

Cognition and its Computation
Prof. Rajlakshmi Guha
Prof. Sharba Bandyopadhyay
Biotechnology and Bioengineering
Indian Institute of Technology, Kharagpur

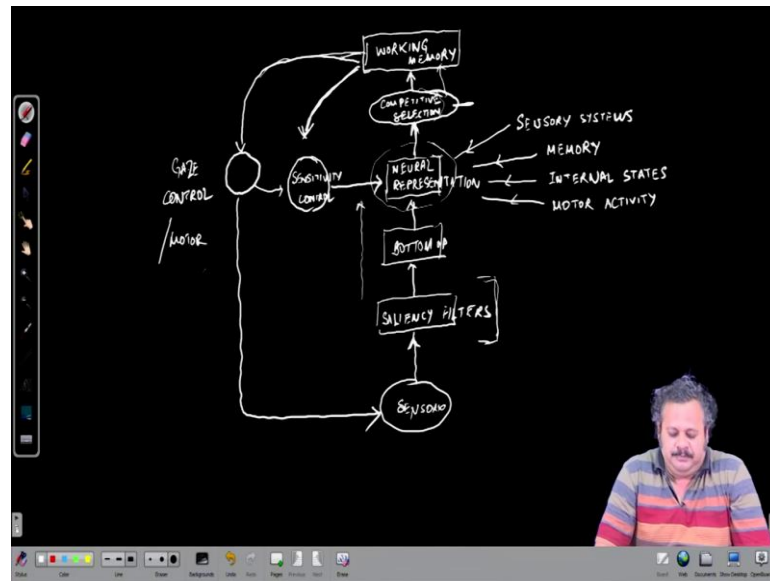
Lecture - 31
Neurobiology of Attention, Working Memory

Hello. So, we have completed our discussions on brain circuits that have to deal with the sensory processing a bit of the motor processing and then reward circuits and also the circuits involved in executive function. After that you have been introduced to the topic of object recognition and perception and you have also been introduced to the idea of attention previously.

And so, now, we go into more details about how attention actually comes into play through neural circuits in terms of activity and how it produces the effects that we think is based on attention. So, if you think about real world scenario when you are paying attention it is about focusing on a single process it could be observing a particular thing, a particular object, it could be listening to a particular persons voice and understanding that it could be actually also moving your hands in a motor function that you pay attention to.

So, it can be on variety of domains that we can focus our attention and as we have discussed earlier the seed of control of attention is in the prefrontal cortex. The various components of attention can be briefly summarized in terms of model propounded by Hudson and Terry Moore in the recent decades.

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And so that involves basically a sensory world outside, this is our sensory world that we are interacting with that is providing our inputs through our sensory systems through the periphery and producing response patterns and finally, leading to our representation of objects. So, that we implement through a bottom up set of processes and before that there is also something that we will call saliency filters that amplifies the a particular salient stimulus in terms of the responses in the bottom up representation and passes it on.

And we will discuss this saliency filter and how that is important and how it is computed by the neural system in the next lecture. But so, I ideally we have finally got a neural representation which we have discussed in terms of the neural sensory circuits and so on. So, this neural representation is modulated by variety of factors for example, other sensory systems.

Now, it is not just dependent on a single sensory input other sensory systems also influence this neural representation of a particular sensory system. Secondly, memory can modulate the representation, thirdly the internal states that is let us say hunger or our state of motivation our all these things come into play in terms of neural representation. And also motor activity can alter our neural representation of the sensory world for example, if we are running we have movement of the same field that we are visualizing when we are standing and so the representation changes based on the motor activity.

So, from neural representation there is a process of selection based on relative saliency of the different inputs at play and that is what we call competitive selection and we will discuss this a little more in a little in little later. Then a particular object or particular process or particular item of interest goes into what we call working memory.

