Cognition and its Computation
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Lecture - 16
Coding by Neurons

Welcome. We have so far, introduced you to the neurobiology of computation and we have also discussed the role of the key player in this computation which is which are synapses. And particularly chemical synapses, is what we have discussed neurotransmission through chemical synapses. How information is conveyed, from one neuron to another. And we have also talked about adaptation of neurons or even neuronal circuits.

So, to speak based on changes in the properties of the synapses, specifically we have talked about the strength of the synapses changing over time based on the input and the output activity of the neuron. And, this is this basic mechanism is called synaptic plasticity. And later on in our course we will see how important and how this plays a big role in terms of learning, in memory, in basic cognitive aspects and what have you.

So, before we go further, we have in another lecture you have learnt about the basic structures of the brain, the basic anatomical structures and so now, we will delve a little deeper into the way the brain processes and stores information about the external world, from which we make decisions and we learnt things and so on. I mean, so, it is the sensory world that provides a way for the brain to gain information about what is happening around us.

And, so, for that purpose we will be discussing the sensory circuits involved in this and this is basically, how it is represented, how the sensory information is represented along the different pathways, different sensory pathways. And, these lectures will provide you the tools to understand the basis of perception in the brain about the external world.

Although, when we talk about sensory circuits, we will be talking about the 5 senses primarily. There is a whole other system in the autonomic nervous system, where there are also sensory neurons. And we will not be discussing them here. So, and in fact, most of the autonomic nervous system we would not be discussing although they that whole system also plays a big role, primarily the sympathetic and parasympathetic system the whole flight or fight reaction that is governed by the systems..

And then there is the sensory system there are also or sensory neurons there, where there are sensors that like sense internal properties of let us say the blood like blood pressure and blood oxygen, levels of carbon dioxide contents of the gut and so on. There are many such sensors there also. However, our discussions in this course will be limited to the primary 5 senses which is audition, vision, somatosensation, olfaction and gustation which is taste.

So, in order to start these discussions we have to introduce a new concept first of all and that is, what we mean by information being coded by neurons. So, as we have said that with the basis of all computation is spiking mostly, that spikes convey the information that is computed by a neuron based on the inputs to it and then it goes on to the next stage neuron where, it is integrated with other information coming in from other neurons and so on.

And so, there is a hierarchy that is present throughout the pathway if we consider all the sensory pathways, we start with the basic peripheral level where the peripheral nervous system through the means of some sensors interacts with the external world either physical or chemical; chemical meaning the olfactory sense and the taste sense the in our through our mouth tongue.

And so, these sensors play a critical role in providing the information of the external world. So, it is the properties of these sensors that ultimately determine, what from the external world is actually being conveyed to the central nervous system into the brain based on which the all the computations are being performed and we perceive the external world.

So, if we start our discussion of the auditory system, we will talk about the connection with the external world being through the cochlea in our inner ear, when we talk about the visual system, we will talk about the retina which serves as the region where the external world is sensed and then through spikes information is conveyed into the central nervous system.

Similarly, in somatosensation, there are many many thousands of receptors that actually process or sense different kinds of somatosensation like pressure, vibration, even the relative position of muscles and so on, and which is conveyed which to the central nervous system in the somatosensory pathway, which provides us a sense of our entire body as well as the sense of touch and what we are feeling and so on.

Similarly, in the olfactory system, there are olfactory receptor neurons, which are essentially ligand, which essentially have receptors that are sensors for olfactory's or ligands that bind to those receptors like we had talked about ligand-gated ion channels like the AMPA receptors. Similarly, we have such receptors in the olfactory periphery, in the olfactory epithelium, in the underlying region in the nose.

And then, in the tongue we have also the many gustatory receptors like those for salt and SAR that is hydrogen ion sensing, sodium chloride sensing and many the other kinds of sweet and bitterness sensors. Similarly, we also have the umami sensors, facts sensors and so on so, which gives the final percept of taste. So, as we said that for this we have to introduce this term code, where we mean that the activity or spiking of the neurons convey some aspect of the sensory stimuli.

And the, and that is encoded in some form in the spiking activity of the neurons. So, we will talk a little bit about this before we totally jump into the sensory pathways. So, that we are clear on what we mean when we say that, the rate of the neuron increases or the timing of the spikes are synchronized across neurons and so on, which is how some of the ways that we understand that neurons encode information about the external stimuli.

