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**Animal Eyes**

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We are, this evening, going to discuss animal eyes, and I am often asked this question, “What does my dog see? What does a fly see or a honeybee for that matter?” and it is an interesting, perplexing question that has exercised the minds of many, many intelligent people in the field of optometry, vision science, and a lot of new research and data has come out. I am going to go through some of that today. If I miss out your favourite animal, I apologise, because we could just do this on three or four different species of insects and be here for the rest of the afternoon quite easily.

Here, we see the beautiful eyes of this insect, made up of many, many facets, called a compound eye. Interestingly, there are other eyes present on this animal. It has seven, and I will tell you about those later on.

If you are interested in this subject, there are a number of very good publications and overviews and reviews, which are listed on this slide, in particular a very good introduction would be Michael Land and Dan-Eric Nilsson, and in fact, any work at all that they have written, I would recommend you to read.

There are many types of eyes. We have already seen that there are these compound eyes. We also see that, even in the fossil record, we have evidence of compound eyes. We have eyes that are camera eyes, and all these eyes look superficially the same, but in fact, they are derived from completely different sources and they are completely different groups of animals.

If you want to swim through a sticky fluid, such as the sea, you want to make yourself shaped like a torpedo, and you need some stabilising devices. In fact, you want to look a bit like a fish. This thing that looks like a fish in fact is not a fish, it is a reptile; and this thing that looks a bit like a fish is in fact not a fish, and it is a mammal. This thing that looks like a camera eye is in fact a camera eye but it is from a cephalopod; this thing that looks like a camera eye, with an iris that moves and changes, is actually from a jellyfish; this is a camera eye, and this is actually from a true fish; and this is a camera that is from one of my colleagues…

This is called evolutionary convergence, and that is the independent origin of similar traits, and what it is telling us is that there are only a few ways that you can build to move through sticky water and this happens to be one of the best ones, and if you have it, you are likely to survive in that niche and not be eaten by something like this, and therefore you will pass on those fish-shaped genes onto the next – it is not an accident that nearly all fish, certainly in the superficial zones of the sea, look pretty much the same. And that is the same story for eyes.

Now, if we are going to design an eye, it is quite interesting to see the same evolutionary convergence in place. There are only really a set number of ways that you can design an eye, and since the vast majority of animal species have eyes, that tells us that having eyes is really, really important. We take them for granted on a daily basis, but in fact, if we had not have had eyes, we would have been what dinosaurs euphemistically call lunch and we would not be here today. So there is an evolutionary arms race that goes on, and in the Cambrian period, when sophisticated eyes started to develop, they developed very quickly indeed, and it may well have been the invention of predation and predators that led to this rapid evolution of eyes.

Eyes can be single-chambered, sometimes referred to as simple eyes, even though there is nothing simple about them, or they can be multi-chambered or what we call compound eyes, and there are various different types of these. You could have a pit version, like a pinhole camera, and you can have that in the compound version as well. You can have a refracting one and you can use lenses to refract in various different ways. Apposing, appositional eyes, above, su-positional, and there is various ways that you can do this. These are very interesting eyes because, unlike our camera eyes, these give you an erect image not an inverted image. You can also reflect, and there is various different ways animals use to use reflections to get an image and a formed image on their eyes. So, that is it – nearly all eyes look something like this cartoon, and that also is very interesting as well.

Just very briefly, I will just run through, for the non-physicists in the audience, what refraction is and what is happening with these systems with light. If we have a substance here that is more dense than a vacuum, air or water, as it comes through, the light rays slow down and then they speed up again, and if that is curved, they slow down and they skew, and they can come to a focus somewhere over here eventually. These are the waves of light, and we imagine the waves of light by looking at the troughs or the peaks, and they curve, and we can see this shape if we look at a harbour, watching ocean waves coming in, and light does exactly the same. We trace that out using a ray because it is easier for us to think about rays than to think about waves, but essentially, rays are just going at 90 degrees to the wave front.

If we have a system where we have less dense material here but dense material on here, let us say water, we can get refraction and we can get a focus. If it is very dense, we can actually get a focus inside it, otherwise we get a focus here, and we do know from Ancient times this was known. Pliny records that he read all the books of Rome through a bowl filled with water, which he used as reading glasses as he got older.

If, however, the outside is the same as the inside, you lose this power of refraction, and you do not end up with a very good focus, and this would happen, for example, with a pit eye in the ocean, and remember that eyes evolved in the ocean. So this is not very good if you want to get really good focus, and if you want to get good focus, you have got to invent a lens that is going to focus these rays in water.

