Computational Neuroscience
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Week – 06
Lecture – 26

Lecture 26: Stimulus to Response Mapping(Coding) - III

Welcome. So we in the last week we had concluded with the idea of the spike triggered average and we showed that the spike triggered average is proportional to the estimate of the cross correlation between the output spike train produced by the stimulus $X(t)$ where $X(t)$ is Gaussian white noise stimulus let us say and our $P(t)$ is the observed spike train. So just a recap of our model again which is our $X(t)$ we have our $H(t)$ that we want to find of this LTI system and then we are getting $Y(t)$ a proxy sort of to the membrane potential and then we have a static nonlinearity which can be arbitrary that produces the driving function $\lambda(t)$ for the point process generator which is producing the $P(t)$ which is summation our $\delta(t - t_i)$ and these t_i's are our observations over the period capital T that is over that period we are observing N_T spikes and the spikes are occurring at time points t_i. So the few results that we have so far is that our $R_{YX}(\tau)$ is proportional to $H(\tau)$ or the impulse response itself that is this LTI systems definition and that is true in the case of $X(t)$ is a white Gaussian noise process and it has a variance σ^2 then we know what the constant of this proportionality is. We also showed that our R_{PX} if we cross correlate or estimate a cross correlation of R_{PX} which is $\hat{R}_{PX}$ then that is proportional to what we call the spike triggered average which is nothing but $X(t_i - \tau)$ and this is summing over all the spikes and to capital N_T and this is nothing but the STA or spike triggered average. So now we are left with the task of connecting from P to X then λ to X then Y to X.

So we will go over these steps sequentially but to make the first step we had introduced the idea that we can convert the $P(t)$ from the spike train observed at the spikes observed at time points t_i and we have another process Q which is binned in small enough bin size δ then we said that our if we cross correlate R_{PX} that is if we cross correlate p and x get the cross correlation function $R_{PX}(\tau)$ this is approximately $R_{QX}(\tau)$. So the the Q is a variable or the process actually where which takes on values 0 or 1 and our δ is small enough such that probability of the ith bin Q_i equal to 1 is nothing but δ times $\lambda(i\delta)$ position that is almost the instantaneous firing rate there multiplied by the tiny window. So now we know this $\hat{R}_{PX}(\tau)$ estimate to be the spike triggered average that is its proportional to the spike triggered average which means that our R_{QX} is also proportional to the spike triggered average. So now can we compute $R_{QX}(\tau)$ let us say we now need to compute $R_{QX}(\tau)$ so that means it is simply the so again since Q is observations and not we do not have infinite observations we will only have an estimate of R_{QX} then $R_{QX}(\tau)$ is ideally the expectation of $Q(i\delta)$ and $x(i\delta - \tau)$ this expectation is what we need to compute.

So if we start with the expectation of $Q(i\delta)$ we have so that can be written as if now we have essentially capital M bins and there are this is going to be this needs to be summed over all the bins that is $i = 1$ to capital M where if this is the total time t our t is nothing but $M\delta$ and so the average it is replaced by the average for all the bins this expectation for each of the bins. So now if we if we compute this expectation we can do it in this particular way where we introduce a dummy variable if we consider let us say only the inside of the summation we introduce a dummy variable a and let us compute the expectation under a of this expectation $E[Q(i\delta) \cdot x(i\delta - \tau)|x(i\delta - \tau) = a]$. So this expectation can simply be written as this from basic probability and so our $x(i\delta - \tau)$ can be replaced by a so what we have here is E_a and we have expectation of $Q(i\delta) \cdot a$ so that is we have a outside and expectation of $Q(i\delta)$ given that $ix(i\delta - \tau) = a$. So essentially we are introducing this a and then integrating it out by getting this expectation. So now what is the expectation of $Q(i\delta)$ $Q(i\delta)$ that is independent of a now that is Q we know that the probability of $Q(i\delta) = 1$ is $\delta\lambda(i\delta)$ and so we can say that otherwise it is 0 so we can simply say that it is E_a and a times if we now have this x compute this expectation it turns out to be 1 times $\delta\lambda(i\delta)$ so 1 times $\delta\lambda(i\delta)$ given $x(i\delta - \tau) = a$.