So, working memory is something that is intricately linked with attention. So, it is the memory it holds a very little information for a short period of time and it is it involves the current situation, current context and current information that we are dealing with in our current action. And so, what is what information is in working memory is what we are paying attention to and similarly what we are paying attention to is what is in our working memory.

So, vice versa it is linked intricately with what we call attention and this working memory has the ability to modulate a number of items a number of elements, say a particular one is a gauge control circuit or rather a motor related control that we can use to direct our attention that is orientation, turning our head in a particular direction to listen to someone. Or when we turn or when we make us a card to a particular move the eyeballs towards a particular location in order to pay attention to that particular object those are those can be determined by working memory.

And what attention does is through this working memory can actually do sensitivity control which we will discuss in a little bit. Sensitivity control and that control basically alters the neural representation the gaze or some motor output also can cause the sensory control because we are turning our attention to one particular thing when we orient towards one particular object.

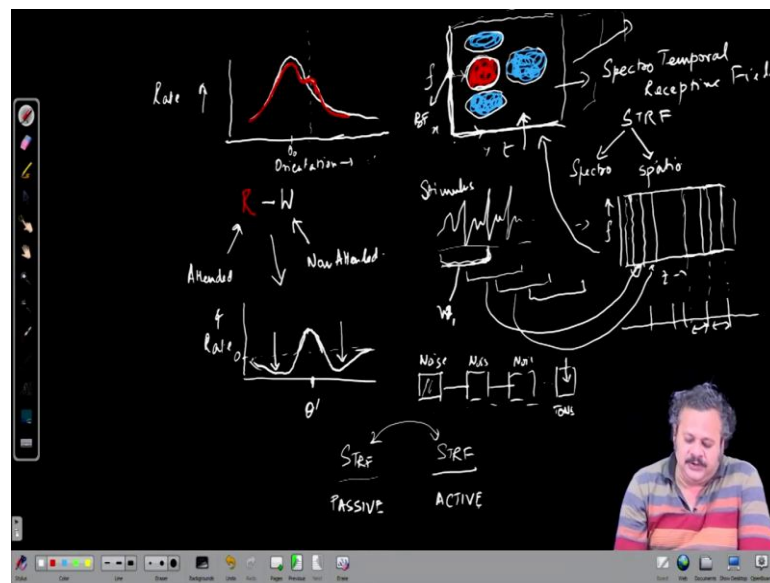
And so, our focus visual focus goes on to that object and actually changes the sensitivity of the representation or sensitivity of the neurons towards the objects or elements of the object in that location. And this also finally, plays a role in shaping our sensory world that is what we are paying attention to this motor output. So, this neural representation or basically what we will call representation of at the higher level is not the only thing that is controlled actually throughout the attentional mechanism might be influencing all along this bottom up pathway.

And shaping the or relatively shaping the different neural representations and focusing on one particular object and enhancing the representation of that to so that it is it

becomes relatively more salient in this competitive selection process and goes into or stays in working memory. So, this is sort of the overall structure or framework to study attention and we will take a few examples and show that these ways of neural representation or shaping neural representation through attention generally works in a way that enhances the contrast of a particular feature over other features or enhances a particular object over other objects in general in terms of representing it.

So, what I mean by that is if we think of orientation tuning curve in the visual v1 area.

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So, this is orientation angle of a bar orientation of a bar and this is let us say the rate responses based on the degree orientation angle of the bar in the receptive field of a neuron. And let us say it is tuned to a particular orientation θ_0 . So, what I mean by contrast enhancement is that if we are paying attention to a particular orientation then usually it is the it is an enhancement of the representation of this orientation and suppression of the representation of the other orientations around it.

So, if I draw an altered orientation tuning curve that is let us say with attention the representation is changing then it would be something like this I mean it may be exaggerated, but maybe if we take a population of neurons like this we will get this kind of an effect.