Here is the problem. We evolved in water with these eyes, then we come out of water and, bingo, we are back in this situation again, where we are in the air and water, and this eye would be hopelessly over-powered for us, so we have to make adaptations, as terrestrial animals. We make the lens a little bit thinner, we change the shape of the cornea, and ultimately, we get the focus back onto the retina.

Now, all optical systems are imperfect. If you remember, as a child, when you opened a cracker and you had those little binoculars or magnifying glasses and you held them up to the light, you saw coloured circles around the edge of them or very, very blurred images. Well, one of the blurred images have spherical aberration, and the light focuses at different planes. So, if you have a very spherical lens, you are going to get more spherical aberrations. The other problem with them is you get chromatic aberrations, is that not all wavelengths of light behave in the same way, and red light is rather lazy and focuses far back here, blue light focuses very aggressively, so we have got to deal with these problems because they are inherently part of the optical system. You have noticed here that, with a large pupil or a large aperture, they are worse. So let us make the aperture small. We have a problem now, and the problem is, when it gets small, is this thing called diffraction. You may remember from high school physics when you had to put powder on water and then you put various things in here. Here come in the plane waves and look what happens here… They spread out, and you get a bright, a dark, a bright, dark, and a bright. This is called an airy disk. If we plot it out, if we have a large pupil or a medium-sized pupil, we don not get too bad a point focus – it is a bit of a spread. But as we make the pupil smaller, we get a bigger spread and this gets worse. So we have conflicting problems here if we are going to design an eye.

The other thing we have got to do is that we have got to measure acuity and it is no good putting the dog in glasses and “Read down the chart” because it is just going to go “Woof!” and you say “Rex” is all it is going to hear too, so the Snellen fraction is not appropriate. So, if we are looking at animals and measuring animal eyes, one good way would be to look at gratings, and these gratings can be either static in choice chambers, they can be rotating round and we can look at the behaviour – you can imagine having goldfish in a bowl and rotating a grating round it and watch which way the goldfish swims, and various other things that can entertain scientists endlessly for years on end, in between applying for grants.

If we are going to measure in cycles per degree, we can then talk about spatial frequency. So, the frequency here is one cycle per degree, for example. Here, it is double, and here we have two cycles for every degree of visual angle. This one only has one. So, we are going to talk about cycles per degree instead of Snellen acuity, but I will covert it back to Snellen acuity later in the talk so that we get back to the anthropomorphic way of thinking about these things.

And you will remember that one minute of arc is subtended by the Snellen letter at six metres or 20 feet, so 20/20 is just American for 6/6, because they still work in feet in these measurements.

How does that convert to cycles per degree? Well, we can have a look. This is the sine wave we have got here, we have measured this angle, then we come down and it turns out to be about 30 cycles per degree. So, human vision you could say is 30 cycles per degree, would be about 20/20 or 6/6 vision. We actually, theoretically, can see much better than that, but because of the optical aberrations I showed you before, we see somewhere between 30 and 60, which is the theoretical limit of the human eye.

When we are dealing with some animals, we cannot even use cycles per degree, so what we have got to do is theoretically work out what they might see by looking at that retinal spacing, and this is called the acceptance angle. For an insect, we can look here at the spacing between the various receptors. For an animal, like a human, we can look at the spacing between the individual receptors, and this is what happens. So a human can detect these bars at this distance, whereas an eagle, which has much closer packed receptors, can detect it much further away.

And here we have a multi-focal insect eye that cannot see detail or spatial frequencies as well as camera eyes can, so they have to be a little bit closer to see the same images.

The cone spacing at the fauvia is about 2.5 microns for a human and this would give us this theoretical 60 cycles per degree. Using the theoretical acceptance angle, we can grade animals according to how well or what their acuity might be. Now, before I go much further, I want to tell you that acuity is not the most interesting thing about vision, by a long way. It is the thing that stops you driving, but it is not what you use for driving, and that is the irony of it, but we will come onto that later.

So, an eagle has terribly good vision. A human has reasonably good vision, as far as the animal world is concerned, but most birds would think us pretty pathetic. An octopus is fairly good too. Cats, much worse than ours, probably a half or worse for acuity… Various gastropods, honeybees, more gastropods, fruit flies, until we come down here to a lowly flatworm called planaria, which has one of the simplest eyes in evolution whatsoever, and you can see there is hundreds of fold differences between the visions of these various creatures.

