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Lecture - 22
Sensory Circuits: Olfactory and Gustatory

Welcome to the last lecture on Sensory Circuits as we have been discussing all the parameterizable stimulus spaces and their corresponding sensory circuits their hierarchy. And to some extent the kind of features that neurons in the those particular systems respond to or encode. So, for the sake of completeness we go on to the chemical senses we will briefly describe them and not go into too much detail, and is necessarily to give you an idea of the all the sensory systems.

And specifically in this case the chemical sensors which do not have stimuli that can be easily parameterized. I mean; in fact, they cannot be parameterized maybe parts of those stimuli or some set of stimuli can be parameterized. So, let us say if we think of the carbon chains, I mean the olfactant’s that have carbon chains, then we can think of the length of the carbon chain as a parameter and people have done such parameterization.

However, there is no clear understanding in terms of a topography or a spatial map in both the system the olfactory system and the gustatory system. So, in as you are probably aware the gustatory system starts from the nasal cavity and it is it we have the sensory epithelium or the olfactory epithelium in the nasal cavity in the upper region.

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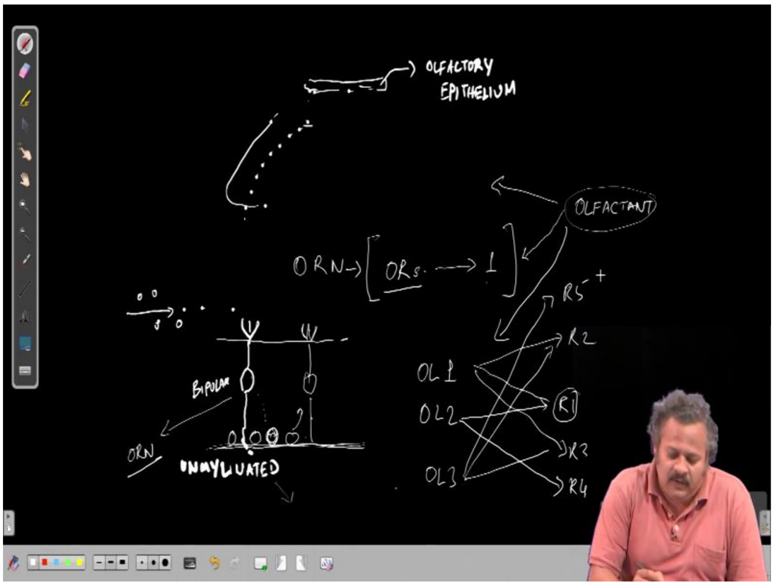

So, if this is the nose then as we breathe in the air comes in and then there is sensory or epithelial region or the olfactory epithelial region where the transduction of the stimuli happen or the olfactants happen. So, if we think of this particular region as a flat structure and we have the olfactants which are molecules that are coming in with the air that we breathe.

Then there are non-motile cilia that project out of the olfactory receptor neurons that are the primary sensors. So, the olfactory receptor neurons which lie just above the olfactory epithelium the surface of the olfactory epithelium are bipolar in nature and they then project with unmyelinated axons small diameter axons that go into the central nervous system.

So, this particular region has other supporting cells that support the structure and most importantly there are basal cells in this region in the epithelial tissue, which serve as progenitors for new olfactory receptor neurons. So, these are the olfactory receptor neurons and is one of the unique features of this particular system is that there is turnover of neurons. That is olfactory receptor neurons can die and it causes the basal cells to be converted into new olfactory receptor neurons.

So, one of the one of the few places where we see actually development of new neurons even in the adult stage so, that is called neurogenesis and this makes it an attractive system to study for other reasons especially developmental biology and also for regeneration of neurons, which is not found pretty much in most of the other regions of the brain. So, these cilia here and the olfactory receptor neurons in general have the olfactory receptors ORs.

Olfactory receptors are essentially proteins; that is, just like ligand gated ion channels or ligand gated proteins that are metabotropic receptors the not ion channels, but metabotropic receptors here. And the each olfactory receptor neuron generates or expresses only one kind of olfactory receptor, each olfactory receptor neuron produces only one kind of olfactory receptor.