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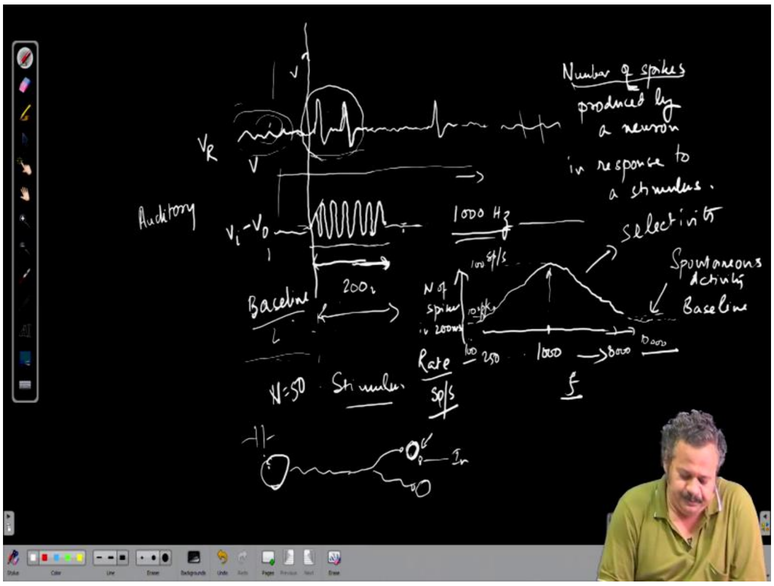

So, let us say, I mean if we are recording from a neuron, that is we are able to identify the time of spikes if you remember, what when we said that there is a spike let us say this is V rest of a neuron in some pathway in some sensory pathway, let us say auditory and we are recording the activity of the neuron, which we mean that the V that is the V in minus V out of the neuron.

And, so, it is at V rest in the beginning and let us say in response to a stimulus. So, this is voltage here for the above the plot above. And this axis is time for the plot above and below and let us say we have a presentation of a sinusoidal frequency that is a tone sound. So, let us say we hear the whistle, let us say of a person which is at let us say 1 Kilohertz or 1000 Hertz. And let us say it lasts for a brief period of time that is let us say 200 milliseconds, ok.

So, this is lasting for about 200 milliseconds. And then there is silence again and previously also there is silence. So, we have this V rest and let us say we are able to measure the action potentials that occur in response to or rather in the same duration as the tone presentation as we see and then it goes back to V rest and let us say spontaneously there is some action potentials also that can occur.

So, we say that a neuron is responsive to a stimulus or it encodes some aspect of the stimulus, if there is a significant change in spiking activity. When we say significant, we mean statistically significant, change in spiking activity and when we say spiking activity, we will qualify that more in a little bit significant change in spiking activity during the period of the stimulus, sometimes even after the period of the stimulus and so on.

So, what we mean by significant? Is that it is statistically significant? And by activity, we mean usually one of the two things. That is either the number of spikes the number of spikes produced by a neuron in response to a stimulus. So, this means that we have to compare the number of spikes that are produced during the presentation of the stimulus and compare it with a control period of time that may be long after the stimulus is over in this region, how many spikes are occurring or a significant amount of time or just before the onset of the stimulus.

So, if let us say there are no spikes here and we get 2 spikes in response to this 1000 hertz tone, we still cannot say whether the neuron responds to the tone or not, in terms of the number of spikes. Why so? Because, we have introduced the idea that the responses can be stochastic or can change from time to time and this stochasticity or variability rather, not change from time to time or there is very it is rather variability is present and overall mean remains more or less constant.

Overall mean across multiple repeats of a stimulus, that is we have to perform the experiment over and over again, a large number of times and there are ways in which we can basically qualify, what is large? In what case that is based on how much variability is there in the spiking responses?

And. So, based on the information of multiple such repeats of the same stimulus, that is this is let us say repeat 1, we present again then we say it is a repeat 2, 3, 4, 5, 6 let us say N up to 50 so let us say in this example up to 50 repeats. And then, we find out what is the average number of spikes that occurred in response to the stimulus during the stimulus, that is within this 200 millisecond period and compare it with the same 50 times of the period just preceding the stimulus, which we call the baseline which we call the baseline.

So, only when there is a statistical significance in the stimulus period and baseline period, in terms of the number of spikes then we can conclude that the neuron encodes some aspect at least some aspect of this particular stimulus. We still cannot completely say which aspect of the stimulus, but with variety of other ways of probing, we can conclude that it is actually the tone frequency that may be being encoded by the spikes, number of spikes produced by the neuron let us say by varying this frequency over many many different frequency regions or frequencies.

We can see how the response or average response in terms of number of spikes changes for the different frequencies. And then we can conclude, yes, ok, so this neuron probably has some selectivity to particular frequencies or it is tuned to a particular frequency if the response varies with frequency. So, let us say if we did a 50 repetitions and found that there is a significant response in number of spikes by the neuron produced by presentation of a 1000 hertz tone, this axis is frequency.