Now, apart from acuity, as we mentioned, we need to talk about contrast. Here is a high contrast target, and here is the same target with low contrast, and if it is big enough, you can still see it. But here is a high contrast target and here is the same target in low contrast, and it is a damn sight more difficult to see. This is like driving in the fog. We are starting to lose the ability to see things. And this plots out, and it turns out that, if things are very, very fine, we cannot see them at this level of contrast, and if they are very, very coarse, we cannot see them either, and there is this sweet-spot which is defined by this contrast sensitivity curve.

We can do that at a particular spatial frequency with this Pelli-Robson chart, and this is used clinically, and you can see, as we come down here, that eventually people stop being able to read all the letters here, and possibly only one or two letters on this line, and no letters as the contrast starts to fade into light grey, into white. So that is contrast sensitivity.

There are other things, like movement and so on, and I will deal with those under the specific examples.

The other thing that is interesting about animals is that most animals use a completely different vision system from ours that evolved 700 million years ago when vertebrates and invertebrate lines diverged. What happened was that we use this way of packing our visual molecules, and this is called a ciliar or a hair receptor, and if you want to remember this one, this is the one that looks like Marge Simpson, so she has got the big purple hair coming up, and that one is easy to remember. Whereas, invertebrates, for their eyes, use this system, which are little villi. Now, villi are little things like you have in your intestine, for example, and they are little tiny finger projections, and they pack it in like this, so this is Bart Simpson. What is interesting about these two different ways of packing, the biochemistry is different as well.

We use a system activating this G protein where we break up this circular molecule and open some channels with a second messenger that allows stuff to flood into the cell, changing the polarity, which then allows us to convert light into a chemical, then back into an electrical signal for transmission further down, an ionic electrical signal.

Insects and other invertebrates, but insects in particular, use this system, where the G protein, a different G protein, activates this enzyme that splits lipids. Lipids are fats in the membrane, so it damages the membrane. The membrane contracts, and as the membrane suddenly contracts, it physically opens the channels. So this is instantaneous, and this is why you cannot swat a fly with your hands, because they can see faster than you can move. They can see much faster than we can. So, what they are losing out is what we call spatial acuity, i.e. the number of bars you can see in a given distance, they are speeding up in temporal resolution – they have got much faster ways of seeing, and this is one of the reasons why.

The other thing that a lot of animals can do, they can see polarised light. Now, polarised light is a bit freaky because we cannot see it, so what we have got to do is imagine it. Light can vibrate in its wave-form in many different directions – up, down, left, right, sideways, and a few others for measure as well. But if we pass this light through polarised grating, we get rid of all these vibrations in all the other ways, and we only allow through light that is going in a particular angle, and that is called polarisation. In fact, our atmosphere does this for us from the Sun, and as light is scattered through the atmosphere, it becomes polarised, becomes linearly polarised, as it does if it is reflected off water, and you end up with this vibrating in the same plane. And what is interesting about a lot of insects is that they use these Bart Simpson or rhabdomeric receptors, and you can see they connect as gratings and simply, as the light going down here, they can detect polarised light in these different planes. It is a little more complicated than that, but essentially, if you can remember that, it will be helpful when we talk about it later.

Now, a little bit of Greek to deal with the pelagos, the open sea, and epipelagic means upon the sea, and this is the sunlit zone. This is where most of the interesting stuff that we think about in the sea goes on. It is where all the food production occurs. You can have photosynthesis, you can have plants, you can have lots of animals, and you get jellyfish, tuna, sharks and dolphins. They are all basking and enjoying themselves in these warm, superficial layers of the sea.

This layer becomes a little bit darker and murkier, and when we get down to 500 metres, about here, we get very depleted of oxygen, and therefore we need to develop things like efficient gills. We do not want to move much unless we have to. It is established with swordfish and squid, wolf-fish, and some species of cuttlefish, and also, we develop bio-luminescence, that is we start to make light ourselves, like zooplankton do, and if we cannot do that, because we are a vertebrate, we borrow them and we help them and they live in with us and therefore we can shine and see things.

If we go down to the bathypelagic, which is deep, now this is a really strange, weird zone. Here is cold and it is totally silent. There is no light. There is no plant life. The only source of food is what is coming from above, food-fall, or other animals that are living in this zone as well. Marine snow, and here we have these gorgeous looking creatures, hatch-fish, giant squid, some of the smaller squids, and some octopuses.

