# Cognition and its Computation

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## Lecture - 20
## Sensory Circuits: Auditory - II

Welcome. So, we have been discussing the Auditory nerve fibre responses in our section or discussions of the Auditory Circuits, part of the sensory circuits. So, we discussed that the tuning curves or the receptive fields of auditory nerve fibres and we will see that neurons along the auditory pathway also have a tuning curves and that is how we define the receptive field of auditory neurons.

Now, in terms of intensity as we last discussed, there is a broadening of tuning in the auditory nerve fibres that is if we play a same sounds a range of frequencies.

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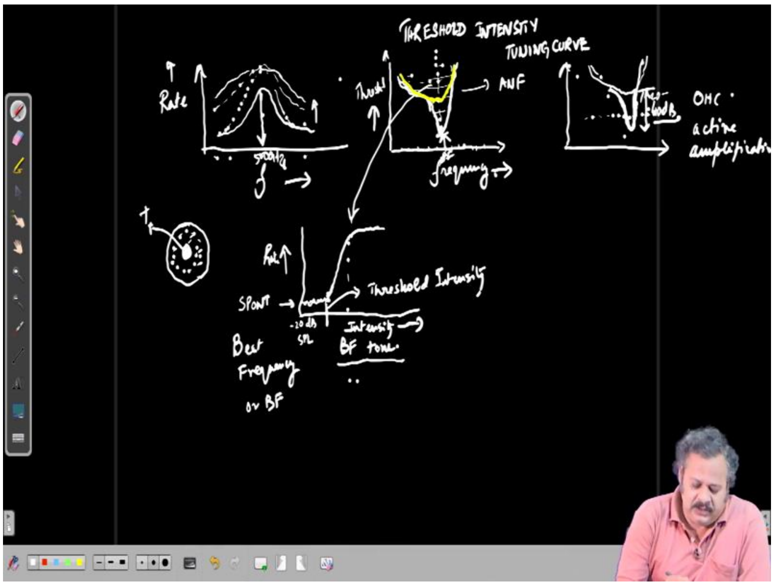

So, if this is the frequency axis and we play a range of frequencies one after the other with interval and record the rate responses of spikes or number of spikes occurring during the stimulus presentation in that window, we divide that by or normalize that by the time, then we can get a tuning curve of an auditory nerve fibre like this; where, let us say this is our 5000 hertz.

Similarly, if we play the same sound set of frequencies along this axis at a higher intensity, we will find that the responses will increase and there is a broadening gradual broadening of the responses and finally, there will be saturation of responses. So, each curve that I have plotted here is essentially a different tuning curves as a function of intensity of the sound. We did not have anything like this in the visual system in terms of the receptive field changing with intensity absolutely, I mean becoming much broader and so on.

Here, the case is different in the sense that the receptive field or the description of the receptive field changes based on the stimulus itself and so, this is a non-linear system in that sense. Of course, in the visual pathway also the receptive fields are non-linear, but it is not ah. So, I mean it is not at least at the stage of the lateral geniculate nucleus and the retinal ganglion cells.

It is not so largely dependent on the stimulus intensity there. Actually there what we will have what we saw is that when we have a centre kind surround kind of receptive field that is on centre of surround, it essentially makes it intensity invariant. In the sense that its it does a normalization; in the sense that it subtracts out the intensity on the outer side because of the inhibition coming here and the plus in the middle.

So, the minus is in the surround and plus in the middle make it more or less the luminance invariant that is even if I make the stimulus or the picture brighter and brighter, this kind of centre surround receptive fields inherently takes care of that increase in brightness; at least to a great extent. So, on the other hand, here it is slightly different in the sense that the sound intensity increasing, changes the nature of the receptive field and this is actually true throughout the auditory pathway in neurons in the cochlear nucleus and beyond.

We will see that this is generally true even in the up to the auditory cortex from the cochlear nucleus up to the auditory cortex. So, another important way of describing the tuning curves or receptive fields of auditory nerve fibres is what we call a threshold intensity; threshold versus frequency curve which is also tuning curve. So, that is threshold intensity tuning curve; threshold intensity tuning curve, where for each and every frequency when we are recording from a single fibre, we obtained the intensity;

this axis is a intensity or rather threshold at which intensity we face a threshold for that frequency.

That is let us say we are recording from a fibre and we are playing a stimulus at this particular frequency which we will call the best frequency or BF and if we play a best frequency tone along the with at different intensities, best frequency tone at different intensities. So, this axis is intensity and this is sorry this axis is intensity and this axis is the best frequency tone intensity and this is the rate.

