Computational Neuroscience
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Lecture – 23

Lecture 23 : Receptive fields and models of receptive fields

Welcome. We are into our lectures on neural encoding and decoding. In the previous lectures, we talked about statistics of spike trends, the variability in spike trends that spike trends generally follow a Poisson process like characteristics and spike counts follow generally a Poisson distribution over a certain interval. We also discussed about defining stimuli as random variables or random processes depending on the situation and how we will be treating the stimulus world in the case of encoding and decoding as a random variable or random process and how we will then try to connect it with another random variable or random process which is the spike trends. When I say random variable, the response space, if it is simply spike count over a certain window in response to stimulus whose parameters are changing, then the response is simply a random variable which is the spike count in response given a particular stimulus. However, in general, it will be a random process because we are recording from spike trends and we discussed the issue where the response measure is based on a response rate in a time window and the size of the window can vary and go down to very small values and even be a continuous time process or a point process in continuous time.

In order to go on further, what is it that we want to understand about the relationship between let us say the stimulus and the response? One way to approach is a descriptive kind of relationship which simply tells us what the receptive field of a neuron is. So if we are recording from a sensory neuron in an intact animal, let us say either an auditory neuron in the auditory pathway which you are familiar with in terms of a hierarchical pathway or the visual pathway or somewhat of sensory. These three as you may recall are the parametric, parametrizable or parametric stimulus physical stimuli and we also have the chemical stimuli which are olfaction and gustation where we do not have a parameterization of the stimulus space. So these have no parameterization possible so far.

So essentially in these cases, we have to resort to this idea that a neuron responds to odorant A and odorant B of a set of odorants A, B, C, D let us say and maybe we can also add to it that to the odorant A, the neuron responds with certain number of spikes per second and to the odorant B with another certain number of spikes per second or even talk about temporal pattern of spikes that is by changing the time window of binning of the response space. So along those lines, even in the auditory and visual and somatosensory stimuli, we can have a descriptive definition of the receptive field that is how it actually all started. So for example, we can have let us say we are recording from a visual neuron and we are representing in this rectangle the entire visual field of view in front of us and or the animal from which recording is being performed and we are essentially getting spikes and now we start to flash lights at a small resolution along this entire window and we measure the number of spikes occurring to light flashes in each of those positions X and Y. And we find that in this particular region that is when we have flashes of light here or here or anywhere within this circular region, the neuron responds to the light flashes. Then this circular or region is sort of the receptive field of the neuron that we are recording from.

So there are a few things here. One is the number of spikes we said that the neuron responds and so with it as in we discussed in the previous lecture, we must have a response measure that is essentially for now it is the time window or time resolution of the response and the other thing is how to understand that there is a response. So let us think of it in this way that there are spikes occurring in neurons spontaneously as well. So that is without any stimulation due to simply noise or other fluctuations going on from other connections coming in where there is activity, we have spiking as a baseline. So let us say we are recording and we obtain spikes at certain windows.

So this time period let us say is the baseline or in other words during this period we are not doing any stimulation and let us say in this period the light flashes are coming on and here also we find spikes occurring at certain intervals and then it responds again with its spontaneous activity. So to conclude that there is a response here in response to the stimulus in this particular window, so this is the stimulus, we have to compare it with the baseline where there is no stimulus and assume that preceding stimuli even before the baseline are in no way affecting the responses in the baseline. That is it is indeed a true baseline, I mean theoretically a true baseline as if there is no dependence on anything happening in the past. So to compare since we know that these are random variables that is the spike count in an equal sized window in the baseline as the stimulus window. So let us say this is the stimulus window and this is our baseline window, the cyan and the red they are of equal sizes.

So we need to compare whether the number of spikes occurring in that same window in the red window and the cyan window are different or not. Since these are random variables we have to take help of statistics and we also have to do repetitions to get a better estimate or at least a good estimate of how many spikes we can expect from the stimulus and how many spikes we can expect due to in the baseline period of an equal amount of time. And as I have drawn in this picture there are four spikes and four spikes in both cases. So by just looking at this we cannot conclude whether there is a response or even we cannot conclude that there is not a response that definitely there is no response that also we cannot conclude. So it also means that here we are considering the response measure to be the number of spikes in whatever window size we are considering.

It may be that by changing the response measure there may be a way by which we can say that they are different in the baseline and the stimulus. So that could also mean that there is a response at least in terms of the spiking happening that we are observing. So for example when we are talking of, so let us go to a new page and let us say that the response measure is by count or simply the average firing rate which is the number of spikes by the time window that we have. $R = \frac{N}{T}$ So we perform this stimulus presentation over and over again on multiple trials. Let us say we repeat one, two, this is the i-th trial, let us say we do capital N trials.