Then we have the abyssopelagic zone, really at the bottom. Very few creatures can live down here. Most of them do not bother with eyes because they are pointless, and they tend to be transparent, and the weight and pressure means there must be some body designs as well that can accept that.

Let us go back up to these warm, sunlit epipelagic zones. You may remember this from a previous lecture. This is just a one-celled animal. It is one of those planktons that some whales like to eat and ultimately dependent on – everything we eat from the fish comes from these animals. But some of them themselves are predators, and this is one. This one sits at the bottom of the water. It can sense light. It has got a focusing mechanism here. It has got a pigmentary layer here, which means it changes the colour of the light, and it has got a receptor here for light, and when it sees something coming above it, it leaps up and it eats it, and it is really quite astonishing. This is all in one cell, so it is not an eye. It is within the cell, and it is quite a complicated thing.

When we develop the first eye that is truly an eye, it has got to have a cell, at least a cell, and funnily enough, there is an animal that has one cell that is an eye, one neural cell, and one pigment cell to screen, and here it is. Why do we have that screen? It needs to know whether the light is coming from above or below, and so, if you put a pigment screen in – otherwise, it would be firing all the time – it only fires when light is coming from a particular direction where it is not screened. You will see its little finger like projections in here which are packed. And what happens with this is it fires, the light comes in, and it fires off, and it is connected to a contractile band here that starts to move, and it start to beat its little hair-like things and it turns, like the boats in Oxford and Cambridge Boat Race do, as you can see. This rather elegant mechanism of responding to light and moving towards the light is really the basic level of animal vision.

The next level is to have more cells packed into the pigment and that would be a pigment cup eye that we see here in this very, very basic flatworm here. These are called lateral ocelli or stomata, and there is various different types of these, and we see them in many, many types of animals, and they work like this. Because of the pigment, this cannot be seen unless it moves here, where it can be seen, and suddenly it lights up and the animal can then make a response to this shadow against the light or the light against the dark, depending on what it wants to do.

Now, 85% of the phylum of animals have eyes like this. They may have other eyes as well, but they have eyes like this. Some of them, this is the only eye, and those animals tend to have limited visual demands. They tend to live under leaves if they are on land, or they tend to live at the bottom of ponds, and all they have to do is to detect where the light is and move towards it, and detect if a shadow is coming over them, i.e. a predator, and move away quickly back into their burrow or under the stone or wherever it was they were hiding. So, a very simple, basic eye, possibly from which all other eyes could have originated, as we showed in my last lecture on the evolution of the eye.

Several receptors can actually occur within these pigment cups, and so we can actually end up with a significant response to relatively dim light, compared to that single receptor that we saw earlier.

Planarians are these small flatworms. They are rather cute. They have got eyes and they have got little ears, and these ears can detect the currents and the eyes can see the light, and if you chop them in half, they regrow, and if you chop out their eyes, they regrow their eyes, so they are rather fun things for scientists who like to do that sort of thing to experiment on, and they have found out some very interesting things, including some of these genes about regeneration and maintenance. When we understand how these genes work, this could be very helpful for us because it may help us, for example, cure macular degeneration if we are able to turn on genes that can make retinas from de novo or, for people who are born blind from congenital defects, it may be able to help them develop an eye. So there is lots of interesting work that will come from this lowly animal, so they are not just of interest just of how they see, they are also of interest biologically and they are also interesting to us, but not as interesting as these critters, which are delicious.

The main thing about molluscs is they have all different types of eyes, and many of them have eyes, some of them quite complicated pit eyes and large eyes, some of them have lensed eyes, here and why do they have all these eyes? Well, it is of course what I said before: it is because they are delicious and people like to eat them, and not just people, lots of other animals like to eat them as well. They have, very interesting eyes, in that some of them can use these ciliary receptors, which is not what we expect with an arthropod – we expect them to use the rhabdomeric receptors. So there are things breaking the rules here, and we will talk about that.

A pinhole camera, you will remember from your childhood, can actually make an image on the back, and this is exactly what happens. The sort of image that can be made would be about 2.3 degrees when the pupil is small in this animal, but it can also enlarge its pupil, dramatically, to let in a lot more light, but now you can see, instead of stimulating just a few receptors, it is stimulating a lot of receptors, so the acuity goes down, and what it can differentiate has to be a lot bigger.