And let us say this axis is a number of spikes in 200 milliseconds of the frequency presented, which can be also converted into the rate of spiking that is essentially dividing the number of spikes by the duration over which those the stimulus is occurring and so we can also have rate or spikes per second in the Y - axis here and this axis is frequency. So, by varying the frequency let us say, from 250 hertz to 8,000 hertz let us say, we get the rate of the neuron to change in some manner.

Let us say this is 100 spikes per second and let us say this is 10 spikes per second. And let us say beyond that, it remains at 10 spikes per second. This is essentially the spiking activity measured in the baseline, that is it is present even if the stimulus is not there or a stimulus to which the neuron does not changes change its response, you we get that 10 spikes per second which is also spontaneous activity.

So, neurons also have spontaneous activity, which is essentially what we mean by Baseline activity, that is when there is no stimulus then the activity of the neurons if we quantify that using random 200 millisecond windows and find out how often it spikes in those 200 milliseconds. So, let us say we get that and that is 10 spikes per second and then we see that even if we play a 100 hertz stimulus, it is 10 spikes per second so, it is not any different from baseline.

And, when we play 10 kilohertz or 10,000 hertz then also the response or the number of spikes or rate is 10 spikes per second. And so, that is there is no response in terms of number of spikes produced by the neuron to 10,000 hertz or 100 hertz. But, it insignificantly increases its response 2000 hertz.

And, so, there is a tuning of this form and this is what we mean by a selectivity of a neuron selectivity of a neuron to a particular stimulus feature or this also says that the neuron encodes frequency in this case, through the number of spikes in response to the stimulus in response to the frequencies, different frequencies that are played.

So, here what we are assuming though is that the number of spikes is the basis of the neural code. That is, the information about the stimulus is being conveyed by the overall rate during the stimulus presentation where the stimulus in this case is a tone of a particular frequency.

So, it is not necessary that this number of spikes changing with frequency always mean that the neuron is actually encoding this stimulus. This is a very, I say this because; this probably would not be there in textbooks that you will be referring to. But it is not necessary, that we mean that it essentially means that the neuron encodes for the frequency. It is only a coincidence it can be only a coincidence.

It is a correlational observation, we always have to remember and we will mention this time and again later on also is that, a correlational observation for a stimulus and the change in response in number of spikes does not necessarily mean that information is actually being used by the organism or the human being or the animal from where we are recording you know in those neurons that it is being used by the animal in terms of frequency understanding.

So, it may be that there is actually something else that is more important to the neuron and we are seeing this as only a side effect, seeing this being the change in the number of spikes produced by the presentation of a frequency. And actually, what really matters is that the neurons that receive these spikes. The neurons that receive these spikes; remember, we have we are recording from a neuron the V in minus V out and we saw spikes in this.

And this neuron is has an axon that goes and targets couple of other neurons. And let us say that these spikes ultimately do not produce any change in the neuron to which they are projecting. This can easily happen. And, so, or maybe it is being totally shut-off by some inhibitory input that goes on to the next stage neuron every time that tone is being played.

And, so that means, so some inhibitory synapse is stopping all the spiking information from the pre-synaptic neuron in this particular post-synaptic neuron which has another synapse which is let us say inhibitory and it is stopping this neuron from firing whenever these tones are presented. So, that means, that this tuning or the selectivity that we talked about and we assumed that the neuron is coding for the frequency is being used is not necessarily true.

However, the it is going to be very difficult also to prove. Not difficult, I mean the further experimentation is required in order to really prove that, yes, this is in fact being used by the organism and that we will require experiments that implying cause that imply causation and that is the use through some behavioral output from the organism based on the stimuli.

And by manipulating the activity of the neuron in response to the stimulus somehow externally and then we see a change in the behavioral output, only then can we conclude that. The other thing is that, we can always come up with many different kinds of code being present in the stimulus.

