Computational Neuroscience
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Lecture – 51

Lecture 51 : Adaptation

Welcome. We have discussed about plasticity and both short term and long term. We have shown how to implement short term plasticity or long term plasticity with variety of rules in networks or at least in single output and multiple input cases. And shown how variety of developments of over Hebbian learning. And so now we would like to once look at the implications of such kind of plasticity in terms of the computation that is being performed or phenomena that are outcome of such plasticity and how that affects neuronal processing and how we can implement those kind of changes into the models that we have been talking about. So let us first start with discussions on short term plasticity.

So we know that these are temporary changes just a small recap in synaptic strength. So we know that we know the phenomena that if we have a presynaptic neuron we make it fire an action potential and we measure the post synaptic neurons response to that action potential and we do this repeatedly for a few times. So we see decay in the synaptic strength based on the EPSP or IPSP or there is a facilitation in that synaptic strength that is which are the two cases for potentiation and depression in the short term plasticity. And if you leave the system for a while undisturbed then you get back your original EPSP sizes.

So we will discuss two particular phenomena which are exactly based on opposite kind of stimuli I mean not exactly opposite but conceptually opposite kinds of stimuli. One in which we have low probability stimulus and a high probability stimulus. So and in other case we will have one particular stimulus that has very high probability and the others many others have low probability of occurrence. And this is also somewhat what we I mean with these kind of paradigms once we go into the discussion you will realize that both are actually essentially what we know as adaptation. So we know of many phenomena that we call adaptation essentially it may be short term plasticity or long term plasticity because the word adaptation essentially would mean it does not actually differentiate between the temporary change or permanent change.

So if you enter a dark room for example and you are in there for a little longer initially you would not be able to see anything and gradually you adapt and then you get to see at least the major structures in there in the dark room and with minimal light. Similarly when you are hearing a sound for a long time gradually its sensation reduces and these are all replicated in the responses and can be explained by these short term phenomena. So particularly here let us consider these two cases where in one case we have what we call is an oddball paradigm and that is given by so we essentially have two different frequencies let us say f_1 and f_2 in the auditory domain. So let us say one particular frequency is presented repeatedly multiple number of times so this is time and with a sufficient gap about let us say 300 milliseconds or so we are playing a particular sound that particular frequency and some very on rare occasions let us say 10 percent of the time we present f_2 and so on. So this is basically how the stimulus if represented in frequency and time would look that there is energy in this particular frequency periodically at certain intervals and sometimes that particular frequency is missing and replaced by a higher frequency let us say f_2.

So what the phenomena that we will talk about is called stimulus specific adaptation. So in this case what happens is that the presence of this f_1 which is also called the standard tone and the other is the oddball or the deviant tone because of the repeated presentations of the standard tone the neuron that which we are recording from is its inputs are adapted to f_1 the synapses that are providing input along the neurons that are responding to f_1 they get adapted and the ones that are responding to f_2 they are totally unadapted because it is not presented at all and when we play the f_2 sound there is a much stronger response. So that stronger response can however also happen if let us say as we recall tuning of the auditory neuron let us say this is frequency where this is f_1 and this is f_2. If the neuron's tuning curve let us say this is rate if the neuron's tuning curve is something like this where f_2 by itself produces a very strong response then of course even it does not matter whether we are presenting it rarely or frequently I mean in spite of being presented frequently it may have a very strong response. So it is we have to take care of the phenomena that it is not the inherent tuning of the neuron that comes into play when we are thinking of this stimulus specific adaptation and we have to control for that tuning.

So essentially what is done is these are played in a pair of stimuli that is wherever you have the f_1 in another set of stimuli you play f_2 as the standard and f_1 as the deviant or the oddball and so on. So in this case f_2 is standard and our f_1 becomes the deviant. So now in both the cases we have responses to f_1 I am sorry we have responses to f_1 either as a standard or responses to f_1 as a deviant. Similarly we have responses to f_2 as a standard and f_2 as a deviant. So if you come up with a measure of what whether there is stimulus specific adaptation or not and whether the neuron selectively prefers responding to any deviant tone then we need we can create a measure like this where we take the response of f_1 as deviant and f_2 as deviant and then we subtract out response to f_1 as standard and summed with f_2 as standard and then we can normalize it by the sum of these things so that it stays between minus 1 and 1.

So as you can see in this measure that if this measure is plus 1 it would mean that this f_1s plus f_2s is simply 0 that is our there is no response to f_1 or f_2 or f_2 as the standard. However when those same stimuli are occurring as deviant they have some positive response and that would lead to a plus 1 deviant detection or CSI I mean this measure of stimulus specific adaptation there are multiple ways to name it one of them is CSI or which is cumulative selectivity index. So here if you now think of the other extreme where the CSI is minus 1 then I am sorry this is common selectivity index common selectivity index. So if it is minus 1 that means that our response to f_1 and response to f_2 is 0 as deviant. However whenever it is presented as a standard we have responses positive responses.

