we have different function here which is a function of τ and that is the auto correlation function τ in there so this is also a convolution but it is only that this is a convolution between $H(\tau)$ and $R_{XX}(\tau)$. So what we show here is that in this kind of scenario where we have wide sense stationarity and we have a random process as input and output is also a random process of an LTI then the cross correlation function between the output and the input is related to the auto correlation function of the input through the impulse response just like the output of the system is connected to the input of the system through the impulse response through a convolution here we see that even the auto correlation or the cross correlation function is simply the convolution of the auto correlation function that is the cross correlation of the input itself with itself and the impulse response. So in a sense what we have here is that our $R_{yx}(\tau)$ is nothing but $H(\tau)$ convolved with $R_{xx}(\tau)$. This is the auto correlation function, this is the cross correlation function of the output with the input and this is the auto correlation of the input.

Now if we assume that our input, because the input is our choice at least for these cases, we can create the input ourselves and play that kind of stimulus, use that kind of stimulus and record the spike trends from the neuron. So if we create the stimulus to be such that our $x(t)$ is Gaussian white noise then this relation $R_{yx}(\tau)$ with $R_{xx}(\tau)$ becomes much more simpler and much more simple and that is because when we say Gaussian white noise process, if the input is a Gaussian white noise process, it simply means that at every instant we are drawing the value of the random process from a Gaussian distribution and if every instant the value is independent of any value elsewhere of that process. So that means if we think of the auto correlation function, that is how the expectation of $x(t+\tau)$ and $x(t)$, since these are totally unrelated they are independent of each other, so this is always 0 for all τ not equal to 0. And in fact what we find, what we can show is that at τ equal to 0 we will have an impulse from the definition of this expectation for our process when we do the integral it will simply turn out to be an impulse at 0. And so the auto correlation function of a white noise process $R_{xx}(\tau)$ is nothing but $\delta(\tau)$ and it can be scaled by σ^2 depending on the power or the variance of that Gaussian from which we are drawing and that determines the power in that noise or the energy in that noise.

So this σ^2 is nothing but the standard deviation or the variance of that Gaussian white noise. And here we will also assume that our μ_x is 0, the mean value is 0. The 0 mean Gaussian white noise then we have the auto correlation function

$R_{xx}(\tau)$ is simply $\sigma^2\delta(\tau)$. So that means if I were to draw, if this axis is τ, if I were to draw this is 0 then the auto correlation function is simply in red it will be 0 everywhere other than at 0 here and we represent the impulse at 0 with this arrow and this height is taken to be σ^2. So now the convolution of $h(\tau)$ and $R_{xx}(\tau)$ that we have here if we now use the auto correlation function as described here then our $R_{yx}(\tau)$ now becomes the convolution of $h(\tau)$ and this $\sigma^2\delta(\tau)$.

So and convolution is nothing but an integral and the σ^2 can come out of the integral and here we have essentially $h(\tau)\delta(t-\tau)d\tau$. So we have changed the variable to t now I am sorry we have to do it with τ so this because this is τ we need to have this t here and I am sorry we will have $\tau - tdt$. So $h(t)$ and $\delta(t-\tau-t)dt$ we showed that from the property of the Dirac delta function or this delta such an integral is simply the value of the function $h(t)$ evaluated at this argument as 0 that is at t equal to τ. So that means this simply becomes $\sigma^2 H(\tau)$. So in essence what we have now had is we have we have removed the input function from here or input process from here because of it is because of the white Gaussian noise assumption about the stimulus or in fact in our control that is the stimulus.

So that is gone and $R_{yx}(\tau)$ is simply proportional to the impulse response in the case of white Gaussian noise input. So the first relation that we have for LTI and this kind of situation is that our R_{yx} is going to be proportional to the impulse response of the system. So if we recollect here if this is our model at the top of the page then the if we somehow can get the cross correlation y and x then that is going to be proportional to the impulse response and that means we can get an estimate of the impulse response of course within a scaling factor. So if we have access to this $y(t)$ which is the membrane potential for that we would require to patch onto a neuron and know that $y(t)$ but here we are given the problem of recording the spikes extracellularly. So we have those all or none events and we are recording only this $p(t)$ only this $p(t)$ here that is the spike train from this spike train we need to be able to somehow connect it with this $R_{yx}(\tau)$ or hence our $h(\tau)$.

