Computational Neuroscience
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Lecture – 59

Lecture 59 : Spike Timing Dependent Plasticity - a theoretical Perspective

Music Welcome, so we have been discussing theoretical aspects of neural coding and plasticity. That is how from theoretical principles many aspects of neural coding like representation of stimuli or even plasticity can be or outcomes of plasticity can be derived based on theoretical principles. So we had introduced this topic with the idea that it is probably not feasible or possible to perform all sorts of experiments with all kinds of neurons in all the systems, be able to record from all the neurons and so on and so forth. And since there are no current laws that govern these sort of functions, we need to come up with principles, optimality principles or some other principles based on which we can actually predict how the behavior of a neural system should be or a particular aspect of a neural system should be. If evolution or some whatever way the system has developed has been following some set of rules or some common principle. And so far what we have talked about is essentially information remaining intact which is either being able to reconstruct the stimulus or maximizing mutual information between the stimulus and the response with minimal amount of energy.

That is sort of what we have been discussing so far in terms of receptive fields or how receptive fields should be in the visual system and auditory system at least at one particular level of the system. And those can be extended for further cases or further higher up in the hierarchy of that particular system. And we have looked at one example where we have explained the outcome of plasticity through theoretical principles. So now if you recollect our idea of spike timing dependent plasticity or STDP, let me just remind you that we have a presynaptic neuron and which is projecting onto the spine of a postsynaptic neuron, dendrite is here, this is the dendrite, this is the axon of the pre, so this is the presynaptic neuron and this is the postsynaptic neuron and this is the output of the postsynaptic neuron.

And we know that if we have a spike in the presynaptic side and a spike in the postsynaptic side with a gap of delta and if this association is done for a long period of time, for multiple times then this synapse strength is modulated or it changes based on this delta. And so the general Hebbian plasticity rule that we have is that if this axis is delta, which is post minus pre, that is positive is that the post is larger than pre, that is the postsynaptic neuron spike occurs after the presynaptic neuron spike, then we have a potentiation and otherwise we have a depression when delta is negative. So post minus pre and this is the change in delta or weight of the synapse. This is the synaptic strength change. So as we had discussed that these rules are pretty synapse specific and it is also dependent on state of the neuron, that is upstate or downstate and variety of other situations, I mean firing rate regime and whether we are considering single spikes or doublets of spikes or triplets of spikes and so on.

And those rules are different for the different cases. Similarly the type of synapse, whether it is from a particular excitatory neuron to excitatory neuron synapse or excitatory to inhibitory of a particular kind or inhibitory to excitatory of a particular kind or region of the cortex, the functional region that we are in, these spike timing dependent plasticity windows are different. So it is, remember that we had talked about these experiments as with long term plasticity, these require a long time of data collection from a pair of neurons that are connected, patched together. Or patched simultaneously. So these are very very difficult experiments also.

So it is impossible to be able to derive such learning rules for each and every type of synapse in each and every region of the brain. And so we require theoretical principles to guide us in terms of what should be the way that these synapses should be adapting based on certain principles. And so the first work regarding this was by Galchechik about 20 years ago. So this is the first time such work was done. And the work that Galchechik did was, showed that if relevant mutual information between the input and output is maximized, then the spike time dependent plasticity rule that emerges, just like we have been talking about what receptive field emerges for minimal activity and maximum information retention, here what learning rule emerges.

We find that it is indeed the Hebbian plasticity rule, that spike time independent plasticity rule that emerges out of these theoretical principles. So the way the problem is set up is that we have an output as a function of time y_t, w_i, there are capital N, this is representing the capital N synapses onto the output neuron from capital N inputs, which is x_i, x_1 up to x_n. Each of them is a function of t, are what the inputs are. And so all of the inputs are active simultaneously and each of them are weighted by w_i and we get the output. This is the standard way we have looked at the rate based representation with the output nonlinearity of the neuron being absent when we are operating in the linear regime of maybe that sigma in nonlinearity or what have you.

And here what the input activity $x_i t$, the input activity $x_i t$ is represented as a synaptic input, where $s_i t'$ is representing the spike times in the input and $f_\tau t - t'$ is representing the kernel that or the postsynaptic potential that emerges out of the spike in the input. So as explained here, this $s_i t$ is simply as we have always represented a spike train, it is the summation $\delta t - t_{spike}$ or where t_{spike} are the spike times of in this case the i th input spike train. And the f_τ which is constrained to be summing to one can be an exponential decay or can also be some other form. In this case they have considered it to be an exponential decay and this is a pretty standard way of formulating the whole problem. So the real question is, this is what we have so far is a standard representation of neuron's output based on input spike trains which are converted into postsynaptic potentials by and weighted by the synaptic strength.