So how many trials we need to do also depends on how variable the responses are and based on knowledge from previous experiments and so on we have an idea for the structure that we are recording from how many repetitions are good enough. In other ways you can also think of it in this way that if we see that by increasing the number of repetitions we are not changing the response spike count, average response spike count or average response rate then whenever at whatever capital N we are seeing a sort of convergence of the rate of spikes we can consider that we have sufficient number of repetitions. And similarly preceding each of those repetitions we will again have a baseline period which we had in the cyan lines and so we have rate B_1 in baseline rate or spike count B_2 I am using it interchangeably here and rate b_i and b_N. Similarly we have in the response window R_1, R_2, R_i and R_N. So now we have to ask this question whether this set of responses or baseline values and the set of responses, sorry set of responses they are significantly different or not.

So remember that a response can be an increase from baseline, can also be a decrease from baseline. That is the neuron may be inhibited due to a stimulus and it may be inhibited significantly such that the number of spikes occurring is lower than baseline, substantially lower than baseline or if a stimulus is exciting it may be above the baseline. So these we do based on statistical test, hypothesis test where we simply ask the question whether the mean of the observations R_1 to R_n is higher than or first is different from the baseline observations B_1 to B_N. And we basically now compare the means of these two. So we have statistical methods for it.

Usually we use a t-test assuming that the distribution is Gaussian like which is the case when we have a sufficiently large spike rate and we assume that the rate is continuous random variable. Then the Poisson converges towards a Gaussian distribution. It can be approximated close to a Gaussian distribution and so it becomes a test of whether the two Gaussians are significantly different or not and that depends on how variable the two distributions are. So let us say this is the distribution of responses where this axis is rate and let us say this is the distribution of baseline windows where these B values are indicated by the cyan distribution. So B_1 to B_N are representing this cyan Gaussian window or Gaussian distribution and R_1 to R_N represent this red Gaussian distribution.

Now we essentially ask the question whether this mean value and this mean value are significantly different or not and that depends on how much overlapping region we have in this region. That is because that is the region where if we observe a rate in this particular range then we cannot be sure whether it came from the baseline or whether it is same as the baseline that is came from the baseline distribution or it came from the rate distribution or the response distribution. Similarly if the rates are in this range which it is highly unlikely that the number of spikes observed come from the baseline distribution or that there is probably response in there and if the observations are in this range we can obviously be sure that it is coming from the baseline but again there may be another window where we can say that the responses if it were much lower than that if there was a rate distribution on the left then it would be lower than the baseline distribution. In this case it is on the right hand side so we are not worried about that part so it is an excitatory response. So the details of the measures that are involved in calculating this whether there is a significant response or not that is a statistical problem and we have functions in available to us by which we can do this statistical comparison and say with certain confidence or with a certain probability that indeed there is a response and usually we use confidence level of 95

And so from those kind of tests we can conclude that there is a response or not and so if there is no response that is if the rates the mean rates are the same or the baseline distributions and the rate distribution are highly overlapping and so we cannot say with confidence that there is a response then we can only conclude to this point that there is no response if we consider rate as the response measure that is the overall rate over the entire time window which is essentially the spike count also during that entire time window of the stimulus. We are assuming that the time windows are constant in the same in the baseline and in the stimulus period and in every trial. So it may be as I was saying that there is a difference in the responses at a finer resolution of time and that comparison requires further kind of measures where we will be talking about them later on when we discuss discrimination along the same line and say that okay there these are discriminated by the neuron in terms of the responses produced and the timing of the spikes. So for the most part when we are considering when we are considering the rate response we do not pay attention to the specific time of the spiking and so it is the response is independent of where the spiking occurred if which is what it is when we have a fixed Poisson process that is with a fixed rate homogeneous Poisson process and in the other case we can have an inhomogeneous Poisson process. So in the homogeneous Poisson process we have a fixed λ in the response period and the fixed λ in the baseline period which is what we were comparing here.

This is the λ_r estimated from the data this is the $\lambda_{baseline}$ estimated from the data. However the response may be actually $\lambda_r(t)$ which is an inhomogeneous Poisson process or as we had also said that by discretizing time as δ_i in the ith window post the stimulus. Similarly the λ_b can also be $\lambda_{baseline}$ as a function of time or in the δ_jth window in the baseline period and so this requires comparison over the entire time and those comparisons are different. So the point that we are trying to make is that saying that there is no response based on the spike rate is does not necessarily mean that there is no response for any kind of response measure. So that needs to be kept in mind.