So which means that there is no selectivity for the deviant response. So neurons in the auditory pathway are shown that many neurons show positive value of the CSI which means that they have this kind of selectivity to a deviant sound and we will now just see that at least in one kind of model it can be shown that it is based on short term depression. So we should also add that the evidence builds in favor of that idea of short term depression based deviant detection phenomena based on the fact that as we go higher up in the hierarchy this CSI values of neurons gradually actually increase and become more and more positive. So once we explain the model we will see that if we cascade the model further and further we should be getting higher and higher CSIs and so that is one of the ways of thinking about whether this is true or not but there are other ways also by which this can be explained but all of them require some sort of short term depression. So let us see how to explain this so I would put it very simply here.

Let us say this is the frequency axis we have F_1 stimulus here we have F_2 stimulus here let us consider a neuron that is tuned equally to the F_1 and F_2 or they respond equally strongly to F_1 and F_2 so let us say the rate responses of the neuron it is F_1 this is F_2 it is tuned in this particular manner. I am sorry this is F_1 this is F_2 let us say so it has almost equal rates on both sides of the best frequency of the neuron. So this is the final output neuron whose spikes are being measured and as we have briefly mentioned that there is something called tonotopy let us assume that there are inputs coming spatially and also the connections are such that there are parallel frequency inputs coming in to the final neuron and so let us say there is a neuron at a lower stage that is tuned in this manner there is a neuron at this stage that is tuned in this manner there is a neuron at this stage that is tuned in this manner and so on. So now let us say all of these three are providing inputs to this same neuron so when we are repeatedly playing F_1 as standard what is happening is due to that short term depression phenomena that we have talked about the output of this neuron whose this is neuron 1 this is neuron 2 neuron 3 output of this neuron the synapse that is connecting to the output neuron let us say this is the output neuron this synapse gets adapted and also this synapse gets adapted and also maybe this synapse also gets adapted. However because this third neuron is not at all activated by F_1 it is this synapse is totally untouched so this is totally unadapted so while the responses to F_1 and F_2 F_1 are going on and gradually decreasing due to the adaptation in these synapses all of a sudden when the F_2 stimulus comes in there is an immediately a strong response to F_2 and this response once and then again this synapse will not be adapting again because we are switching back to F_1 so again F_1 is still adapted and you are getting small responses to F_1.

So overall what we will see is that whenever F_2 is occurring it is occurring with a high rate and overall F_1 is occurring at a adapted rate so that response of F_2 is stronger than of F_1 because of the short term depression in the synapse that we are that convey the F_1 information to the output neuron. Now just the swap can be considered by simply looking at the other way round where we are playing F_2 as standard and F_1 as deviant and basically in that case then neuron number 1 is not at all responding to F_2 when F_2 is occurring as standard and so when F_1 occurs as a deviant that synapse this particular synapse is unadapted in this case and whenever F_1 occurs this unadapted synapse allows a strong input going in to the output neuron causing a strong response to F_1 as the deviant. So this observation that we see is called deviant detection and there are few other ways to think about these problems based on other paradigms of this input and some of them can be explained by this short term depression others require top down input to come in and so on. So in short this phenomena that we are seeing stimulus specific adaptation or deviant detection is actually a very well studied and long observed phenomena in the auditory system and actually is present in other sorts of systems as well and is what also is known as or at least forms the thought to form the basis of some phenomena called mismatch negativity. So mismatch negativity and this has been used in a number of ways from diagnosis to understanding particular kinds of processing in the brain and an explanation for why this may be occurring at least part of it is based on the short term depression that we have learnt about and so implementing this is quite easy now for you if you want to implement this you just need to implement these three or I mean I can have an array of neurons it is very easy to implement these three or four or five neurons and in these synapses you need to incorporate simply short term depression may just the easiest model that we have talked about which is the three state model that is sufficient to show this phenomena computationally on in a basic network model and it can be as you can now think about it if we have multiple models of this phenomenon multiple such cascaded structures with gradual more and more I mean more and more neurons overlapping and this getting wider and so there are inputs coming from further away which are responding to F_1 but not to F_2 and so it gets stronger and stronger this kind of deviant detection phenomena.