So I hope you appreciate why we introduced this a that is to be able to separate out this x and compute this expectation and now we go back the same step by removing the a and that turns out to be simply our expectation of and the δ can come out δ times $\lambda(i\delta) \cdot x(i\delta - \tau)$. So the forward step that we did here we are simply doing the reverse of that step here and now what we are left with is δ and expectation of $\lambda(i\delta) \cdot x(i\delta - \tau)$. Now this is a familiar expression for us this is simply our $R_{\lambda X}$ so if we now write this is simply δ times $\hat{R}_{\lambda X}(\tau)$. So we have now an additional result from here R_{PX} $R_{\lambda X}$ and that R_{PX} is approximately equal to $\hat{R}_{QX}(\tau)$ and now we are saying that this cross correlation between q and x that is the input and q is proportional to the cross correlation between λ and x that is essentially what we show here. So you can see that we are gradually coming towards R_{YX} so what we have so far is that our spike triggered average is proportional to our R I mean the spike triggered average is R_{PX} which is proportional to R_{QX} which is proportional to $R_{\lambda X}$ and we know that our R_{YX} is proportional to our $H(\tau)$ that is what we are after.

So now we are separated by this nonlinearity this static nonlinearity which can be arbitrary and so if somehow we can show that this $R_{\lambda X}$ is proportional to this R_{YX} let us say if we could somehow show this we do not we have not done it yet. If we somehow show this then we can now say we would be able to say that our impulse response of the LTI that we are trying to obtain is simply the simply a scaled version of the spike triggered average of the stimulus. So this is the remaining disconnect in concluding that and so for that we need a special kind of theorem which is what which is called prices theorem. So that we will just assume this and show that if we have partial derivative of the expectation of $g(x, y)$ $\partial\rho^n$ will tell all the terms shown that is the same as expectation of $\partial^2 n \partial x^n \partial y^n$ of $g(x, y)$. So here x and y are jointly Gaussian zero mean $g(x, y)$ is any function that is differentiable and well behaved and ρ is the covariance of x and y which is nothing but $R_{YX} - \mu_x \cdot \mu_y$.

So in our case where we have this x our $h(t)$ and y and then we have our static nonlinearity and then $\lambda(t)$ our λ let us say $x(t)$ $y(t)$ $\lambda(t)$ then we are saying that our stimulus by stimulus design we can take $x(t)$ to be white Gaussian noise that we can play such a stimulus to the neuron depending on the system it will be a visual white noise or auditory white noise and so on. So in if this is the case then x and y because this is an LTI x and y turn out to be jointly Gaussian and our μ_x is 0 this is we have 0 mean white Gaussian noise. So this R_{xy} R_{YX} and minus $\mu_x y$ simply the ρ becomes R_{YX}. So our ρ the covariance is nothing but R_{YX}. So I am dropping the τ here to for simplicity of expressing the terms here and as we have said the nonlinearity let us say this $y(t)$ is going into the input with this nonlinearity producing this $\lambda(t)$ which can be represented simply like this that λ as a function of y that is λ as a function of $y(t)$ because it is a static nonlinearity this λ is simply I mean the output $\lambda(t)$ is simply $\lambda(y(t))$ and since we said that this nonlinearity can be arbitrary then we can of course write out this nonlinearity as a polynomial which is as an infinite order polynomial that is coefficient $a_k y^k$ where k goes from 0 to infinity.

So we have our $\lambda(y)$ given so these are all the terms that are given so far and we are assuming the nonlinearity to be an arbitrary nonlinearity here we know now that our ρ is simply R_{YX} and so now what we need is to choose $g(x, y)$ that will allow us to show the connection between λx and yx $R_{\lambda X}$ and R_{YX}. So if we if we take this $g(x, y)$ to be simply x times $\lambda(y)$ or $x\lambda$ then and $n = 1$ then the left hand side of this equation here of the prices theorem this is let us say equation a that turns out to be $\Delta\partial\rho$ of the expectation of $x\lambda$ so and that is simply $\Delta\partial R_{\lambda X}\partial\rho$ $\partial R_{\lambda X}\partial\rho$ so that means it is and that is the same as $\partial R_{\lambda X}\partial R_{YX}$. So R if $\partial R_{\lambda X}$ and

