Introduction to Complex Biological Systems
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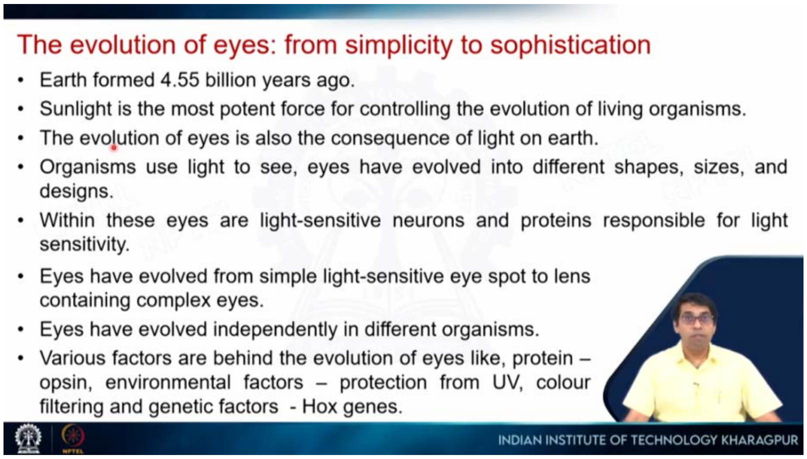
Lecture 39
Evolution of eye

Welcome to this lecture on introduction to complex biological systems. This week, I'm teaching evolution, the history of life, and in this lecture, I'm going to talk about the evolution of eyes. Eyes or the eye is a fantastic organ, and there are all these different types of eyes that we see in nature. So this is the eye of a spider, an elephant, the eye of a gorilla, owl, goat, octopus, and human. We are going to compare the eyes of humans and octopuses in detail later on. Cat and beluga, so it is a whale-like fish. Donkey, mosquito, drosophila, mantis, and lobster.

So I'm also going to discuss these eyes, the dragonfly and mosquito eyes. These are compound eyes. So it turns out that this organ accomplishes vision. However, if you look at this, these entire look so different, which means that nature has come up with the same solution in multiple different pathways.

So you can consider that these are examples of convergent evolution. As we have seen, Earth was formed 4.5 billion years ago and sunlight turns out to be the most potent force for controlling the evolution of living organisms because sunlight is the energy source and we are trapping this energy to perform all the work that we do, anything that goes on this planet. Evolution of eyes is also the consequence of light on Earth because organisms use light to see, eyes have evolved into different shapes, sizes and designs.



Within this light, there are light sensitive neurons and proteins responsible for light sensitivity. So I will discuss the architecture of our eye in details in the next few slides. Eyes have evolved from simple light sensitive eyespot to lens containing complex eyes. Eyes have evolved independently in different organisms. So in the previous slide, I showed you all the different types of eyes or different looking eyes in these different organisms.

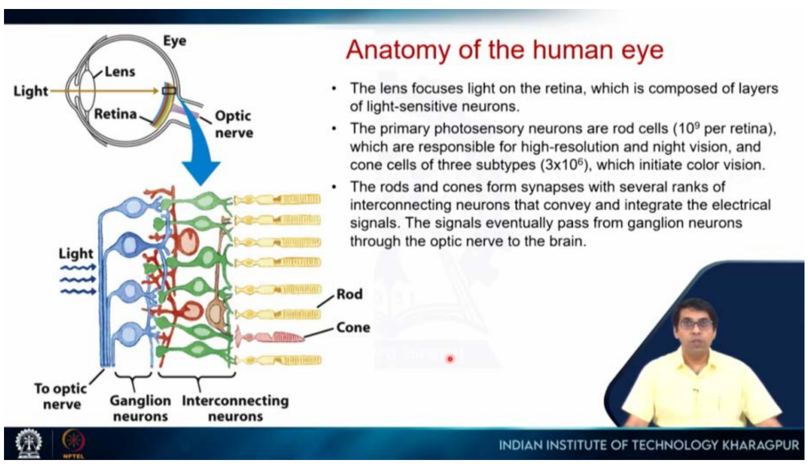
So they have evolved independently of each other. Various factors behind the evolution of eyes are like proteins. So evolution of proteins for example opsin will drive a design of an eye's environmental factors for example animals that live on land versus animals that live in water their environmental factors are different. So that will also drive their evolution protection from UV color filtering and genetic factors like the hox genes so all of these together will have impacted the evolution of the eye and that is why we see so many different designs. In fact, if we talk about evolution, it turns out that there are three major factors that drive evolution. The first one is utilization of energy.

So every organism needs to find a source of energy for survival, and that energy we get in the form of food consumption. So the search for food is something that drives evolution. An organism which has a better eye will, of course, be able to locate food better and hence will have a better chance of survival. So the search for food will drive the evolution of the eye.

Second is the predator-prey relationship. So every organism is a predator. It eats something, and it can also be prey because it can be eaten by something. As a predator, an organism has to locate its prey, and as prey, that organism has to evade its predator and all of these things can be done better if your vision is good.

So this predator-prey relationship will also drive the evolution of the eye. The third factor is reproduction. So for higher organisms, an organism has to find its mate. So here also, vision plays a very important role.

So energy source, predator-prey relationship, and reproduction, all of these three things together drive evolution, and the evolution of eyes has also been driven by these three factors. So here is the anatomy of the human eye. So this is the human eye, and the major portions of the human eye are shown. So we have a lens. There is this retina.



So the lens concentrates the light, and it focuses it. The light falls on the retina, and then an image is formed. That image is converted into an electrical signal, and that electrical signal is conducted by these optic nerves to our brain. That is how we perceive or see something. Now, the lens is also made up of proteins but its function is to direct the light in here. So there is a pinhole that results in sharper images. The lens will bend all the light and concentrate it on the retina and this is the architecture of the retina.