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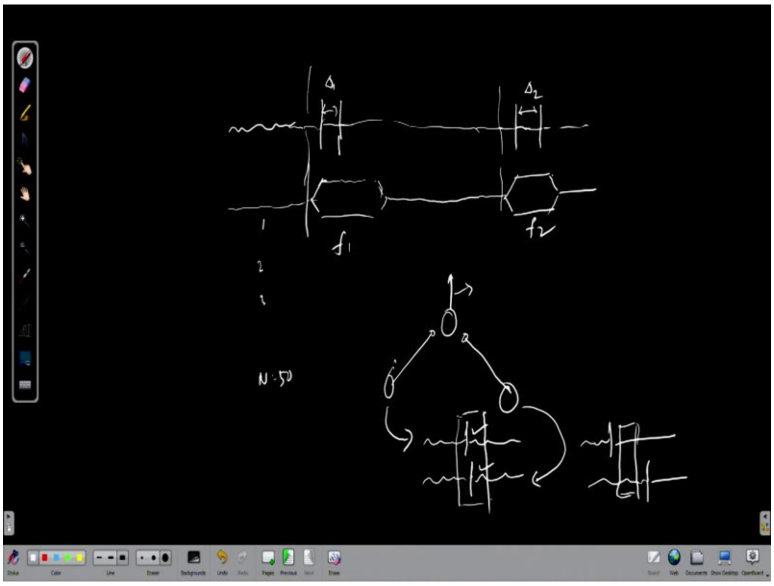

So, in the responses rather; so, let us say that, we have a presentation of again let us say a frequency f 1, at a particular time in this window this is f 1. So, and this is the baseline time, let us say there are no spikes and in this period, there are 2 spikes, f 1 and then with a long gap again we will present a sound f 2 and let us say that again in response to the f

2 sound there are also 2 spikes, but the gap is more. And let us say that on every trial or every presentation of f 1, f 2 remember 1, 2, 3 up to capital N equal to 50 we get the exact same responses.

And the spikes are separated by the same amounts delta 1 and delta 2 in every trial. So, from this it appears that the delta 1 and delta 2 the gap between the spikes encode information about f 1 and f 2, which is a valid observation and valid correlational observation that we can say. But again, it could be that both wherever this particular neuron that we are recording from, wherever they are projecting or whichever neuron they are projecting they cannot tell these delta 1 and delta 2 apart.

They may be responding only to the first spike and then because of some other input getting shut-off completely. And so, the delta 1 and delta 2 produce no change in the post-synaptic nerve. So, similarly we can this delta 1 and delta 2 can be there can be other ways many complicated ways that we can think of, that by varying the stimulus and we see particular observations occurring or particular events occurring in a pattern and we say that this observed pattern is the code for the stimulus.

So, that for that we actually have to also remember, that it is the post-synaptic neurons job not our eyes job or our thinking’s job to understand whether those 2 spiking patterns are different or not. And, so, whatever we say suggest as a code for the particular stimulus parameter or particular stimulus feature, that we are trying to understand we must remember that it has to be decodable or rather a neuron that is receiving those spikes through synapses, input synapses on it should be able to tell the different situations apart, biologically.

Not because by eye we can see that they are different and you know in a particular manner as we change the stimulus. So, any decoding mechanism that we talk about, also has to be biologically plausible. And or rather it that a post-synaptic neuron should be able to do that in the brain, only then can the meaning of code be clear or rather useful.

So, with this I will say that the number of spikes or rate responses turn out to be a very good measure of what aspect of the stimulus or stimulus features that are neuron encodes, because it is easily decodable by a post-synaptic neuron, in the sense of the way we understand neurons so far, it is easily decodable and for many many observations and many many behavioral outputs we have been able to relate the rate of neurons with the behavioral output.

And manipulation of the rate of neurons which those kind of experiments we have been able to do only in the past few decades. With the manipulation we have been able to establish causation in terms of the rate information being actually used by the organism or the animal in producing a particular behavior or producing or having a particular percept that is based on the rate information.

Similarly, there is a lot of evidence where we have found that, particular spike timing also plays a role in terms of encoding aspects of stimuli. For example, we will talk in the auditory system about something called phase locking and it is there in higher order higher regions of the brain also, not just in the lower order regions of the auditory system where there is phase locking, phase locking to other activity that is going on.

And it is also decodable based on coincidence detection or synchronization across neurons and, so, if a neuron, if 2 neurons are firing at the same time and they are projecting on to another neuron, a particular our postsynaptic neuron. So, let us say this neuron is projecting onto one neuron and another neuron is also projecting onto this neuron. And, so, if the activity of this neuron has a spike in this region this particular time and the activity of the other neuron has a spike only within a certain window of each other, only then the post-synaptic neuron fires an action potential.

Individually, they are not capable this particular spike or this particular spike. If they are apart in time by more than this window, of some amount that can vary from neuron to neuron, then the post-synaptic neuron does not fire any action potentials or rather it does not detect the presence of the spikes. And, this is this coincidence detection mechanism is a involved in decoding particular spike timing based information about stimulus features.

So, with these ideas, of spike rate and spike timing as ways by which neurons encode information and can be decoded by post-synaptic neurons, we will delve further into now the sensory systems, where the first topic would be what we will call receptive fields and in the auditory and visual systems and so on. So, until then, we will continue the discussions in the next lecture.

Thank you.