And it is true that olfactory receptors it is not I mean they can be bound, I mean the olfactory receptors can recognize multiple types of receptor multiple types of olfactants. So, it is not that each olfactant is going to bind to only one kind of receptor; each olfactant may bind to many different receptors sometimes only one receptor.

And thus, there is a sort of in general a divergent kind of activation when an olfactant comes in. So, there are about 1000 types of olfactory receptors and so, based on a combination of what olfactory receptors are stimulated by each olfactant that is encode that encodes the identity of the odour or olfactant.

So, we have let us say olfactant 1 and olfactant 2 may stimulate receptor type 1 and receptor type 2 and receptor type 3. Olfactory receptor 2 may now have going to let us say can stimulate receptor 1 and receptor 4. Another OL 3 may now stimulate olfactory receptor 3, and olfactory receptor 2, and may be olfactory receptor 5. So, based on this tremendous combinatorial expansion, a huge number of olfactants can be encoded. And this is the fundamental basis of how olfaction or olfactants are encoded in the activity of the neurons in the next stage.

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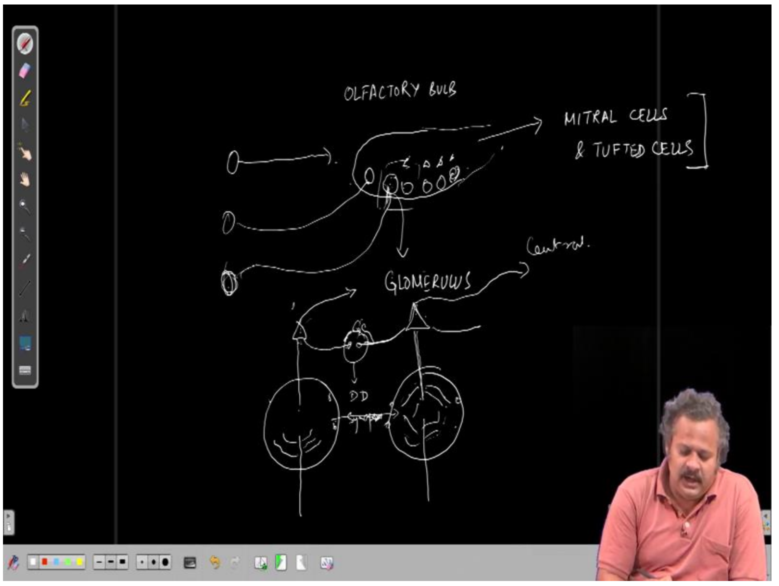

So, the olfactory receptor neurons project into go across the cribriform plate and project into a structure called the olfactory bulb that lies just above the olfactory epithelium above the nasal cavity. So, it is it has shape more or less like this and the olfactory receptor neurons project on to specific structures that are called glomerulus, glomeruli glomerulus each glomerulus. So, there are multiple glomeruli along the olfactory bulb side and a single type of receptor or olfactory receptor neuron with a single type of receptor projects to usually 2 glomeruli.

And it is here based on the inputs to the glomerulus; so, the glomerulus is a structure where the axon terminal of the olfactory receptor neuron ends and branches in sense of collaterals. So, if I draw if I expand this region here the structure is that there are many collaterals of the axon that invades the glomerulus that are generated and projects. So, this structure is essentially full of synapses and the olfactory bulb projects out via two types of cells called the mitral cells and tufted cells.

These are the principal neuron types of the olfactory bulb and these are in the inner side of the olfactory bulb and they send each of them send a basal dendrite. If this is a tufted cell, they send a basal dendrite into this region into the glomerulus. They may send dendrites to more than 1 glomeruli and so, there is an intricate structure of synapses that is formed from the axon endings and the dendrites of the mitral cells or tufted cells. Their output axon goes out into the central nervous system in further into the central nervous system.