∂R_{YX} I mean $\partial R_{\lambda X} \partial R_{YX}$ is a constant that is the $R_{\lambda X}$ as a derivative of $R_{\lambda X}$ with respect to R_{YX} if that is a constant that would mean that R_{YX} is proportional to $R_{\lambda X}$ which is exactly what we intended to go after in order to complete this chain that is if we that is derivative of $R_{\lambda X}$ with respect to R_{YX} is constant that means they have a linear relationship that is they are proportional. So here if we now go forward with this assumption of $g(x, y)$ to be $x\lambda(y)$ and look at the right hand side so the right hand side is expectation of we said that $\partial^2 ng(x, y)\partial x^n \partial y^n$ and our $g(x, y)$ is λx and our λ is nothing but summation $a_k y^k$ that is we have equal to expectation of now n is 1 so ∂^2 and we have here essentially x times $\sum_{k=1}^{\infty} a_k y^k$ $\partial x \partial yn$ is 1 as we had done in the previous on the left hand side. So now if we do this partial derivatives so what we will be left with is simply expectation of a_k I am sorry expectation of with the derivative with respect to x this is gone and now with the derivative with respect to y will be left with $\sum_{k=1}^{\infty} a_k y^{k-1}$ and we can take the summation out that is $\sum_{k=1}^{\infty}$ expectation at a_k times expectation of y^{k-1} and we know that our xy is jointly Gaussian and x is Gaussian so y is also Gaussian and so this is simply the $k-1$th central moment of a Gaussian and so it is a constant. So the sum of a_k times a constant can be shown it converges and so this turns out to be a constant which is what we intended to have intended or we required to have to complete the change. So what finally we have is our λx ∂r_{YX} is a constant which means that our λx is proportional to r_{YX} and so we are done in the sense that if we get the spike triggered average then that spike triggered average is simply proportional to the $H(\tau)$ that we are after. So this connection is made and so we are done showing that indeed the spike triggered average can be used to estimate what our $H(t)$ should be. Now that we have something proportional to the impulse response using that we can find out empirically what this nonlinearity would be that is given the set of data of $x(t)$ and $H(t)$ with convolution with estimated $H(t)$ will get a number of $y(t)$'s and I mean we will get samples of $y(t)$'s and use using the connection between $y(t)$ and $\lambda(t)$, $\lambda(t)$ estimated from our $p(t)$ we can with repetitions of the stimulus we can find an empirical sort of function that transforms y into λ.

So this whole idea can now be extended to different kind of forms where the stimulus $x(t)$ is multi-dimensional that this is a vector or the stimulus I mean many different many dimensions. In the case of the auditory system let us say we can have this $x(t)$ to be simply the spectrogram or how the energy at different frequencies is changing over time. So in that case the stimulus this becomes x simply becomes a vector of elements for different frequencies and goes over time. So that is if this axis is frequency and this is time we have at each time point we have different frequencies and they have certain values that intensities for each of these frequencies and that is varying over time and we can design that to be Gaussian white noise making them independent of frequency bins and time we can then do the spike triggered averaging on the spectrogram itself that is a vector random process here. Similarly when we talk of the visual system our x will be a two-dimensional matrix or rather the pixel values in my entire field of view.

So it is instead of one vector like this it is going to be simply a matrix of white noise image for all the pixels that is our $x(t)$ and this is changing with time. So I am basically each frame of image is coming successively and that is our $x(t)$ in each time instant and so we can similarly do the spike triggered average for the visual system and get estimates of the impulse response. In this case the impulse response is going to be as you can imagine a video that is a set of frames of images over τ so that means it is a with the receptive field itself is a video and in the spectrogram case the receptive field would be a two-dimensional matrix where we have frequency on one axis and τ on the other axis just like the spectrogram itself and so in the somatosensory system also you can extend this similarly just like visual stimulus over certain patch of skin let us say we can have pixelated values of pressure or whatever the mode of the stimulation is and we with the Gaussian white noise assumption and the design of the stimulus accordingly we can use spike triggered average for the somatosensory system as well. So with the spike triggered average as we had earlier said the they are good spike triggered average turns out to be good in the periphery like in the auditory nerve in the retinal ganglion neurons RGN even in the LGN some neurons in $V1$ like the simple cells it can be modeled well similarly from the auditory nerve in the auditory system they are well modeled well predict the behavior of different types of neurons in the cochlear nucleus that is the next stage in the cochlear nucleus some neurons even in the inferior colliculus and so on. However as we go into the primary auditory cortex and beyond and here also as we go beyond $V1$ or even the complex cells of $V1$ we cannot use the spike triggered average to model their behavior very accurately.

However as we had mentioned we can still linearize those systems over a small parameter space and predict the behavior within there and maybe combine it across different points in the parameter space to get a larger model. And finally as we will later on see like in the auditory cortex and even in the higher order visual cortices even though the spike triggered average is not a very good model to predict responses of the neurons to new stimuli we will see that with behavior certain learning the spike triggered average can change that is the receptive field itself is changing due to some phenomena of learning or some perturbation to the system and we will see that those although they are not good models they are instructive in the sense of understanding and going after what mechanisms are there behind those kind of plastic changes. So even in the higher stages the spike triggered average is useful even though not as models but as other descriptions of mechanisms that may be underlying. So that we have now gone across the forward problem one aspect of the forward problem that is going from the stimulus to the response. We will now in the next lecture try to understand the backward process that is from the response to the stimulus and one particular aspect of it is reconstructing the stimulus and basically try to see what is going on in the sense of that what is producing these spikes.

So these are useful in brain computer interfaces and shown this kind of decoding methodologies that is going backward from the spike train to the phenomena that is causing the spike train. Thank you.