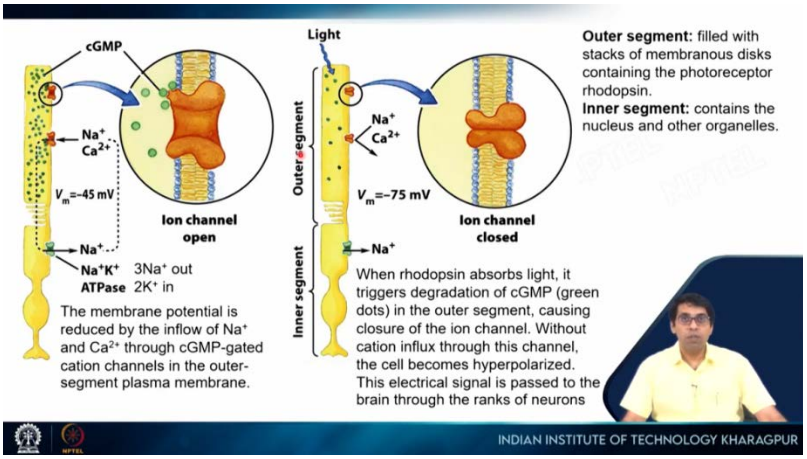
So our retina is primarily made up of neuronal cells. So there are two types of neuronal cells: rod-shaped cells and cone-shaped cells. So the lens focuses light on the retina, which is composed of layers of light-sensitive neurons. The primary photosensory neurons are rod cells and cone cells. So it turns out that there are 10^9 rod cells per retina and $3x10^6$ cone cells per retina.

Rod cells are responsible for high-resolution images and night vision. However, these rod cells cannot discriminate between colors. So they give you high-resolution images, and they can also help you see in the dark, the night vision. The cone cells can distinguish between the three primary colors. So the colors that we see are because of the cone cells.

They initiate color vision. Rods and cones form synapses with several ranks of interconnecting neurons that convey and integrate the electrical signals. The signals eventually pass from the ganglion neurons through the optic nerve to the brain. So these rod cells and cone cells connect through these interconnecting neurons, the green ones, and then these ganglions and then these are the optic nerves, which go to the brain.

So this is an amplified image of what you see here. Now, there is something very interesting that I should point out, and I will again discuss this in more detail later on. The design of this is inverted, inverted in the sense that these are the cells which sense the light. However, light is coming from this direction. So light is coming from this direction so it passes through these optical nerves and all these neurons and then it will reach the rod and cone cells.

It would have been better if the rod and cone cells were on this side and these other cells would have been on the other side and we will see that is exactly the case for organisms like octopus. So we will compare the eyes of humans and octopuses and we will see that they are very similar however this particular arrangement is inverted and this inversion makes the octopus eye much better than the human eye. Another fact that shows up here is you see these optical nerves which are coming out here and because of these optical nerves there are no neuronal, this rod and cone cells in this particular region. So that particular region creates a blind spot. So our retina has a blind spot where if light falls, no image will be created and that blind spot is absent in the eye design of octopuses. So let's look at these rod cells and cone cells in more detail. So this is a rod cell and it is divided into two segments. One is called the outer segment and the other one is called the inner segment. So this is the outer segment and this is the inner segment and in these segments, there are all these ion channels. The outer segment is filled with stacks of membranous disks containing the photoreceptor rhodopsin. Rhodopsin is present in the outer segment. I have already talked about rhodopsin and will discuss it again in today's lecture. The inner segment contains the nucleus and other organelles.

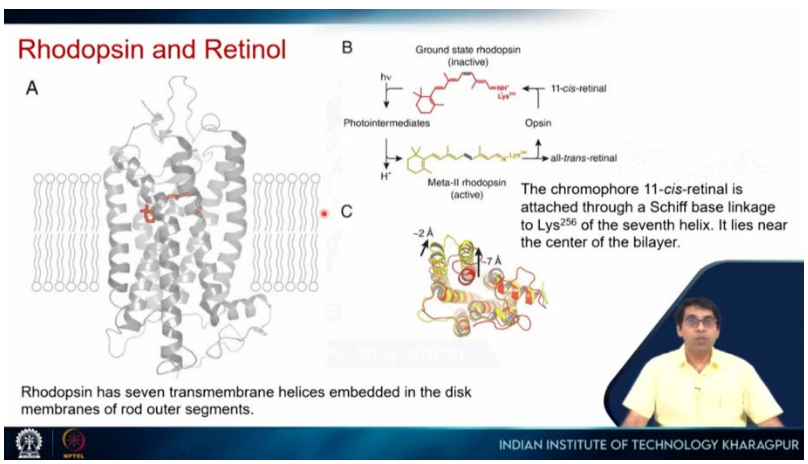


The nucleus, mitochondria, and all those organelles are present in the inner segment. This is the working part of this cell or the neuron. The membrane potential is reduced, so there are these ion channels.

This is the sodium-potassium ATPase. What it does is hydrolyze ATP, pump out three sodium ions, and pump in two potassium ions. The net charge difference is plus one on this side. It pumps in two potassium ions and pumps out three sodium ions. Now, the sodium ions, which are in higher concentration here, flow in through these sodium-calcium Ion channels. So these sodium-calcium ion channels are open. These are in an open state and will allow the inflow of sodium and calcium ions. This equilibrium results in a voltage difference of 45 millivolts across the membrane. This ion channel opens when cyclic GMP binds to it.

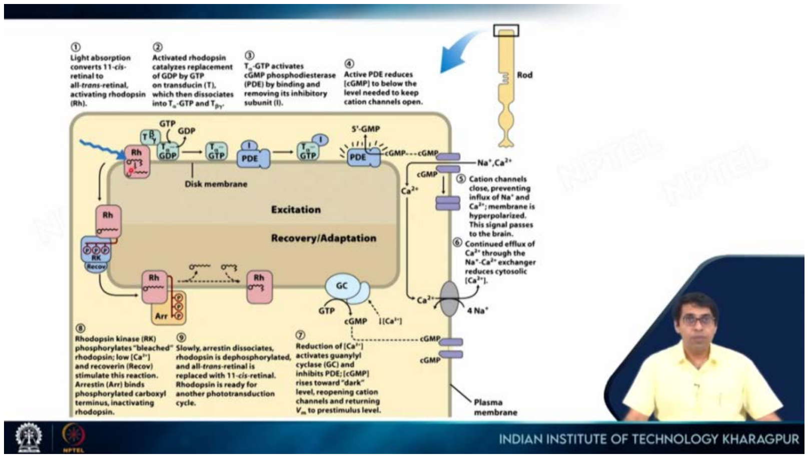
So it turns out that roughly three cyclic GMPs need to bind to this ion channel for it to fully open. When light falls on this cell, it is detected by the rhodopsin. That's another protein which is in this part. Rhodopsin absorbs the light and triggers a reaction where cyclic GMP is degraded, so it is hydrolyzed, resulting in a drop in cyclic GMP concentration. If the cyclic GMP level drops, it will not bind to the channel, and the channel will close without continuous influx through this channel, because these sodium and calcium ions were going in. So these positive ions are not going in, but they are still being pumped out so there will be a charge difference. So the membrane becomes hyperpolarized. This electric signal is passed to the brain through the ranks of the neuron seen in the previous slide. A potential is generated and passed to these neurons, then through the optic nerve to the brain.