They also have lateral dendrites that connect with other olfactory other tufted cells or mitral cells and form dendro-dendritic synapses. Dendro-dendritic synapses; that is, synapses that occur between dendrites unlike what we have learnt so far this is slightly different. So, it is just that the pre synaptic side the dendrites and the postsynaptic side both have the required machinery to perform as a synapse or the pre synapse and the post synapse.

And there are other granule cells that modulate inhibitory neurons that modulate this kind of transmission and can lower the transmission and serve as a stabilizer if there is over excitation. Similarly, there are many inhibitory inter neurons that are present on the edge of the glomeruli that is periglomerular cells and so on which again provide inhibition to the glomerulus and try to stop too much excitation.

So, now again with a combinatorial code this the glomeruli then activate the tufted cells and mitral cells, which is passed on to the central nervous system and that hierarchy is a bit different from what we have learnt so far, because this is a much more primitive sense.

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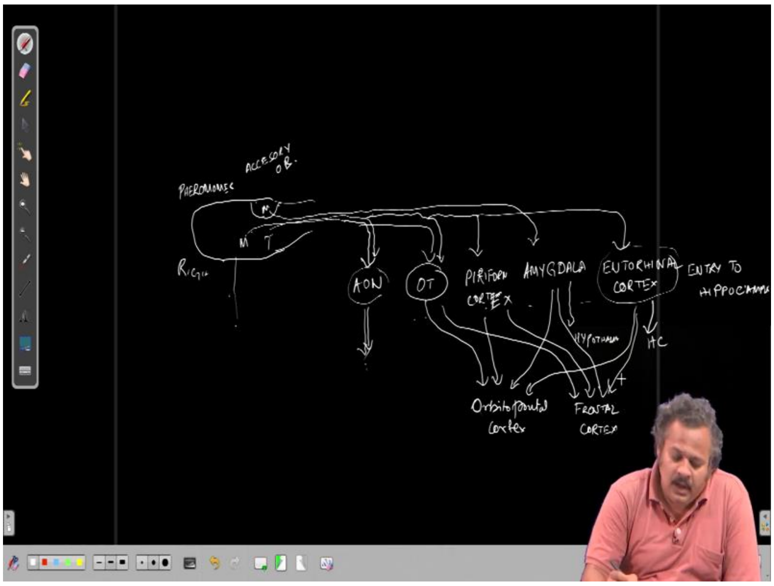

And was one of the earliest structures in evolution in terms of the sensory systems both olfaction and taste. And so, if we think of the mitral cells and the tufted cells; the tufted cells project out into the anterior olfactory nucleus. This is a nucleus in the olfactory pathway which projects onto the other side's olfactory bulb, that is if it is projecting two if the right olfactory bulb, we are considering the right olfactory bulb here. Then through the anterior olfactory nucleus projections go on to the left olfactory bulb.

They also project on to another structure a nucleus called the olfactory tubercle. And there is another set of mitral cells that come from a specific region of the olfactory bulb called the accessory olfactory bulb. And the mitral cells here project onto only the amygdala, which is part of the limbic system and involved in emotion processing, which you have learnt about in brain structures. And this pathway is specifically for pheromone processing for basically social cues and cues for in a meeting context; so, that projects directly into the amygdala.

The main projection start from the mitral cells and the mitral cells project on both to the anterior olfactory nucleus as well as the olfactory tubercle, then into the piriform cortex then onto the entorhinal cortex; and this is the gateway to the hippocampus; so, this is the entry to hippocampus which is as you will learn more is involved in memory; so, this goes to hippocampus.

The as you can see the olfactory inputs from the olfactory bulb from which gets inputs from the periphery directly go into the cortex instead of going to the thalamus or other structures. And then the thalamus and then the cortex, the usual hierarchy we have learnt about in the other three sensory systems; so, that in that sense it is very different.

Now, there are this amygdala there is a projection into the hypothalamus and overall these four structures further project into the frontal cortex in general. And specifically, the orbitofrontal cortex, which is a multi-sensory structure and involved in decision making and it gets inputs from the gustatory system also and of course, from other senses. So, all these have projections into the orbitofrontal cortex and these also project to the frontal cortex.