People have done experiments on nautilus and this is the one where they put it in a fish-tank and spin round stripes of different sizes and you can work out actually what the nautilus can see, and it turns out the finest stripe has to be about eleven to 22 degrees and that is the finest vision it can get.

Now, why did the animal develop this vision to see rotating stripes, because that does not happen in the real world, what it did was to keep it still and stop it rotating in its world, so stabilising, what we call an optokinetic response. We actually have an optokinetic response as well, which is when you spin yourselves round when you are a kid and then you stop and then you are sick, and somebody looks in your eyes and they see your eyes doing this. This is related to this mechanism that is very, very old.

Although it can see things and it can see things fairly well through its pinhole pupil, it is very, very dim compared to a fish eye, and opening lets in more light, but it drops the acuity down and it cannot see very well. Does it care? No, because it lives in the deep ocean, and as I said before, this is living in very dim light, not much happens down there, not much moves, and what moves does not move very quickly. So they are very well adapted visually for where they live. I mean, they would be hopeless trying to catch the Tube or run around or do this lecture, for example, but where they live, they are fine, and they do not need to go any further and evolve a lens.

Pinhole eyes also occur in these animals, which are giant clams, but they just did not develop one pinhole, they developed a multiple in their outer mantle. So, this is the really delicious edible bit, and then just here behind it is a little pinhole eye, another bit of delicious mantle, another eye, another bit, and they have got hundreds of these things arrayed round each of these cusps, and these are very, very good at detecting things coming towards them, because what they do not want is to have their mantle nibbled by passing fish. A 10cm fish at 42cm will trigger the response. So it only has to be crude, but that is good enough because those are the sort of fish that can do you a lot of harm.

They have these symbiotic algae that we mentioned before that live in the mantle tissue, so it has got to have access to sunlight to allow those algae to make the food that it needs to grow. So they do not want to close all the time, so they do not want an eye that is too sophisticated. If they had an eye that is going to close with every passing particle of dust, they would starve, so they need to have it open most of the time and then only close it when a fish or another predator approaches.

Take all those pit eyes and bring them all together in one place and you have evolved a compound eye, and that is exactly what is happened with these arc clams, and here is the compound eye. Here is a compound eye of it and it is essentially a lot of pit eyes brought together. It also has pit eyes as well, very much like the giant clam that we saw early, but this is the eye we are interested in now, and you will notice that it has ciliated receptors, which is very unexpected for an arthropod eye. It does not have any lens, so it has got a very poor resolving power. Each of these holes may only have one or two of the receptors in, so it has a very large field of view, about 30 degrees, but that is enough for it to perceive spatial movement and trigger closure of the shell if a large shadow is detected.

What is interesting about ciliated cells like ours, as we pointed out in my first lecture, is that they are not interested in light. They are active in the dark, and light turns them off. So, it is a very, very good defence mechanism for these animals to have.

We have said these pinhole eyes suffer because they cannot make a very good focused image and things have to be relatively large to be seen. So, here is the unfocused image that we focused down here, or the eye would have to be incredibly large, implausibly large, to pick up an image from it, which is what the nautilus does, and has a one centimetre, an enormous eye for such a little animal in the shell, but again, still not big enough to get a true focus.

What we want is to do a lens, so we make a lens, and now look at this – we are focusing quite well. It is only four times the radius of this, where the focused image is, and so we have got a nice little blurred circle here, much better than this, and we can start to see things in much finer detail, and this is done.

Here is a cross-section through a snail eye, gastropod snail eye, with one of these spherical lenses.

Lenses do not necessarily have to be made out of congealments of protein. They can be made out of what is around in the environment, like aragonite. Aragonite is a very interesting, transparent chemical crystal that has two refractive indices, and that is very handy if you spend your time in the inter-tidal shore, like these West Indian fuzzy kitans do, because it means you can see underwater and you can see when the tide goes out. Again, it is the same thing: these things do not want to be eaten, they need to clamp down when a predator arrives. You can do visual experiments on them, and funnily enough, people have, and one they have found out is that, if they put a black disc, three centimetres or larger, it clamps down, and that is about 9 to 12 degrees, which for us, a human eye, to make it so it would be about twenty moons, stacked up, would be how big the thing would be. Now, a moon, at arm’s distance, is half the size of your fingernail, so it could be vision that would be seeing this, where as we can see much finer than that indeed. So it is pretty coarse, but it is sufficient for these things, which have survived from the Cambrian period through to today, and rather beautiful structures, as you can see.