So the question or the formulation is that what should we maximize is that we consider that there are m plus one input patterns that is let us say which are represented by i like so. If there are input patterns like that, $x_i i$, i goes from one to n then the system has to be able to discriminate all these m plus one patterns in the best possible way. Which is essentially maximizing the mutual information between a specific set of patterns or input that is driven by a specific set of patterns and the output activity y_t. So here what is important is that just in the previous example in our last class that we talked about we had essentially two stimuli and if we have those two stimuli it is very easy to intuitively think of it as the one that is producing a lower activity is going to be strengthened. The one that is producing a higher activity can be weakened so that the overall activity keeps on is minimally used.

So here also the same kind of idea is there but there are large number of patterns and so in another space they have to be sort of maximally separated. And with the y under certain assumptions again with large uncorrelated inputs behind the output spike train you can actually assume that this y is given a particular input pattern the eta-th pattern is Gaussian in nature. And each of them can be the probability of them can be weighed by p_η. And so the overall mutual information in this case assuming a continuous function continuous output y is the difference in the differential entropy of the output and the differential conditional entropy of the output given the particular input that is present. So the h_y given eta or a particular input pattern is Gaussian and with the h and then we can actually show that with gradient ascent where our derivative of the mutual information the term here with respect to w_i under correlated activity between y and x defined by these correlation functions or correlation matrices rather you can come up with the gradient that will show us that if we have to keep on increasing the mutual information then the weights have to change the Δw the weights have to change along the gradient of this mutual information.

Or I_y given eta. And while this expression that we have is not completely intuitive what this term actually shows is that we will have two basic terms in this expression where one will be leading towards potentiation and one that will be leading towards depression. And if we have a long enough time window over which this operation is happening that is we are updating the Δw or the w then the overall average change in the weight as a function of the learning time and the presynaptic time. So this is the timing of an output and this is the timing of the input or presynaptic spike. So it is drawn in the opposite way we are used to $t_{post} - t_{pre}$.

$t_{pre} - t_{post}$ here it is $t_{pre} - t_{post}$ and the theoretically derived learning window from the previous examples is showing that same potentiation on average when the post spiking follows the pre spiking. And there is a general depression in the synaptic strength following the post spiking that is preceding the pre spiking which is exactly as what is represented in our Hebbian spike time independent plasticity rules. So on principle on average this is clearly showing the same sort of idea that we have observed experimentally although it is obviously not exact because we have something like this as the learning rule. But those may be derived from other small assumptions or other small changes which may actually imply certain aspects in the processing. So this is only one example that has been shown.

So some work along the same lines if you have an inhibitory neuron projecting on to an excitatory neuron that is an inhibitory synapse. If you have the exact same kind of format same kind of formulation and show the entire process you can actually show that it is exactly the opposite and this inhibitory to excitatory plasticity would turn out to be anti Hebbian. That is it would be something like this as opposed to what we are seeing in this particular case which is excitatory. So and indeed there are inhibitory synapses that are anti Hebbian in nature not exactly like this but in the same way that we have shown earlier that there is a flip of the entire learning window. That is it is a sort of reflection along the horizontal axis.

So again in this example that we have talked about and the example that I am just mentioning here. It is a fairly simple kind of network where we have these capital N input trains and we have this capital N synapses. And we have the output here. It is not and the update rule is only on these synapses. So there are a few more considerations here.

That is what the assumptions that we have made are in a particular firing rate regime. If you read the paper in details that describes this whole process and that they are Gaussian in nature. So what if the assumptions are changed? If we consider the down state versus up state which would mean that we have a higher firing rate regime. What happens in that case? Here we are considering in this example we are considering just an inhibitory set of inputs in isolation on an excitatory input. What if we consider a network in this manner where we have an inhibitory interneuron in general and we have a common input driving both of them.

Can we derive under this scenario the plasticity rules that will emerge for these three synapses under sort of similar principles. So this is a common motif that we have in the cortical circuits. That we have an inhibitory interneuron. Of course it is not just one neuron to one neuron kind of inhibition. There are multiple ways you can set this up with multiple number of neurons, multiple number of inhibitory neurons and so on.

So these are sort of the questions or ways in which these problems can be taken forward. Let us also say, let us now put in the particular functionality of the inhibitory neurons. Let us say that this inhibition is subtractive in nature versus this inhibition is divisive in nature. Would we get the same kind of learning rules? What would be the difference? So that is simply like a prediction of what the plasticity learning rules would be for a particular kind of inhibitory neuron like let us say the parvalbumin positive and the somatostatin positive. What are the difference between their inhibitory neurons that are expected from these kind of theoretical principles.

So this is only to get you started in thinking in these directions of approaching problems from first principles and not having to completely rely on empirical data and relying on experimental abilities and so on. So this is one of the ways in which computational neuroscientists can contribute and basically collaborate with experimentalists where you can discuss with intentions of predictions and seeing observations and then go back and forth between the theory and experiments. So I hope that with these four lectures on theoretical approaches you appreciate the importance of theoretical approaches in computational neuroscience and neuroscience in general. So with this we will end our lecture today and we are now left with one lecture where we will discuss briefly on some of the current topics that require attention of computational neuroscientists and some of the things or directions in which you can take up work and perform research. Thank you.