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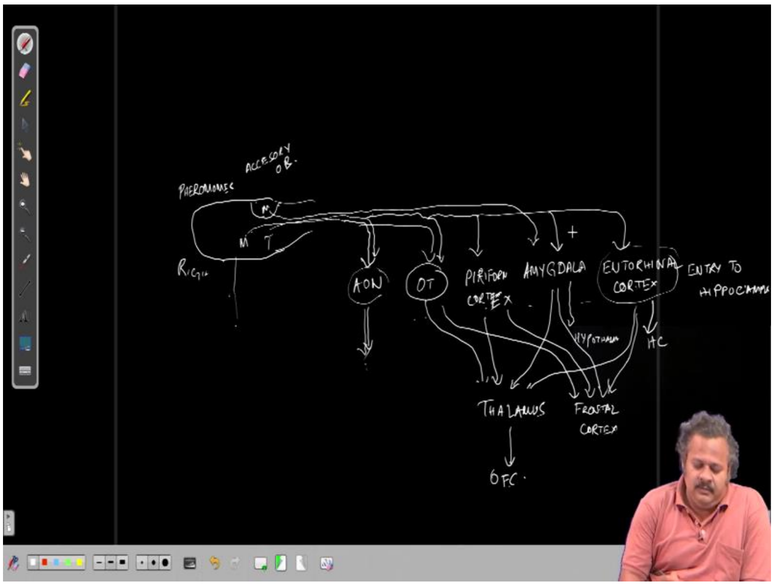

So, as you can see I am sorry just step this is there is a thalamus that is the medial dorsal nucleus of the thalamus to which these project which goes on to the orbitofrontal cortex. So, as you can see; so, from the cortex it goes back to the thalamus into the olfactory cortex and similarly again entorhinal cortex back to the thalamus into the cortex as well as other regions of the cortex.

In this sense the olfactory pathway is completely different in its structural arrangement, hierarchical arrangement. And the basic idea of representation of odours is based on the divergence of olfact each olfactory stimulus on two parallel paths as well as convergence on to single paths from multiple olfactants. And this kind of divergence and convergence is generally true throughout the pathway, which can be experimentally determined.

So, we these olfactory system is probably the least studied and hence a lot remains to be explored I am sorry I did not mark the amygdala. So, lot remains to be explored and can serve as a basis for really understanding how our brain encodes stimuli and is involved in processing information. And finally, providing percepts and hence cognition, because here since there are no easily parameterizable stimuli here.

And in the other cases since stimuli are parameterizable, we as humans or neuroscientists in general have adapted our understanding of the physical world based on sound pressure waveform or pressure, vibration for the somatosensory system. And illumination intensity and etcetera I mean it is a way we tend to understand the physical world from our understanding of physics and the mathematics involved with it.

Here because there is no such parameterization, it is unbiased a system that is sort of unbiased by the ideas of human knowledge. And so, in this kind of a system it sort of that neuroscientists are forced to think of a way how the brain tends to understand the stimuli, which is slightly different from how we have studied the all the other sensory systems other than of course, gustation.

So, with this note I will switch the discussion on to the gustatory system and for the sake of brevity and since we will not be talking too much about these systems later on during our lectures on attention perception and other aspects of cognition we will keep these brief. However, I must warn you that they are no less in any way any less in terms of affecting our abilities and our cognitive abilities and influencing different kinds of behaviour and so on.