So the other kind of case that we have we mentioned that we will discuss is that there is now opposite kind of thing that there is one stimulus that is extremely high probability and that is occurring many many times and each of them and each of the others are occurring like the deviant very few times. So let us see what that would mean so in this case we will consider sound level as the parameter for the stimulus this is also an auditory phenomena that we will discuss however just to get back to the idea this same idea can be used in the visual system somatosensory system and so on. So it is I mean this mismatch negativity is observed in multiple sensory domains and can be explained at least for the first part with short term depression. So let us get back to our other example in this case also we will first talk about the auditory system and in particular in this case it will be the intensity of the sound or sound level. So if you may remember that let us say we have neuron who which is responding to a broadband noise of a certain intensity and that intensity is gradually changed on or increased then what we can we will see in this case let us say this is intensity and let us say this is our rate response from the neuron and the response is so there is some sort of a threshold that is below that intensity the neuron does not respond to the noise burst and then the neuron starts to respond and this saturates and stays here.

This is just like the output nonlinearity of neuron model that we have we had talked about like the spike trigger average followed by an output nonlinearity. So that is providing that threshold and the saturation of firing rate and that is what is being observed is in this case as the at the systems level. So now if we play a stimulus let us say if this axis is intensity let us say this is low intensity let us say 20 dB SPL let us which is around here or 20 dB SPL let us say this is 90 dB SPL. So we are varying the intensity from 20 to 90 here and now we are playing stimuli from each of these intensities randomly over time the same way we were going with f_1 and f_2 instead of f_1 and f_2 we have intensity 1 intensity 2 to intensity capital N let us say let us say from we are going from 20 to 90 that means 7 I mean about 15 or so stimuli if we do 5 dB steps but the occurrence of a band of these stimuli let us say from 55 to 65 dB the sounds in these this intensity range are make up 80 percent of the stimuli occurring in time. So every sound is being repeated sorry every sound is being repeated at certain interval let us do this time interval first.

So in every interval we are getting one particular sound particular intensity noise where in this intensity we are getting sounds more and more often and much less number of times in other intensities and so on. So if we look at the distribution of the sounds intensity so intensity and probability then in this case if we take the sounds that are this particular range of intensities then they occur with the sound they occur with let us say 80 percent probability and the rest of the sounds are occurring with all of them together with 20 percent probability. So this phenomena that we will see now is that this same neuron that had this response which is let us say has a threshold at 20 and let us say it saturates at around 50 dB SPL and then up to 90 dB SPL it is saturated. The same neuron when presented with these stimuli as we have described here we again are playing the same stimuli that were used to collect this particular curve used to obtain this particular curve of rate versus intensity. So now it is so this was obtained by equal number of presentations with large gaps of each of these intensities.

However here in the other case what we are seeing is that a set of intensities were played multiple number of times so we are averaging those cases and the other ones are occurring much fewer number of times. So what we will see is what is known as adaptation to sound level statistics and that is so it is this is 55 to 65 dB SPL then often what is seen is that the neuron shifts its rate intensity function such that the maximum occurrence is put now into the dynamic range of the neuron. So this phenomena actually starts right from the auditory nerve and is present even in the auditory cortex in another form but it is present first seen in the midbrain in the auditory pathway and so this and now if you do the variation of the version of the range of intensities from 55 to 65 if you make it another one that is 65 to 75 let us say then again it can be something like this or now if it is a range 45 to 55 in this range then it may be something like this. So with depending on what particular set of stimuli are being presented with higher probability the neuron adapts such that it is not able to adapt to the higher probability of the neuron. So with higher probability the neuron adapts such that it can devote its resources to differentiate those occurring on multiple occasions in a better fashion over time.

So now to go back at the mechanisms of this at least one particular model it can be shown by again in the same way that this adaptation is occurring through synaptic depression by now in this case if you the assumption is that you will have higher and higher depression as the intensity increases and you will also need a network of neurons that are responding to different kinds of intensities. So this particular phenomena the similar thing in the visual system can also be seen and that is what we call adaptation to contrast stimulus contrast. So in this particular case the particular example that I am talking about is that if these are from the thalamic neurons in the visual system in the LGN. So if you play movie of very low contrast images I mean throughout the movie the contrast is very low that means the range of values over which the pixels intensities vary is much smaller compared to another case where the range of values over which the pixel values vary is much larger. So low contrast let us say if we were to draw a distribution of the values then if this is the mean then low contrast is a sharp distribution whereas low contrast may be something like this and high contrast may be something like this that is it has a wider range of values present.

So in the case of low contrast now if we obtain the receptive field of the neuron we find that the receptive field switches between based on the contrast of the stimulus to different sized excitation regions and inhibition regions and in basically keeping in lines with being able to code the entire range of the stimulus or the entire range of the pixel values intensities in the different pixel values. So this particular example again can be used to study the range of the values over which the phenomena like how we adapt to different intensities under different situations and how the retinal pathway is organized. So so far that we have talked about we have talked about simply the simple models of our of a network that can explain the observed things with short term depression. So, in the next class we will discuss about how to implement models that will incorporate this kind of short term depression in a at a systems level not necessarily with short term depression at synapses, but in a different form. Thank you.