So, initially if at the very softest levels may be minus 20 dB SPL, the neuron will have or the auditory nerve fibre will have a spontaneous firing rate that is spontaneous. Until at a particular intensity, it starts to respond above the spontaneous activity that is what we will call as the threshold intensity.

Remember, we say that the it starts to respond meaning that the response strength is significantly different from what we have in the baseline period and this rate response keeps on increasing and then, saturates at a certain intensity about 20-30 dB above this threshold. And if we get similar curves for not just the best frequency tone, but the other frequencies as well.

That is if this is the best frequency and do this for all other frequencies that we are presenting and find this threshold intensity for all the frequencies, then the softest intensity at which the fibre starts to respond to a single frequency is what we will call the best frequency of the auditory nerve fibre.

So, in other words, it would the curve look somewhat like this with a asymmetric shape usually in the mid frequency to high frequency ranges and is more symmetric in the lower frequency ranges and they have a long tail that is more sensitive than the upper frequency side and this is a typical tuning curve or threshold intensity tuning curve for auditory nerve fibres.

And the lowest threshold at which the fibres responds to a particular tone to that tone that is going to be our best frequency and the rate responses along this line is what is plotted here. So, this is another way to describe the receptive field of the auditory nerve fibres or for that matter any neuron in the auditory pathway. So, as we are we were saying that as we go higher up in intensity, the bandwidth of the fibre keeps on increasing that is the range over which range of frequencies over which it responds that increases and if we gain get the rate information also at the different intensities, we will find that it increases and then saturates after some level.

So, in this picture, we can actually find out what the component for the outer hair cell is and what the components for the inner hair cell is. That is we can segregate the sensitivity produced by the outer hair cell or the additional sensitivity produced by the outer hair cell. So, in a case where we have a fibre and if somehow we could damage the outer hair cell that is or the row of outer hair cells that is related to the responses of this fibre, then based on only the inner hair cell, the tuning curve would be typically like this.

In the sense that it is capturing only this particular part and the outer hair cell causes this steep sensitivity or rather this increased sensitivity of 20-30, even 40 dB SPL or 40 dBs this gain 20 to 40 dBs depending on the frequency and this sensitivity is provided by the outer hair cells active amplification.

If you remember from our previous lecture, we said that the outer hair cell because of their electro motility or the ability to change its length based on the a voltage or the membrane potential, it adds the fluctuations onto the normal fluctuations of the basilar membrane and that sensitivity that increases the sensitivity of the auditory nerve fibre providing this narrow tip and lower threshold.

So, being able to here at the softest intensities are at very low sound levels, it we get that based on this outer hair cells sensitivity introduced at all the different frequencies in this manner. So, in hearing problems, often it is the outer hair cells that get damaged and that is what reduces the sensitivity of hearing, depending on the frequencies in which the outer hair cell damage has been caused and if you remember it is the inner hair cells that produce the final input into the auditory nerve fibres.

So, if inner hair cells get damaged, then there is no actual information flow into the auditory nerve fibres that is the auditory nerve fibres are not going to get the input glutamate on to the synapse at the end of the inner hair cells and so, they will not be firing action potentials and so, there is going to be no information flowing in.

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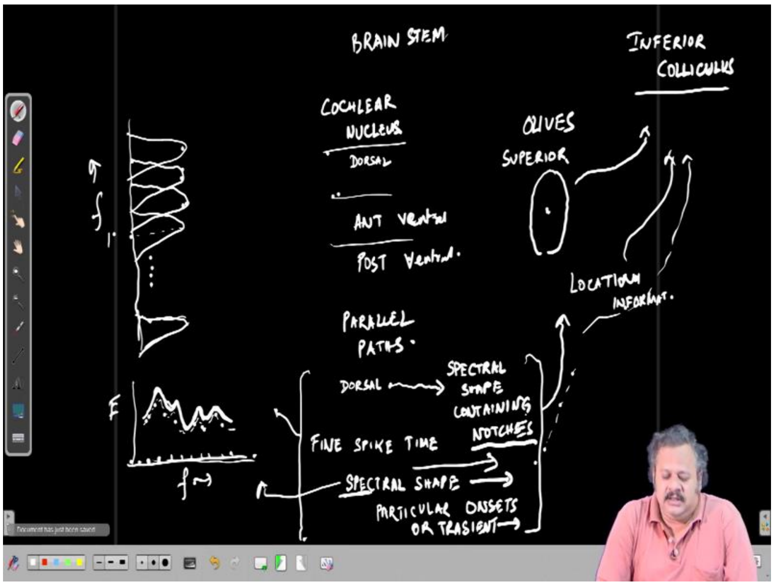

So, in the regions beyond the auditory nerve, we have the first stage as the let us look at that first stage as the cochlear nucleus which has basically three different parts. The dorsal part dorsal cochlear nucleus the and the ventral cochlear nucleus which has two parts that is the anterior ventral cochlear nucleus and the posterior ventral cochlear nucleus. So, these are in the brain stem and these regions are also tono topically organized as we have talked about earlier.