These are beautiful creatures as well. They are not flowers, they are worms, and they have very, very delicate tissue on them, and they live in the ground in these tubes that they make out of mucus and sand. Now, they have got to have eyes, and in fact they do, because they want to retract back into that tube as soon as anything comes by to have a little nose around and find out it is not a plant and it is an animal and eat it. Here are its compound eyes. What is interesting about these compound eyes is, one, they are ciliated again, but two, they are lensed, so they actually can get focus here, and this is going to improve their acuity. They have about 12,000 of these in each of these eyes, so they are rather large and they are very, very good shadow detectors, because, as we have said, they are turned on by the dark, so they are turned on by shadow. So very, very good alarm devices, and Nilsson describes them as “sophisticated burglar alarms”.

The lenses that we are familiar with are within the eye, and here is an eye, and you can see the spherical lens virtually filling the entire eye, and we can see, because it is semi-transparent, the pigment layer even behind it in this slug. Now, different types of slugs and snails have their eyes in different places. Most of them have them on the end of these stocks, but some of them do not and have them at the base of the stocks inside, particularly the air-breathing pond snails as well. So, next time you go and see one of those, dig it out of your pond, have a look at it, and you will notice that the eyes are not here, they are actually at the base of the tentacles.

This fearsome-looking creature is a box-jellyfish, and fearsome indeed – they are rather dangerous. Now, many jellyfish have developed pigment cup ocelli, the very simple eye that we mentioned before, but the box-jellyfish has gone one further. In fact, it has 24 eyes, and it has four different types of eyes, and they are located in four clusters, here, and this has within it four types of eyes. It has got slit eyes, it has got pit eyes, it has got two lensed eyes, one that always points up because there is a little bit of stone in here that acts a buoyancy to keep it there, and one that always points down, and these are camera eyes and they can actually see spatial detail.

Here is one of the eyes. This is the upper-pointing eye, this is the lower-pointing eye, the lens and iris, and there is the pit and there is the slit eye. What sort of stuff could this see? Well, we will look and see where it lives. It looks in the Caribbean mangrove forests and this is the view that we would have exactly here, but if they go out to deep-sea, they starve, because they are hunters. Unlike other jellyfish that float in and out on the tide, passively, these things actually detect their prey and swim towards them to kill them and eat them, which is a rather scary thought, but luckily, they are mostly small and they do not bother us, unless we go for a swim and they sting us, and their venom is so poisonous it can cause tremendous damage to even humans.

So here is a couple of these box-jellyfish floating around here, and this might be what they will see. The down-pointing eye is here to detect the mangrove roots because it does not want to go and swim into one of those and bang its head because it is rather jelly-like and might cause some harm, and secondly, it needs to detect where the canopy is. It wants to swim here, and it does not want to go swimming off here and end up off the shore of Norfolk or something. So, it can detect the canopy, and that is roughly how it will see. It does not see in colour. It has got a single opsin, as far we know, and it detects coarse detail, but that is better than what it could detect just using its pit and slit eye.

So then the question comes: why so many eyes? The reason is, is because they all do different things. This one is the eye for making sure that you go towards the canopy, this is the eye to make sure you do not bang into the canopy, this is the eye to tell you when it is daytime, and this is the eye that tells you when it is night-time, and what happens, if you have got a lot of eyes, you do not need a lot of brain. If you have only got two eyes, like us, you need a lot of brain and a lot of brainpower, and since this animal is only a diploblast, not a triploblast, it has not – that means it has only got two layers in its germ cell, it cannot develop things like hearts and muscles and brains and livers and all the stuff that three-layered animals can. It split off before the triploblastic line in evolution. So this is a very clever and sophisticated way of actually seeing the visual world.

Here is another one. This is so cool, and it is beautiful! We only usually see the inside bit of this, and usually it comes with black pudding and a bit of lettuce, but the bit we do not see, is thrown away, and it is nice to go to a fish market and see it if you can, are these beautiful blue eyes, iridescent blue eyes, and they are there to actually stop animals going in and eating this. If you think that, in the United States, in 2008, they harvested 53.5 million pounds of these things, you can see that it does need to do something about predators. Unfortunately, it cannot do much about us, but it can do enough about the other ones to make sure there is enough left for us to eat. It has these little tentacles that filter feed and so on, and it does not want them nibbled by fish, so it has got to have this abduction response – it snaps shut at the approach, and the abductor muscle is the tasty bit and it protects it. It is very good for you as well – it is low in fat, protein, Vitamin B, selenium… There are lots of good reasons, if you are not a vegetarian, to eat scallops – and not too much mercury either.