So, in a sense if we look at the difference between the red and the white curve that is the red minus white being the attended tuning curve when we are paying attention to a particular orientation in the receptive field of the neuron minus the white orientation tuning curve that is the net effect that attention is providing. So, this is our attended status and this is the non attended status.

So, the difference now becomes that if we are attending this particular theta prime then this difference can relate to a rate change. So, this is 0 change it becomes something like this that is the red minus the white, that is there is suppression or inhibition that suppresses the representation in the surrounding region which is less preferred from the particular orientation that we are looking at and on the other side as well an enhancement of a particular feature in the receptive field.

So, examples like this will come up when we discuss how attention comes into play with how the sensitivity control changes neural representation in a little more detail in the next few minutes. So, if we consider another example which is let us say in the auditory system, if we consider the receptive field of a neuron as a description of what the neuron responds to in frequency and time that is we are representing stimulus over different frequencies and time I will explain it a little more very soon.

Let us say blue represents lower or negative values and the red which would be the center region represents the positive values. So, what we are drawing here is what we often call a spectrotemporal receptive field also known as the STRF, similar sort of receptive field can also be obtained for visual neurons which is also called STRF only thing this is spectro in the case of auditory this S becomes spatio in the case of visual. So, let us try to understand what we mean by this curve here or rather this surface here.

So, we have time on this axis and frequency on along this axis the y axis and the x axis. So, what is drawn here is the average stimulus preceding spikes of an auditory neuron that is if we take a waveform the auditory stimulus is a waveform as we have talked about earlier and we find out in small windows what frequencies with what energy is present in this window.

Then the next window and then the next window and then the next window and so on this provides a way of representing the auditory stimulus that is what we call a spectrogram, a little more detail will be provided in your reading material. So, what we

are essentially plotting is frequency and time if this is the stimulus waveform auditory stimulus waveform then what we are plotting is if this particular window 1 the energy as a function of frequency is plotted in on the surface here in this region, next window of window 2 is plotted in the second slot here, the third one here and so on.

So, now, so this is a continuous thing showing how the frequency content of the stimulus is changing with time and if we find out the average stimulus preceding a spike. So, corresponding to this stimulus parallelly there are events in this spiking of the neuron. And so, the stimulus preceding the spike or the spectrogram preceding the spike that if we take this chunk of this spectrogram.

If we take this chunk of the spectrogram aligned to this spike and for each and every spike like that and average them what we would get is what we call the STRF or it is a representation of the stimulus that is like causing a spike the average stimulus preceding a spike. And generally it turns out to be region where there is a positive where it is positive that is it is producing higher rates and that is akin to the best frequency that we discuss in the tonal response maps that we had talked about.

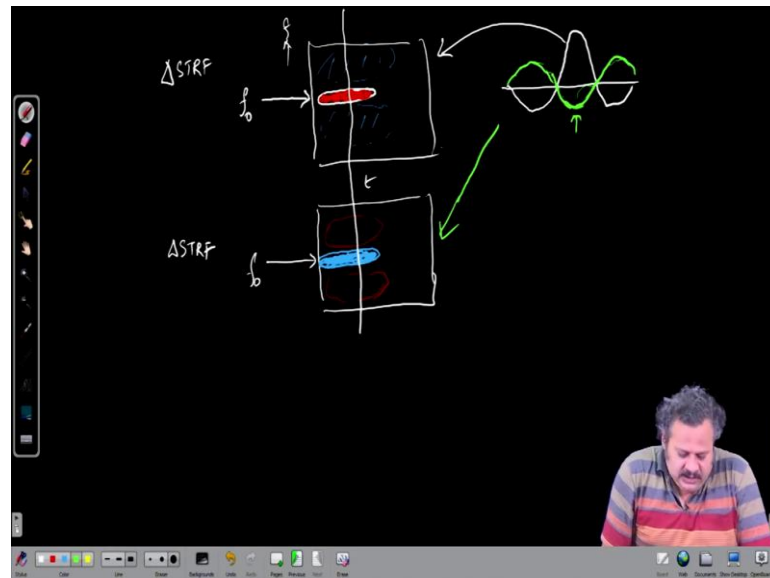
So, now if we consider in this domain for the visual system also we can have instead of frequency and time it would be the x and y dimensions along the 2 axis and then there would be time along a third dimension here and each it would be a video of such images that would be the spatiotemporal receptive field of a visual neuron. So, considering this kind of receptive field also, if we pay attention to a particular tone frequency let us say an animal is trained to find out when there is a tone occurring in a series of noise like stimulus.