So, the auditory nerve input the fibres are essentially providing bank of filter like inputs. So, each auditory nerve fibre is like a filter and based on the best frequency. So, this axis is frequency; based on the best frequency, we have the peak or the tuned region of the auditory nerve filter and the filters change their bandwidth depending on intensity.

So, this representation along the fibres is essentially like a Fourier expansion of the signal. That is not exactly the Fourier expansion, but something akin to it, where the different frequencies in different bands of energy get filtered from the sound and the information is passed on into the central nervous system in the cochlear nucleus and along the auditory pathway, there is a representation of tonotopy which gets more and more broad as we go higher up into the auditory system.

So, in terms of the cochlear nucleus, there are many parallel pathways of auditory information that start off parallel paths of auditory information that start off. In the dorsal cochlear nucleus, we will we know that in the dorsal cochlear nucleus, it the output neurons carry a specific type of information and that is information about the spectral shape containing notches spectral shape containing notches. So, this is a very specialized circuit in the sense that it provides the particular information about how the sound gets filtered by our external ear depending on the location of the sound.

So, if we go into the details of it, it will take up a lot of time. So, in the interest of time, we will just say that there are cues in the sound that are introduced by the filtering done by the external ear and depending on the location of the sound in space, primarily in elevation in the vertical elevation that cue that is introduced changes based on that location.

And that cue is basically the position or the frequency of notches that are present due to the filtering by the external ear and that notch is actually used in determining location in vertical plane primarily and that information is extracted by the final output neurons of the dorsal cochlear nucleus and conveys that information of location based on spectral cues or those notches into the further up into the auditory pathway.

In the ventral cochlear nucleus, now there are other aspects of the stimulus that is passed on and particularly, the spike time based information or fine spike time based information is passed on to the central nervous system by particular neurons in the ventral cochlear nucleus.

Then, more spectral shape based population based spectral shape information is passed on into the central nervous system or further into the central nervous system and there is also information on particular onsets of sounds that is broad particular onsets or transients that occur signalling the start of a sound that is transmitted into the central nervous system.

There are lots of details in which these are computed and we will keep these information in mind as we go on in our discussions later on the auditory scene analysis. So, what we will show what we will say here is that the spectral shape information based on a population of neurons, a particular a set of neurons, the energy at different frequencies of a sound; let us say this is energy and this is frequency. Let us say a sound has high energy at these particular frequencies with peaks.

So, an example of such sounds is speech which has peaks called formants; the first formant, second formant and third formant and so on in fundamental frequency which the information about that is critical in determining the percept of the sound that those peaks have to be faithfully represented or the spectral shape, the peaks and troughs together have to be faithfully represented.

And the spike rate information in the chopper cells particularly those that encode the spectral shape, so they have neurons of the best frequency at different frequencies along this axis. In their rates rate responses actually faithfully correlate with the spectral shape of the sound and so, a critical information is passed on to the central nervous system or the further up in the central nervous system by these neurons.

Now, fine spike timing is also critical in determining the location of the sound as well as many aspects of the envelope of sounds or the cues that actually that is how the sound gets modulated in energy over time or amplitude over time which is also an important aspect of understanding speech.

Though that kind of information with the fine spike times are conveyed by bushy cells in the ventral cochlear nucleus and this fine spike time information is further used in the sound localization circuits, where sound is located or the information about the sound location is determined or extracted from these fine spiked based information for the low frequency sounds.

So, and the onsets or transients that are present in sounds signalling the beginning of a particular bout or episode of sounds, that is conveyed by very broad band neurons.

That is they have very wide receptive fields and get inputs from multiple frequencies of auditory nerve fibres; but very small inputs and all of them together have to be active or many of them together have to be active to produce responses or very if it is a narrow frequency range, then it has to be very loud to make these neurons fire action potentials and these are basically the onset responding neurons and they convey this information further into the central nervous system.

So, the next important step in the auditory pathway is the inferior colliculus and before that there is a side path into which the fine spike time information and the loudness information conveyed by another set of cells which are similar to the spectral shape encoders, are similar to the spectral shape encoders that goes into the olives, another circuit present in the central nervous system.