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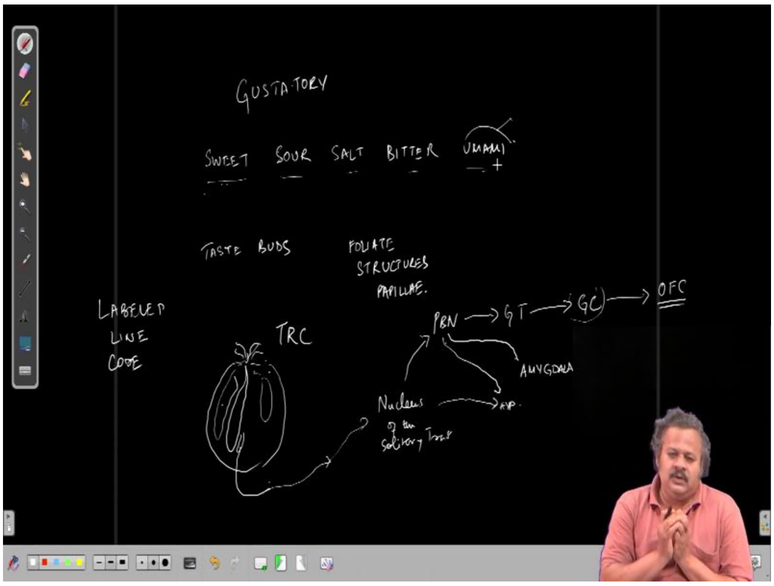

So, the gustatory system is also similarly organized in the sense that there is a hierarchy and the basic transduction of sweet, sour, salt, bitter, umami this is mainly like the taste of meat which is like taste of protein. These are the most studied five modalities of taste; I mean there are subdivisions within it in term in terms of what exactly is the molecule that is sweet. But the receptors that are involved are common for all of them; so, that is why they are sort of clubbed together into the taste that we know.

So, the transduction happens in the taste buds as you may be familiar taste buds that are present in like foliate structures or papillae. And the taste receptor cells the TRCs that are present in are present in the taste buds in this kind of sack like structure with the microvilli like structure of the taste receptor cell extending out into the that the region of the taste part that opens up into the as a pore into the tongue or the palate or the epiglottis, larynx, pharynx all these regions have taste parts.

So, there are other cells of course that are involved in supporting these structures supporting this structure. And these taste receptor cells are innervated by fibres which carry information of the spiking activity or the depolarization of the neurons with spiking activity into the central nervous system. So, there are basically three different nerves that innervate our olfactor our oral cavity and they finally, project into a structure called the nucleus of the solitary tract.

The nucleus of the solitary tract also projects to the hypothalamus for different kinds of processing to do with the feeding behaviour and so on. The next structure in the brainstem that the nucleus solitary nucleus of the solitary track projects onto is called the parabrachial nucleus. And from the parabrachial nucleus it goes on to the gustatory thalamus, which is a specific region of the thalamus that goes into the gustatory cortex which is the main region the primary region in the cortex that is involved in gustatory processing.

And this then projects on to the orbitofrontal cortex in the pre frontal cortical region. And again, this is sort of the hierarchy there are other structures that are involved, which is again the amygdala because of the connection of taste with emotions and the parabrachial nucleus actually projects on to the amygdala as well as the hypothalamus.

So, we will what we know is that there are two hypothesis regarding how these different tastes are encoded in the activity along the pathway. And one of them is a labelled line code, a labelled line code which essentially mean that these different sort of taste the modalities that we started off with they are remain more or less segregated along the path.

While there is some evidence quite a bit of evidence in favour of this it is there is counter evidence also to suggest that there is coding across channels just like in the olfactory system. And that is again a coding based on a combinatorial code that is based on different neurons carrying multiple modality information of the specific taste types. So, again it is in the firing activity of neurons that this taste is encoded and usually the intensity or concentration of the taste is encoded in the increasing firing rates of these neurons.

As an anecdote very in the very recent past, we have a little bit of idea about how the tastants can be organized in the gustatory cortex. And that has to do with pleasantness, where unpleasant tastes seem to be encoded by neurons on one side of the gustatory cortex while pleasant taste producing substances are encoded by neurons on the other side, although there is a great degree of overlap.

So, with these ideas we will conclude the discussion on all the sensory circuits. And next we go on to the motor cortex or the system involving our actions, which is also going to be an important part of how perception finally, produces action or how sensory inputs. And based on some decision we finally, produce action; so, we will take that up in the next lecture.

Thank you.