So, this is a noise like stimulus that is [FL] kind of sound, then another noise, another noise like stimulus and so on and then all of a sudden a tone comes on. And let us say we have to focus and detect the presence of this tone, whenever the tone occurs we have to say; ok I heard the tone.

In such scenarios what people have found is by recording from single neurons in the primary auditory cortex of animals in this case ferrets that in a population of neurons if we can find that STRF of the neurons when the animal is passively listening to these sounds these noises when it does not have to listen or attend to the particular tone that it has to detect or a tone that it has to detect then.

And the STRF when the animal is actively listening for the tone and it has to press a reward or get a water reward or I mean there are many ways of doing the experiment, but basically the animal provides a readout of detecting the tone. And when we compare the two STRFs and look at the difference just like the difference in this orientation tuning curves we saw we again get.

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So, if we look at the difference of the STRFs. So, delta of the STRF that is attending versus non attending minus the non attending one and if this is the frequency of the tone that has to be detected then there is a sharp enhancement of the spectrotemporal receptive field here that is the change in the STRF is an enhancement of this particular region. It is often surrounded by a blurry inhibition around it which again shows that contrast enhancement kind of feature that attention provides.

So, again this axis is time and this axis is frequency and f_{naught} is the frequency that the animal has to detect. So, now, this same experiment so, this result was obtained when the learning is based on a go no go kind of situation where the animal has to stop itself from leaking a water spout when the tone occurs whereas, in another set of experiments where the animal had to approach the water spout or leak the water spout when the tone occurs.

So, the readout of the behavior was different in the two cases, the animal in one case was trained to inhibit itself from a particular behavior and in the other case the animal had to inhibit itself in other cases, but for the rewarding tone it was or rather that for the

detecting of the tone it had to initiate a behavior. And surprisingly the actually the opposite change was observed in the delta STRF.

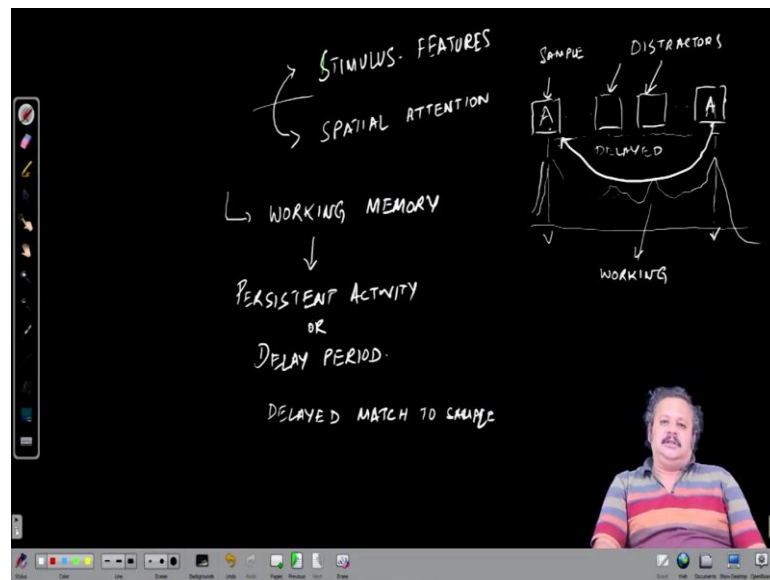
So, that is if f_{naught} again is the frequency that the animal had to detect amidst those noise like sounds then instead of enhancement at the particular frequency there was a suppression of responses of that particular frequency and actually a surround excitation not as large, but again a contrast change.