The superior olives or one section of the olive in the brain stem is the region that extracts sound location information based on cues in the two ears; based on the difference in intensities or difference of sound reaching the two ears that aspect is calculated in the olives and the information is passed on to the inferior colliculus.

So, these are projecting on further with particular sets of information being taken out into the olives that is the medial superior olive and the lateral superior olive, which computes sound location information and passes on to the inferior colliculus as well as the other sets of information also goes on to the inferior colliculus. So, the inferior colliculus is the first stage, where all the information is getting integrated that is the different features that are extracted in the cochlear nucleus turn out to get integrated more in the inferior colliculus.

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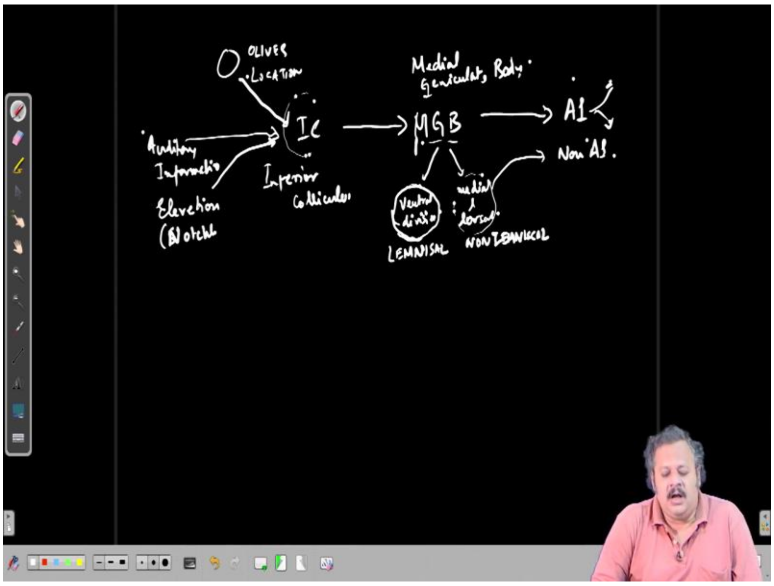

And then, the next stage is the thalamus that is from the IC or the inferior colliculus the projections; the projections go on to the medial geniculate body medial geniculate body as the name geniculate being in there suggest, it is part of the thalamus and it is the auditory thalamus which is the medial division of the geniculate body and that then, projects on to the primary auditory cortex or A 1 and then of course, there are other paths that will be that we will talk about later on from A 1 you know during our discussions on auditory scene analysis.

So, in the MGB actually, there is a particular division that is the ventral division and there are two others that are medial and dorsal divisions. So, this ventral division is the primary path that projects on to A 1; whereas, the medial and dorsal divisions are what we call the non-lemniscal pathway. So, this gets the lemniscal; this is called the Lemniscal pathway which originates from a particular structures just preceding the inferior colliculus and this is the non-lemniscal pathway that goes on to the other regions of the auditory cortex, the outside a one non A 1 inputs.

So, it is the ventral division that come that does whatever computation is need needed to be done or integration that need needs to be done before entry into the primary auditory cortex and projections similar to V 1 projections go into the layer four of A 1 and then get distributed further. So, the sound location information that we had happening in the that we extract in the olives, get integrated into the IC with the normal information pathway, auditory other auditory information and also, the elevation information based on spectral skews or notches.

All these go into the inferior colliculus and the formation of or combination of different aspects start right in the inferior colliculus. Very little is known in terms of concrete I would say concrete ideas of how object is sound object is formed or in the MGB or in A 1, how it is represented that is not fully known.

We will discuss some aspects that we know and in A 1 and the important thing is that the that the reason I am saying it gets integrated is that the location information that got computed in the olives and the elevation information that got computed in the dorsal cochlear nucleus, after reaching IC and then, if we go beyond neurons in the primary auditory cortex have been shown to not be so much dependent on location.

I mean if we look at the location receptive field that is sounds from which regions in the in the space outside us is causing responses in neurons, then we will find that they are extremely large, almost entire half of the auditory field is able to produce responses in single neurons. Usually, such spatial receptive fields are extremely large. So, something that is very important that is encoded, that is computed and encoded in neurons is getting lost by the time we go in A 1, but it is preserved in some other form and it is indicated that it is more present in a population level code that is it is distributed across many neurons.

So, with these discussions, we will finish or conclude our auditory circuit lectures and next, we will continue with the other sensory systems.

Thank you.