So light is converted to an electrical signal by rhodopsin and these ion channels. So this is rhodopsin. We have already seen this. It's a membrane protein. It has these seven transmembrane helices, which are embedded in the membrane and almost at the center of this protein is this particular molecule, which is retinol. We have seen that it comes from vitamin A. Now, retinol that is bound in rhodopsin has this cis conformation. So between the 11th and 12th carbon, This is in the cis conformation. When light falls, this converts to trans retinal.



So it converts into the trans conformation, and that results in this big conformational change in one of the helices. So you see that there is a 7-angstrom shift of this helix and a 2-angstrom shift of another helix. So this conformational change triggers a series of biochemical reactions, which will result in what we have discussed in the previous slide. So let us see what happens here.

So this is the vision cycle. I have already discussed this in one of the previous lectures, but here I am going to discuss it in more detail. So one half of the cycle is the excitation cycle, and the other half of the cycle is the recovery or the adaptation cycle. So, this is rhodopsin; it is bound to the membrane, and this is retinal, cis retinal. When light falls, the cis retinal gets converted to trans retinal, and this results in a tug on or pull on one of the helices. So there is a conformational change, and that conformational change activates this other protein. So activated rhodopsin catalyzes the replacement of GDP by GTP on transducin. So this protein is transducin. The change in conformation of rhodopsin results in the kicking out of GDP from transducin, and it binds to GTP.



So transducin now binds to GTP and then it comes out from here and goes to bind to this protein complex. So this is PDE, or phosphodiesterase. Now, this phosphodiesterase is originally in an inhibited state.

So this I is an inhibitor which is inhibiting this phosphodiesterase. This GTP bound transducin comes and it binds to this inhibitor more tightly than PDE, which means that it will take this out like so. So now the phosphodiesterase is free and it is activated and what will it do? It will hydrolyze this cyclic GMP.

So it will break one of the phosphoester bonds. So it will reduce the concentration of cyclic GMP. As the concentration of cyclic GMP goes down, this gated ion channel, which was allowing sodium and calcium ions in, becomes closed because cyclic GMP concentration has gone down. No cyclic GMP binds here. So this ion channel closes like this.

So this influx is stopped and that results in the generation of this electrical potential which is roughly 1 millivolt and it is carried on through other neuronal cells and the optical nerve into the brain. So this is a continuous efflux of calcium through the sodium calcium exchanger. So this is still happening. So this is still happening, but no calcium is going out, coming in, but calcium is still going out, which means that calcium ion concentration also decreases.

So we have already generated the potential, and that is transmitted to the brain. Now we are in the recovery cycle. So lower calcium concentration triggers this reduced calcium concentration activates this enzyme, which is guanyl cyclase (this enzyme GC). So guanylyl cyclase gets activated because of low calcium ion concentration.

It inhibits PDE, which is this. So it inhibits PDE. So it will stop the hydrolysis of cyclic GMP, reopening the cation channel and resulting in this level. So it will inhibit PDE and synthesize more. It will use GTP to synthesize cyclic GMP, so in a sense, it stops this and makes more cyclic GMP. It will increase the level of cyclic GMP, and those cyclic GMP can now go and bind to this ion channel, opening it. The ion channels, which were closed, will now get opened, and again sodium and calcium ions will rush in through this ion channel.

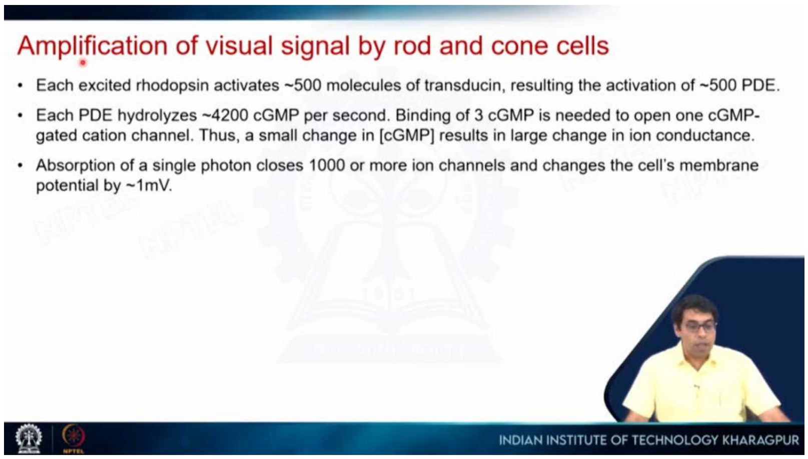
So this raises towards the dark side. So now we are going to equilibrium. Something also happens to the rhodopsin. Now see that rhodopsin is bound to the transretinol. So rhodopsin kinase phosphorylates rhodopsin.

There is already a low calcium ion concentration at this point. So this low calcium ion and recovery, this is another protein that stimulates this reaction. So it phosphorylates rhodopsin. Arrestin binds the phosphorylated carboxyl terminus and inactivates rhodopsin.

So arrestin, this protein, and recov together they come and inactivate the rhodopsin. At this point, arrestin slowly dissociates. Rhodopsin is also dephosphorylated. This trans-retinol is now replaced by another cis-retinol because trans-retinol has to go out, and cis-retinol has to come in.