Now, how does it stop being eaten by other animals? Well, it has got a duplex retina. What is interesting about this retina, you see it has got the ciliated and rhabdomeric. Now, the problem is, it is hopelessly under-focused and light comes in through this lens, causing a large blur circle on these rhabdomeric receptors.

So what is this for, here? Well, it is very clever. It has a reflective mirror, and it reflects the light off, dead into focus on these ciliated cells. We can actually make some estimates of what its visual acuity might be, and also on what its F number might be, which is the dimension ratio that tells us about the light-gathering abilities of this, here. These are the calculations which have been done in the Munich Physics Department, and we can see that it has an F number of about 0.5. How we work this out, we know the focal distance, we know the diameter, we can divide the two, and we get a number 0.5. Humans, for example, in dim light, are at 2.5, and in bright light, 8.5 Fish are 0.8. A good camera, 1.4. The lower the number, the better the light-gatherer, and so what this is telling us, this is an extraordinarily efficient eye at detecting light. It has also got reasonable acuity, of about two degrees.

So, focusing is critical if we want to see things in finer detail, but with a spherical lens, we know we cannot really do that because the focal length is too long, but we know that fish can focus, so how do they focus with a spherical lens? What it turns out is that they use a lens that is differently dense, different refractive indexes at different places in the lens, which means the light can now focus sharply onto their retina at about 2.5 times the diameter of the lens, which is all you need for a fish eye, which is excellent.

Now, we can now get a sharp focus on the retina, and having a slightly flatter lens, we are going to get less spherical aberrations, and this type of lens evolves in cephalopods and fish. Cephalopods are octopuses.

Here are some cephalopods for you, and look at their eyes, beautiful, camera eyes. These eyes look very superficially similar to our own vertebrate eye, but in fact, they are derived completely differently. They are derived from the epidermis, the skin, by in-folding. Our eyes evolved from an out-pouching of the brain, and that is why our retina is inside out and we have a blind-spot, which these animals do not. So they look very much the same as our eyes, but in fact, they are very different indeed. They have rhabdomeric receptors and this means they have the potential to see polarised light, and indeed they do. Squid octopus and cuttlefish are masters of camouflage and they use this outer layer of skin to disguise and change their colours very quickly with these chromophore cells. But what is interesting is the inner one. So, we have multi-dimensionally rotating light that is non-polarised, which comes in, hits this iridophore cell, which is lined up very specifically, and this light then comes off, rather like coloured light off an oil slick: the thicker the oil-slick, the redder the colour; the thinner the oil-slick, the bluer the colour. That is the same here, so the thin plates, beautiful iridescent blue light, deeper layers, the redder the light. Now, what is interesting about this is that it comes off polarised, which is really interesting.

The other thing is, you can block whatever colour you want with an appropriate chromophore cell. So you can now send a private signal that your predator cannot, and the predator of this is a mammal, and that mammal is a sperm-whale. So this animal can now signal to its friends in a private manner that sperm-whales cannot see.

Polarised light is also used by mantis-shrimps. Mantis-shrimps are the delicious food of the previous animal, the squid. So, having polarised abilities here is not of much help, but it has got these sophisticated eyes that sit on the top here and move independently, and look rather implausible. I mean, surely this is just the wackiest bit of design that you have ever come across. They are rather complicated and there are several different layers in it, but we are interested in what is called the mid-band here, which also has layers, and we are interested in one part of the mid-band, which is here, and these are the cells that are specialised to see polarised light. But, what is the point? What they can do is to see circularly polarised light. Not only this light can be polarised in a plano direction, it can also be polarised in a circular direction, and in fact, it can be circularised to the left and to the right, and these shrimps not only can detect that, they also produce it in their shells, and they are the only animals that can detect this and it enables them to privately signal to each other from the safety of the reef without them being seen by their predators that can normally see normally polarised light.

Fish eyes are very similar to ours, and that is not surprising because we evolved from some animal that looked like this some time ago. Unlike our eyes, they are more spherical, the lens, and the retinas have both, similar to us, rod and cone cells, but later in evolution, we lost the ability of colour vision that lake fish and superficial sea fish have – they have much better colour vision than us. Some of them can even see into ultraviolet light. For example, juvenile brown trout see ultraviolet light reflected off the zooplankton that is their food, but when they mature and they become an adult and they are going to eat different things, they lose those cones – they do not need them anymore, and there is no point having them cluttering up your retina, and they do not see the UV light, which does not penetrate so well into the zone where they live in the murky waters.