So now if we consider so let us say we have this system $x(t)$ as input then we have $y(t)$ then we have our nonlinearities the static nonlinearity and we have $\lambda(t)$ and then we have this point process production which is giving $p(t)$. So now if we consider $p(t)$ what we essentially have over time are instances where spikes are occurring that is the t_i's at the different t_i's the spikes are occurring that is all we have and if we now discretize this time axis and create a new discrete variable or process let us say q where we are breaking down this entire time duration let us say we are recording over the period capital T as we have said earlier and so let us say this is 0 to capital T and we break it down into let us say m bins and the bins are of size δ that is our δ times m equals T and the δ is so small that there can be at most one spike in that bin and so we can actually replace the rate with probability I mean we will see in a minute. So let us say we have this δ sized bins here so we have δ sized bins here and there can be at most one spike in each of those bins so the bins are essentially 0 or 1 that is the q_i is either takes on a value either 0 or 1 in the ith bin and the probability of this q_i probability of q_i equal to 1 would simply be our if the rate function is $\lambda(t)$ is simply λ at δi times δ so if δ is small enough so this is simply going to be the probability that q_i equals 1 if δ is sufficiently small because that is the rate that is the number of spikes possible per unit time and since only one spike is possible in a bin is simply multiplying by the bin width we can get the probability of spike. So keeping this relation in mind we can go forward with one more catch here that is since this delta is very small we will assume that our $r_p x$ let us say we will cross correlate the pulse train or the spike train with the input x is going to be close to our $r_q x$ there is a little bit of jump here but for the purposes of this course we will see say that this approximation is valid although there are a number of mathematical treatments that are required in order to make this assumption because we have a delta function in the $p(t)$ from which we are coming to the $r_q x$ but this approximation is pretty good in the sense that if we think that delta is going small and small and small and almost infinitesimally small then our q_i and the process q and the process $p(t)$ are essentially the same the only difference is that instead of the delta function we will have unit impulses in discrete time in q. So this is this is the how to connect these two with each other.

So now let us say we want to compute $r_p x$ from here we have that $r_p x$ that means we have this $x(t)$ and with a number of steps we finally have our $p(t)$ which is equal to summation $\delta(t - t_i)$ and this i is going from 1 to capital n_t. So in order to compute $r_p x$ we need to get the expectation of the product of $p(t)$ and $x(t - \tau)$ or $p(t + \tau)$ and $x(t)$. So since the $p(t)$ is not I mean we will not be getting $p(t)$ over an infinite duration we can only estimate $r_p x$ and let us say that that estimate is $\hat{r_p} x$ and that can be written as our average so $r_p x$ at τ is going to be the average of so $1/n_t$ for each of the spikes integral over 0 to capital t we have $x(t - \tau)$ and summation $\delta(t - t_i)$ i equals 1 to capital n_t and here we have dt. So now if we take the summation out we have $1/n_t$ and summation $i = 1$ to capital n_t and here we have an integral of $x(t - \tau)$ and $\delta(t - t_i)$ and dt.

So again we are posed with the situation where we have integral involving a delta function and another function and so it is simply the evaluation of of the function the other function in this case x at wherever this delta function is valid that is at $t = t_i$. So we evaluate $x(t_i - \tau)$. So this we can replace the integral with with that calculation and it will simply be summation over 1 to capital n_t $x(t_i - \tau)$. So what we have is an estimate of the cross correlation of the spike train spike train and the input. So and what is this this $x(t_i - \tau)$ if you think about it let us say we have this is our $x(t)$ over time this is the the time axis and let us say we have $p(t)$ along this 0 to t as spikes at this time point this time point this time point this time point this time point and so on.

So this is each of these spikes are at t_i so this is our t_1, t_2 and so on and so what we are doing here in this sum that came out to be the estimate of our cross correlation between p and x is that we for and it is a function of τ. So τ will be varying between some minus some particular t to some plus positive some particular t. So here is let us say this is the τ axis and this is $\tau = 0$ and we are we are plotting $r_p\hat{}x$ as a function of τ. So what we need that for each and every τ here on this axis we need to compute this sum and average or and divide by capital n_t. So for each of these τ's if you see that at t_1 if we take for t_1 at a particular τ behind t_1 let us say or a particular τ after t_1 what we will have here is the value of if this is τ this is our $x(t_1 - \tau)$.

If this is τ this is our $x(t_1 - \tau)$. Now for every τ on this axis that is essentially throughout a window of τ around that spike it is simply this $x(t_i - \tau)$ is simply the entire waveform of x over this window. So that is the snippet as a function of τ for t_1. Similarly for t_2 we will have a snippet or window around t_2 which is taking this waveform and similarly for each of those spikes and for and they they are aligned by τ because if we put each of these the the t_1 time point and the surrounding window which is the τ axis and average over all the spikes we are simply taking the average of these snippets around the spike and that turns out to be what we call the spike triggered average. So because given every spike we are taking the window around it of the waveform and averaging that for every spike and so what we will see that since the stimulus this is the relation since the response is caused by the stimulus what we will find is that when we do this averaging the values for values τ greater than 0 this will hover around 0 and come down to noise levels because the subsequent stimulus for that spike does not matter in terms of producing that spike because essentially we are averaging the stimulus preceding the spike and after the spike since the stimulus is not going to produce any spike from the future period we will this sum should go down to 0 and that it does and in the past time this τ with a latency we may get certain kind of function which is the spike triggered average.

So that is this this this particular function is proportional to $r_p\hat{}x$. So now we have introduced the idea of the spike triggered average and we have also said that in our model that we have sorry in our model that we have we want we we need to finally relate the spike train to the cross correlation between y and x and to do that we have for the first step taken is we have looked at the cross correlation of p and x that is the pulse train and x and we find that that cross correlation is nothing but the spike triggered average. So in the next lecture we will now connect the spike triggered average which is the cross correlation between p and x or an estimate of the cross correlation between p and x with the $r_y x$ which is proportional to the impulse response $h(t)$ which is what we are after in terms of modeling this entire system. Thank you.