Now this cis-retinol is present. So it goes back to this state. Calcium concentration has recovered because these ion channels have opened. Cyclic GMP levels are also backed up. So we are back to this condition.

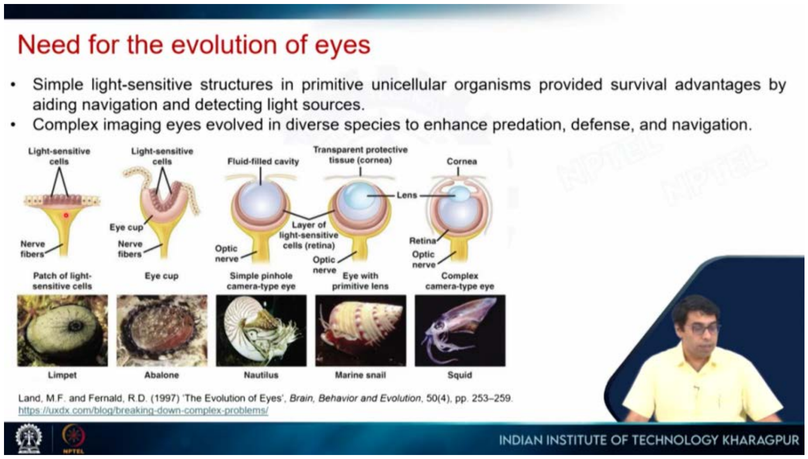
Another photon comes, and then the whole cycle will get repeated. So this is the vision cycle. So, in essence, what happens is that the light energy or the photon is converted to an electrical signal via these enzymes. Now, it turns out that one rhodopsin can trigger the activity of a lot of this protein, which is transducin and the phosphodiesterase and they will catalyze a lot of cyclic GMP hydrolysis. So the signal is amplified, amplification of the visual signal by these rod and cone cells. So each excited rhodopsin can activate 500 molecules of transducin. So each activated rhodopsin can activate almost 500 molecules of transducin.



Each transducin will activate one phosphodiesterase. So one rhodopsin, in turn, activates almost 500 phosphodiesterases. So resulting in the activation of 500 phosphodiesterases. Now, one phosphodiesterase hydrolyzes almost 4200 cyclic GMPs per second. So 500 will hydrolyze this into 500 per second.

Now we have seen that three cyclic GMP binding is needed to open one of this cyclic GMP gated cation channels. So if we have hydrolyzed so many cyclic GMPs, then the cyclic GMP concentration goes down very rapidly and almost a thousand such ion channels are closed. So one photon results in the closing of 1000 or more of this cyclic GMP gated cation channel, which results in a large buildup of ions and results in a potential difference of almost 1 millivolt so there is a large signal amplification because of these biochemical reactions.

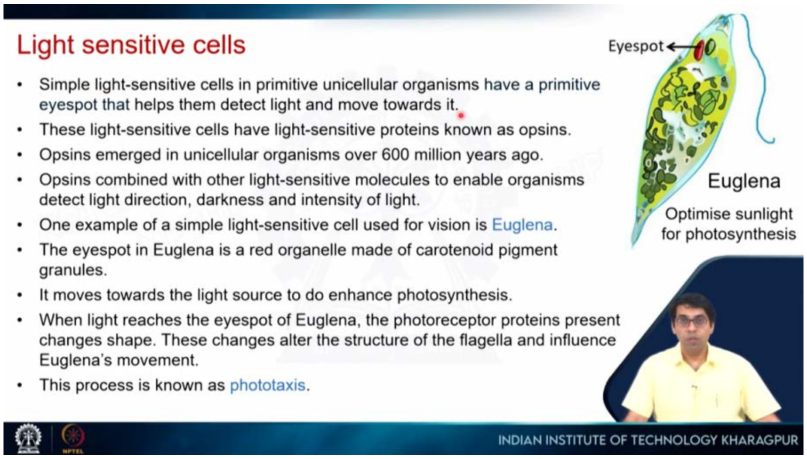
So one photon results in this electrical signal so that was the human eye but it turns out that there are many designs of the eye and some of those are very primitive, but we do see examples of this primitive eye architecture even today. So one is these simple light sensitive cells, there is no architecture, only these light sensitive cells, when light falls on it, that will be detected.



So they can detect light versus dark. A little better design is where the cells are cup shaped. In this case again no image is formed but it can sense light and dark and also some sort of directionality like from which direction the light is coming. Here the design is where it has a pinhole but there is no lens.

So this is filled with water. So if it's an aquatic animal like the nautilus, it will be filled with water. So here it will not form an image, but it can see the shadow of something passing by. So it can see in which direction a particular prey or predator is coming or going. This is a primitive eye with a lens, and this is a complex eye with a very sophisticated lens and a much more complex design.

So this will be something that we have the light-sensitive cells. Simple light-sensitive cells in primitive unicellular organisms have a primitive eyespot that helps them detect light and move toward it. So the only thing that these cells do is that they detect where the light intensity is greater, and the organism will move toward that.

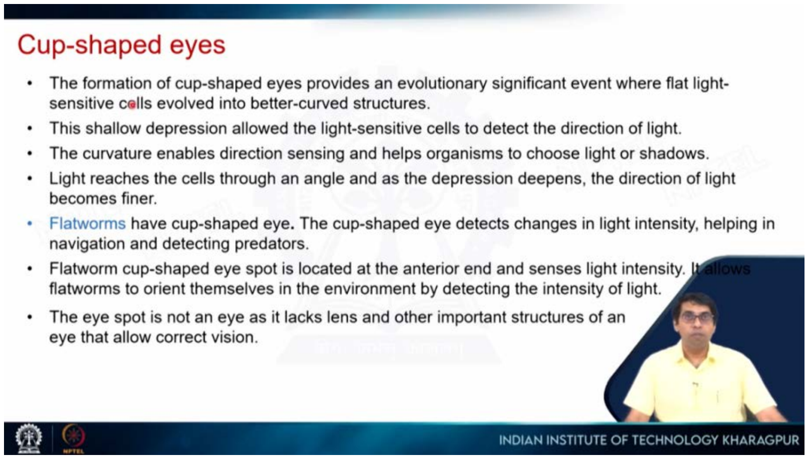


So that will help in better photosynthesis. So it optimizes sunlight for photosynthesis. These light-sensitive cells have light-sensitive proteins known as opsins. So rhodopsin will be an improved or more optimized version of these opsins. Opsins emerged in unicellular organisms over 600 million years ago.