So, if we look at a section through these regions through where the main change is happening we would see two different kinds of contrast features contrast enhancing features, one in which there is suppression of the surrounding enhancement of the middle which is the top one. And in the other case in this particular case we have actually the opposite that is the detected or attended tone has our frequency is that representation is suppressed the red rate responses at that frequency are reduced and the surrounding is enhanced.

But still it is a change in contrast of the relevant frequency and so, what I am trying to say is that it is not always that increase of responses is what is desired to enhance representation of something. It could also be the other way around to modify representation that is by reducing the responses there and doing a differential effect on the surrounding regions.

So, they should be kept in mind and so both excitatory ways of manipulating the neural representation can be used as well with inhibitory ways of enhancing the neural representation. So, in doing so, we will take the example of another case where it is those it is in the case of primates.

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So, we will be talking about a case where so far we have been talking about features stimulus features and changes of its representation, there is also a spatial attention that comes into play. So, these are two different cases and in fact, is mediated by different regions of the frontal cortex or prefrontal cortex.

The stimulus features based enhancement with attention is modulated by the I mean the spatial attention is modular is controlled by the dorsolateral prefrontal cortex whereas, more verbal and stimulus based attention and there in its working memory the seat is in ventral lateral prefrontal cortex. So, we have said that the frontal cortex is controlling this representational changes and working memory is what is directing it or whatever is in working memory makes us pay attention to that is that particular object by changing the stimulus representation.

So, the neural correlate of working memory has been studied in primates and also through MRI, FMRI studies. And what we generally agree on is a neural correlate of working memory is persistent activity or delay period activity neural correlate is persistent activity or delay period activity. So, there are delay period act what I mean by these will be clear in a moment, there are many regions not many, I mean there are more regions than just the prefrontal cortex that elicit persistent activity as if representing working memory.

That is the involvement of one particular feature for a long period of time, long meaning the period of attention on a particular object like it can be a few 10s of seconds and the activity of neurons last throughout that period in prefrontal cortex and also other regions show that similar kind of activity. However, and lesioning of those regions like the prefrontal cortex and other regions also which show persistent activity, lesioning them shows deficit in working memory tasks.

And that is where the delay period comes in that is specific to working memory tasks and we will go into it. The we do not consider the other kinds of persistent activity as reflection of working memory because they are also associated with other sensory deficits or motor deficits whereas, the prefrontal cortex persistent activity abolition is not associated with other deficits, it is only with the working memory task only working memory deficit and the way it is studied is through generally through delayed match to sample.

There are many other ways to study it, but delayed match to sample is what are used primarily in primate and other animal experiments that is a particular an animal is trained to respond to a particular object. Let us say A in its visual field and it has to press a lever when the first object appears then this is called the sample.

And then in intermittent intervals distractors are appear in its particular location of attention and then again at some point randomly after 0 to a few such distractors the same object appears and the animal has to release the lever at this point. So, essentially this A is considered the so, the animal has to pay attention to each of these objects throughout this task until another of the sample appears.

So, this is what we mean by delayed match. So, this is matching the sample matching with the sample. So, the neurons in the PFC show that elevated activity during and persistent activity during this delay period until the animal sees the match and this has been what is considered as the reflection or correlate of working memory in the prefrontal cortex.

As I was saying similar activity is seen in other regions, but abolition of that activity leads to further other sensory deficits or motor deficits unlike the if the activity is abolished in the prefrontal cortex.

So, I think with this we will stop our lecture on Neurobiology of Attention and Working Memory and we will go into further details about how further features are enhanced how a particular system the cholinergic system is involved in attention and how the bottom of saliency filters come into play in attention in the next lecture.

Thank you.