Having said that we will continue here with the idea of simply spike count or response average response rate over the entire time window for the ensuing discussion of receptive fields. So we came to this point of whether there is a response or not based on the response observed or the spike trends observed in terms of flashes of light in that circular region. So let us just recap that so we have this rectangular region which is representing the entire field of view in front of us and we have this particular region when there is light presentation in that circular region then the neuron that we are recording from responds significantly over baseline based on our previous discussion of how to compare and we can then say that we will then say that this circular region is the receptive field of the neuron and this is although we did all these statistics and measure of response and so on this is essentially a descriptive kind of receptive field. In other words we have not understood the relationship between the stimulus and response. We have only identified a region in the stimulus space to which the neuron is sensitive.

That is a fine thing in the sense that we are describing the receptive field in some way but we are not quite quantitatively getting into the idea of the relationship between the stimulus and response. So this brings us the idea of how to model the receptive fields and before we go into the modeling of the receptive fields we then also need to understand that the receptive field, the descriptive nature of receptive field that we say by this region in the field of view to which a neuron is sensitive it is only a boundary. So there may be specific features in the stimulus that is the way the flashes are occurring over all together in that entire receptive field to which the neuron may be extra sensitive. So we may be able to parameterize the stimulus in a particular way within that circular region and then conclude that a particular set of parameters is what the neuron responds best. So for example since we are discussing about the visual system, in the visual system what long ago Hubel and Wiesel showed that in the visual cortex there are neurons that respond to oriented bars, bars of light.

So essentially if in this region we have a bar of light let us say we found that round circular receptive field region now we are qualifying it further as to what within that region describes the response of the neuron best or at least what kind of stimulus within that region makes that neuron fire the most or produce the maximum firing rate or how varying the parameters within the receptive field that circular receptive field the neurons responses are changing. All these are indirectly ways of representing receptive field of a neuron. So it may be that we have a dark region surrounding a light bar like so and it may be moving in a particular direction generally a moving bar. And let us say what Hubel and Wiesel did was that we have this axis horizontal axis and this angle of orientation of the bar is
$theta$ and we are measuring responses as a function of
$theta$. So we have this axis as
$theta$ and if the orientation can vary between 0 to pi or actually 0 to 2 pi if we consider the direction of motion as well.

Now as we vary
$theta$ we measure the responses of the neuron for each of those thetas that we test may be that 0 then 22.5 then
$pi/4$ then 75 degrees 67.5 degrees and
$pi/2$ and so on. So basically we are dividing the 0 to pi into 8 specific or 9 specific stimuli the parameters that is the
$theta$ in this case is being changed from 0 to pi in discrete states. And we measured the rate of response for the 0 angle so when the bar in that circle is horizontal and then it is tilted and in this case it is vertical and in this case it is again horizontal.

And we plot the number of spikes or rate assuming the duration is same along at these points. And what we find in these in visual cortex neurons that are simple cells that they respond with a peak at a particular angle of orientation. And this is called what this is known as orientation tuning that is neurons are tuned to particular orientation of the light bar and this also is a description of receptive field of that neuron. That is which essentially says that it responds strongest to a 67.5 degree oriented bar with pi count as the response measure.

However this does not answer the question that if there were two bars in there that is one horizontal bar. So let us draw it separately. Let us say this is the round region. Let us say now the stimulus is something that is horizontal bar and a bar at 45 degrees let us say.

These two together. So this also can be a stimulus but the answer to the question that what would the response of the neuron be to this kind of a stimulus cannot be obtained from this description of the receptive field. So we need better models in order to be able to describe or better definitions of receptive field in order to be able to describe the relation between the stimulus and response in a more complete sense. I am not saying that we will be able to always be able to do this accurately for every neuron But the objective here is to define the receptive field as a model of the neuron in terms of its response as a function of stimulus parameters or multiple stimulus parameters. So the first thing about it is that it is not that the response is going to be what the response is at 45 degree and what the response is at 0 degree and you add them up together. That is not how neurons generally behave.

However if it were to behave in this manner it would be a very linear kind of neuron but in general this is not true and so we require better receptive field models and that brings in the idea of having models for the neuron to describe its receptive field or its relationship how it relates the stimulus to its response to be able to predict that response given new stimuli. That sort of question is what we would be after in terms of understanding encoding and decoding by a neuron. So in the next lecture we will start with this basic idea of building models. We will start with what I just described as the linear model.