These opsins combined with other light-sensitive molecules to enable organisms to detect light direction, darkness, and intensity of light so one example of an organism which has these light-sensitive cells is Euglena. The eyespot in Euglena is a red organelle made of carotenoid pigment granules. So we have already seen the carotenoid structure in one of the previous lectures. So when there is light, it moves toward the light source to enhance photosynthesis.

When light reaches the eyespot of Euglena, the photoreceptor proteins present change shape. These changes alter the structure of the flagella and influence Euglena's movement. So it has flagella here. So they will start spinning, and it will push this organism toward the light source.

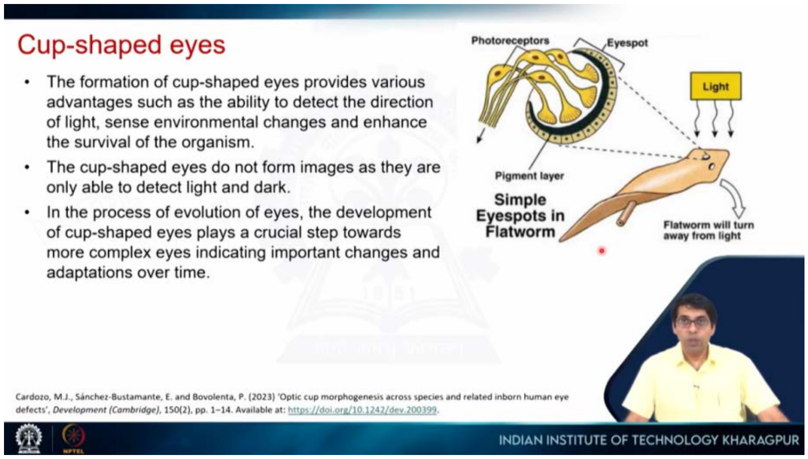
So this movement as a function of light is called phototaxis. So 'photo' means light, and 'taxis' means movement. So we have seen this now, the eyecup so cup-shaped eyes. The formation of cup-shaped eyes provides an evolutionarily significant event where flat light-sensitive cells evolved into better-curved structures.



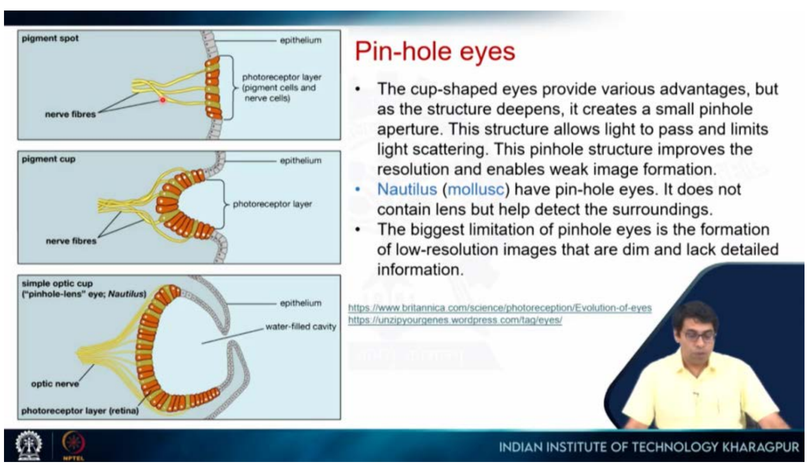
So instead of a flat structure like this, it becomes a curved structure like this. This shallow depression allows the light-sensitive cells to detect the direction of light. So in this case, when light falls, it still detects it, but it is not doing a very good job but here, it can detect the direction of light. So if light is coming from this direction, there will be more illumination here versus if light comes from this direction, there will be more illumination here so based on that, it can detect the direction of light better than these flat cells. Light reaches the cells through an angle and at the depression the direction of light becomes finer. Flatworms have cup-shaped eyes. So that's an example. The cup-shaped eyes detect changes in light intensity, helping in navigation and detecting predators.

So it can detect predators, and it can also detect prey. The flatworm's cup-shaped eyespot is located at the anterior end and senses light intensity. So it allows flatworms to orient themselves in the environment by detecting the intensity of the light. The eyespot is not an eye, as it lacks a lens and other important structures of an eye that allow clear vision. So it is not like a modern eye that we have, but it is called an eyespot.

So this is a flatworm, and it has eyespots here. So what you have is these cup-shaped eyes are the light-sensitive cells, and these neurons are the photoreceptors, so they will transmit the signal. The formation of cup-shaped eyes provides various advantages, such as the ability to detect the direction of light, sense environmental changes, and enhance the organism's survival. The cup-shaped eyes do not form images, as they can only detect light and dark.



In the evolution of eyes, the development of cup-shaped eyes plays a crucial step toward more complex eyes, indicating important changes and adaptations over time. So once this happens, you can imagine that the addition of more components will lead to modern complex eyes. So it is shown here that the pigment spot is flat, and then there are these nerve fibers, which carry the signal. Now we have this cup shape, which is better at detecting the direction of light. In this case, the cup shape is there, but instead of a broad opening, there is a pinhole.

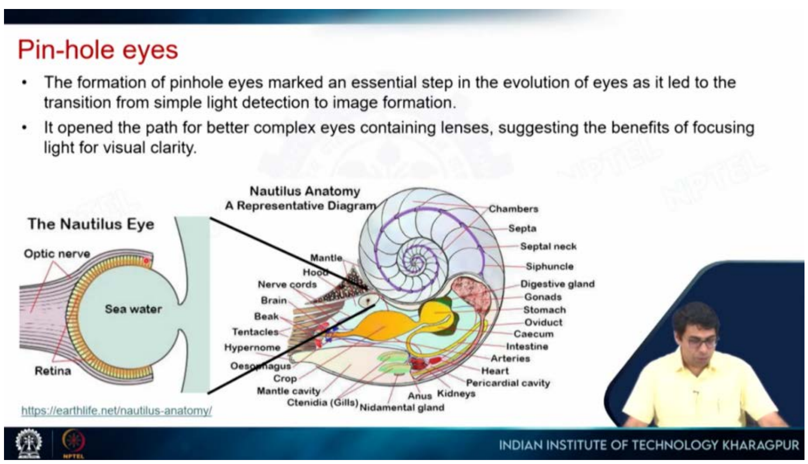


Once there is a pinhole, better images can form, and this starts to become an eye that can actually see images. The resolution will depend on how sophisticated this design is. So you have to add a lens to make better-resolution images. So cup-shaped eyes provide various advantages, but as the structure develops, it creates a small pinhole aperture. This structure allows light to pass and limits light scattering.

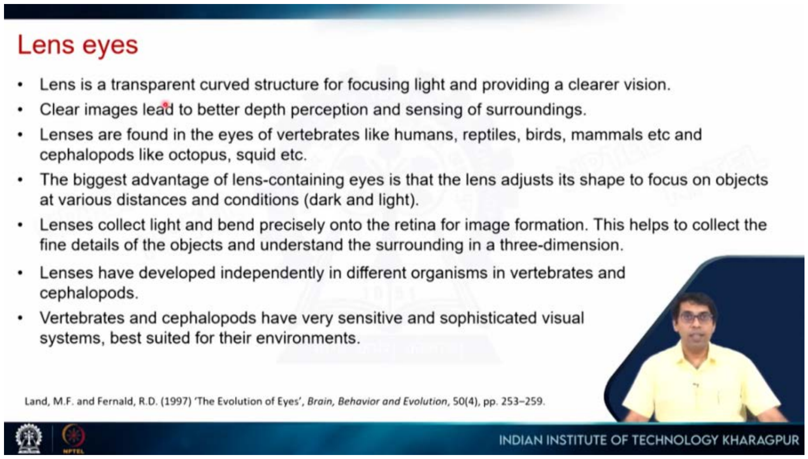
This pinhole structure improves the resolution and enables weak image formation. There is no lens. So this is filled with water. So it will result in the formation of a weak image or a low resolution image. So Nautilus, they have pinhole eyes.

It does not contain a lens. So this is actually filled with water. The biggest limitation of pinhole eyes is the formation of low resolution images that are dim and lack detailed information. So this is Nautilus and this is their eye and this is a zoomed image of their eye.

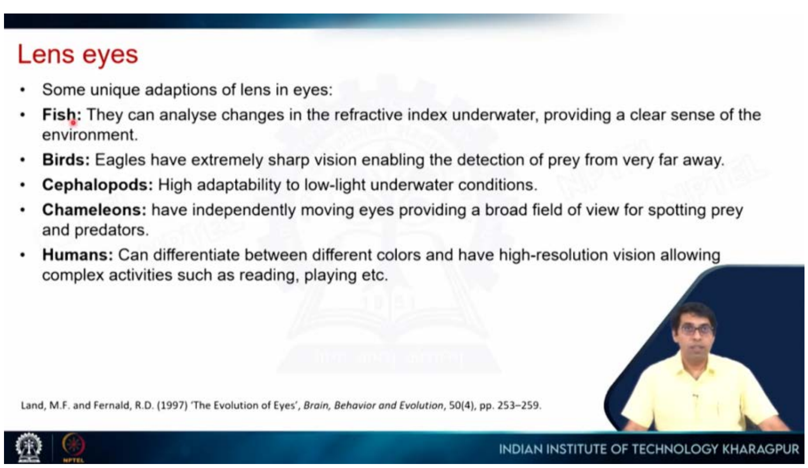
So it forms this pinhole and this cavity, it does not have a lens. However, it is filled with seawater. So you can imagine that it is not going to do a very good job of concentrating the photons and whatever image is generated will not be a very sharp image. The next is eyes with lenses. So these are called lens eyes.



The lens is a transparent, curved structure for focusing light and providing clearer vision. Clearer images lead to better depth perception and sensing of surroundings. So, there are obvious evolutionary advantages to seeing better. Lenses are found in the eyes of vertebrates like humans, reptiles, birds, mammals, etc. and in cephalopods like octopuses, squids, etc.

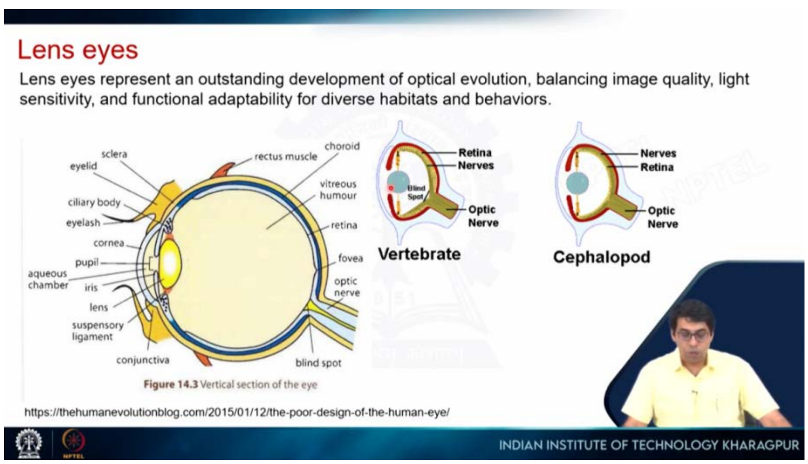


The biggest advantage of lens-containing eyes is that the lens adjusts its shape to focus on objects at different distances and under different conditions. Lenses collect light and bend it precisely onto the retina for image formation. This helps in collecting fine details of the object and understanding the surroundings in three dimensions. So, we get much sharper images because of the lens. It turns out that lenses have developed independently in different organisms, such as vertebrates and cephalopods and we are going to compare the eye architecture in vertebrates and cephalopods. So, vertebrates and cephalopods both have very sensitive and sophisticated visual systems, best suited for their environments but we will see what the major differences are and again, this provides an example of convergent evolution. Some unique adaptations of the lens in eyes, for example, in the case of fish, allow them to analyze changes in the refractive index underwater, providing a clear sense of the environment.



Birds, on the other hand, fly very high, so they have to sense or detect things from a distance. Eagles have extremely sharp vision, enabling them to detect prey from very far away. Cephalopods have high adaptability to low-light underwater conditions. They can go down to very high depths where very little light reaches. In these low-light conditions, they have the ability to see. Chameleons have independently moving eyes, which means that each eye moves independently of the other. In our case, both eyes move together. These independently moving eyes provide a broader field of view for spotting prey and predators.

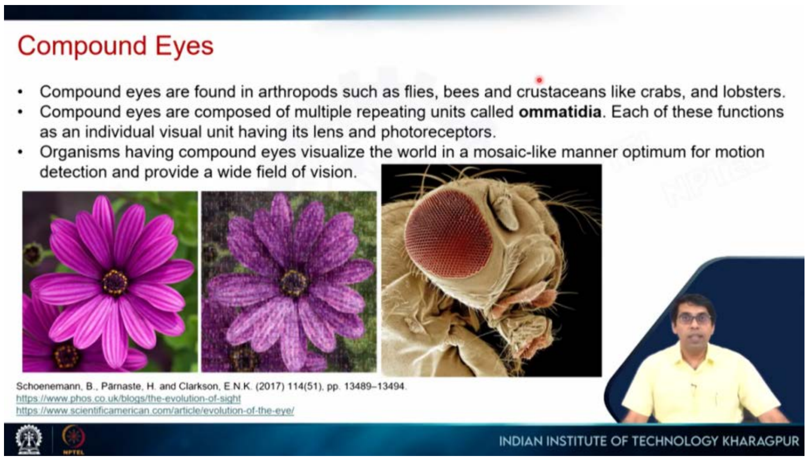
Humans can differentiate between different colors. We see high-resolution images, which helps us in reading, playing, etc. Again, this is the architecture of the human eye. As I pointed out earlier, there is this weird design where the retina is at the back and the nerves are in the front. When light comes through, it goes through this thin layer of nerve cells and then reaches the retina. However, at this position, we have these optic nerves. All of these nerves are bundled together and go to the brain.



There is no retina, no retina cells here. So no rod cells or cone cells and this particular region create a blind spot.

So this is the blind spot in our retina. However, in the case of cephalospods, the design is the way you would expect. Retina is in the front and the nerves are in the back. So even though the nerves are going here, the retina is there. So even though the nerves are there, since the retina is in the front, there is no blind spot in cephalopods.

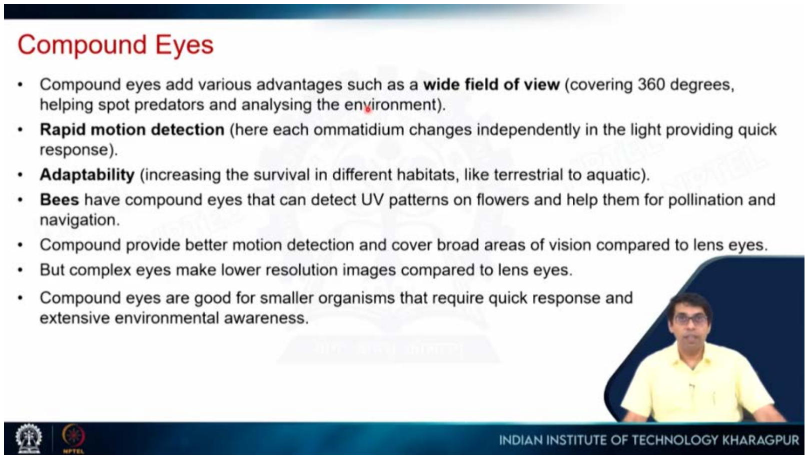
So vertebrates, we have this inverted architecture where the retina is in the back, nerves are in the front, that results in this blind spot. In case of cephalopods, the retina is in the rod and cone cells are in the front, the nerves are in the back and there is no blind spot. There is this other design of eye which is called the compound eye. So this is Drosophila and you can see this compound eye in Drosophila. Compound eyes are found in arthropods such as flies, bees and crustaceans like crabs and lobsters.



These compound dyes are composed of multiple repeating units. So you can see this array of lenses. These are called ommatidia. Each of these functions as an individual visual unit, having its own lens and photoreceptors. These organisms visualize the world in a mosaic-like manner, which is optimal for motion detection and provides a wide field of vision.

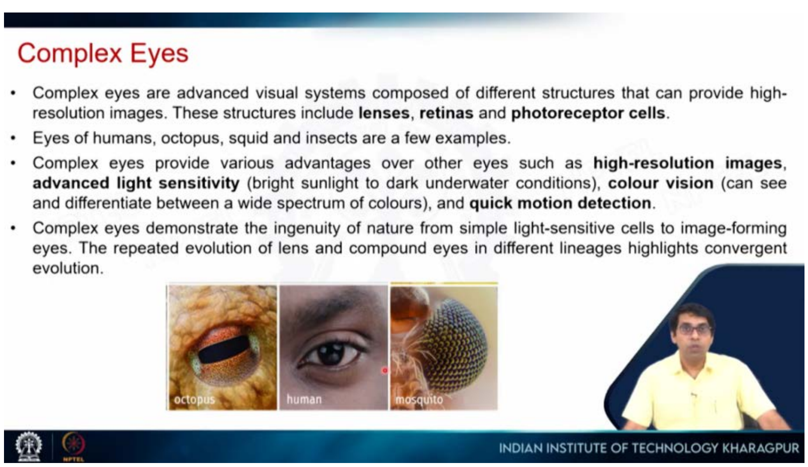
So a flower that we see like this, These organisms will see it like this. However, this provides a much better reaction time for these organisms. So they can detect motion much better than we do. Compound eyes have various advantages, such as a wide field of view.

So almost a 360-degree view helps spot predators and analyzes the environment. Rapid motion detection, since each of them changes independently in the light, provides a quick response time. Adaptability increases survival in different habitats, from terrestrial to aquatic. Bees have compound eyes that can detect UV patterns on flowers, which helps them with pollination and navigation. Compound eyes provide better motion detection and cover a broader area of vision compared to the lens eyes that we have.



But complex eyes make lower resolution images compared to lens eyes. So this will be compound eyes. So with compound eyes, they make lower resolution images compared to lens eyes because of this mosaic pattern. Compound eyes are good for smaller organisms that require quick response. However, complex eyes are better for larger organisms like us and other vertebrates.

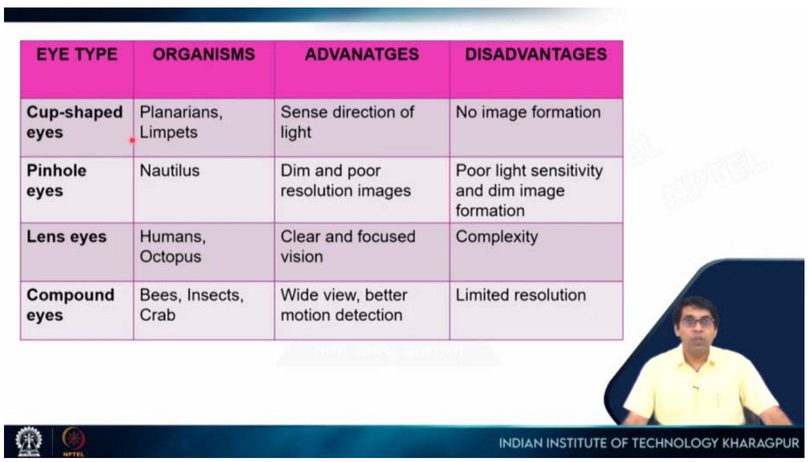
So we have these complex eyes. So complex eyes, these are advanced visual systems. They have structures like lens, retina and the photoreceptor cells. So examples will be the eyes of humans, octopus, squid and insects. Complex eyes provide various advantages over others such as high resolution images, advanced light sensitivity, color vision and also good motion detection.



Complex eyes demonstrate the ingenuity of nature from simple light sensitive cells to image forming eyes. So we have seen all these different designs, there are some very primitive designs and now we have very complex eye designs like this. So on top of that, there are also some protective membranes. For example, we have eyelids which protect our eyes. We have tears which produce lysozyme that fights against microbes and protects our eyes from infection.

Nictitating membrane, a third eyelid in some animals like birds and amphibians, provides extra protection without obstructing vision like you see here. This shields aquatic animals from water currents and saves desert animals from intense and harmful UV radiation. These are the different eye types: cup-shaped, pinhole, lens eye, and compound eyes.

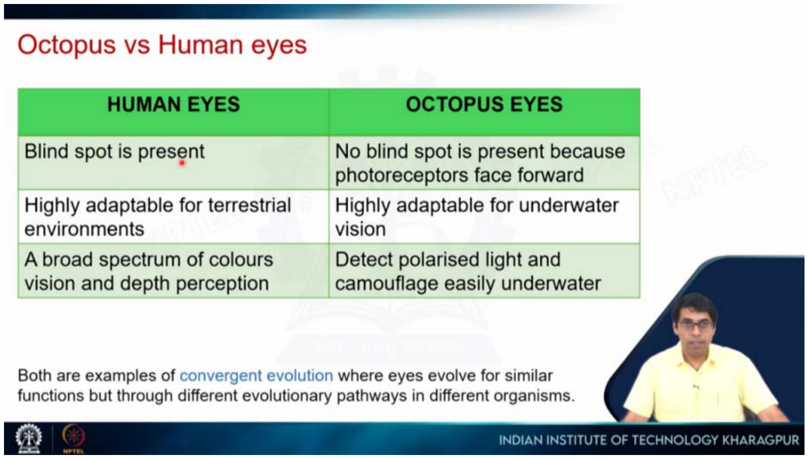
They are found in these different organisms. Their advantages and disadvantages are listed here. You can pause this and go through it. This is a summary of the different eye types. It is interesting to compare human eyes with octopus eyes.



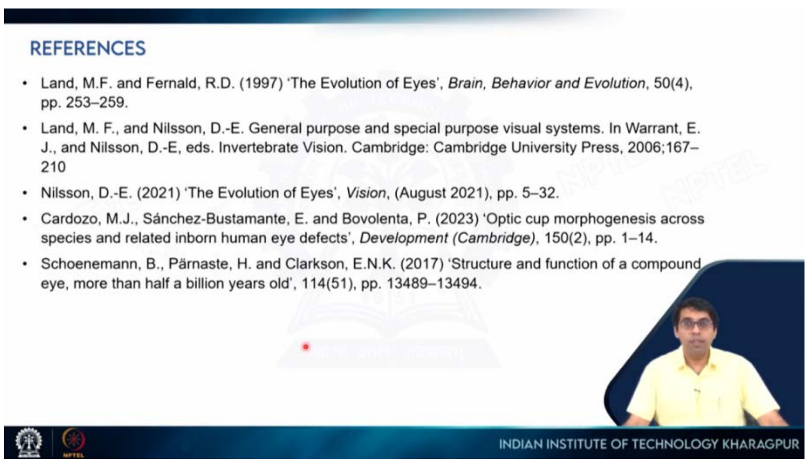
EYE TYPE	ORGANISMS	ADVANATGES	DISADVANTAGES
Cup-shaped eyes	Planarians, Limpets	Sense direction of light	No image formation
Pinhole eyes	Nautilus	Dim and poor resolution images	Poor light sensitivity and dim image formation
Lens eyes	Humans, Octopus	Clear and focused vision	Complexity
Compound eyes	Bees, Insects, Crab	Wide view, better motion detection	Limited resolution

Human eyes have a blind spot, as I showed in the previous slide, because of the inverted design of the retina and the nerve cells. No such blind spot is present because the photoreceptors face forward. They are on the front side, and the nerve cells are on the back side. This is highly adaptable for terrestrial environments. Octopus eyes are also highly adaptable for underwater vision.

A broad spectrum of colors, vision, and depth perception is achieved by human eyes. Octopus eyes can detect polarized light and camouflage easily underwater. So, both of these eye types are examples of convergent evolution.



So, I have listed all these different references in the slides, and I have also listed some of the important references here. You can go through them, and you can also use the books that I have listed earlier.



Thank you.