Now, anchovies can detect polarised light. We are not sure why. Is it because of migration, or is it because they can signal to each other when they are in a school, swimming together? A lot of schooling fish can actually have this ability to detect polarised light.

Deeper-dwelling fish that are at thousand metres, have very special adaptations because there is no light down here, or very little light, and here is a marine hatchet-fish. This is its environment. It is in the dark, with nearby an occasional flash of light from little tiny animals, these bio-luminescent flashes. Now, most bio-luminescence is blue, and there is a reason for that: it is because blue light penetrates through water and red light does not. As you know, when you go under the water if you are swimming at all or snorkelling, the deeper you go down, the bluer things become, and if you have not snorkelled, you can watch it on the telly with Jacques Cousteau and that shows exactly the same problem. In fact, they have to adapt their cameras for colour underwater.

Now, these are not degenerate. These are very sophisticated, and they have evolved in a world with almost no food and very, very low oxygen. These fishes are very weak and they swim very, very slowly indeed, so they do not need to be able to see miles away. They only need to see as far as this animal, or maybe that animal is, just to get there. If they see further out, and they cannot see further out here, there is no point because they can never swim to it and get to it in time to eat it. So, they have very, very good light detection, and some of them have extraordinary adaptations to their eyes.

That actually is not the eye of this fish. That is a protective coating on the outside of the eye to stop the eyes being stung by the tentacles drifting down from jellyfish and in particular from Portuguese men-of-war, which is why this is my favourite animal, because I hate Portuguese men-of-war, and I actually did not know there was something that ate them, but there is. So, although he is not the most handsome of chaps, he really does a rather useful function. Shame there are not more of them…

Anyway, in this dark zone, we have to remember it is cold. There are no currents, nothing moves, and it is almost completely dark, and you are going to evolve some very interesting things to live down here. One of them you might evolve is tubular eyes that point up so that you can see the stuff coming down towards you against the very dim background reflection of the sky above you. Now, there are problems with that, because if you are swimming along and you have got one of these critters below you, you are going to cast a shadow and it is going to see you and it is going to slowly swim up and intercept you and it is going to eat you. So you want to do something to make your underside light, so rather like aeroplanes are painted light blue underneath, so that they are counter-illuminated against the bright sky, so that their predators who are chasing them cannot see them, or it is more difficult to see them. These animals do the same, and what they do is to use counter-illumination. They actually ingest, but do not eat, those little critters that make light, and they line them up on the outside of their body, and as they are up there, they now have the same illumination as the light above and they do not cast a shadow and they cannot be seen.

Now, some of them do this in a rather clever way, and this is work from City University, as we pointed out before, from Professor Ron Douglas, who has done amazing work here, and apparently spends his summer down in deep-sea and submarines where these animals live.

These are interesting because they release a chromophore that is red. Now, these animals do not have red receptors. No animals around there have red receptors, so they cannot see this light, but one of these species can, because it has a red receptor, and the other one that makes the red light does not, but how it sees it is very clever. It actually ingests some animals with chlorophyll pigment and then absorbs the red light into the chlorophyll, which is green, and then signals from that chlorophyll to its blue receptors and green receptors, which now enable the animal to see in the red. So, it can make light – it is like a private search-light that no one else can see, and it can find its prey, and the prey does not even know it is being seen so it does not swim away, and a very interesting way of doing it…

We mentioned about mirrors, and funnily enough, there is an animal that uses a mirror to actually see, in this eye, the downward-pointing eye, part of its eye, and it also has an upward-pointing eye, and this is a brown snout spookfish, viewed from below, an absolutely incredible adaptation to living in the depth of the oceans.

You can develop very large eyes, like swordfish do, and very large eyes have advantages, as we mentioned before, more light-gathering and they, remember, are swimming at deeper depths than most of the other fishes are, and it allows them to see far away. So it is nine centimetres, about the size of a tennis-ball.

But what is the point of very, very large eyes because we are going to get more and more problems with aberrations, and eyes are expensive to build and maintain, so it does not make a point of making the eyes very big. So how do we explain the giant squid, which has an eye the size of a basketball?

Well, it evolved these eyes to escape its predator, the sperm-whale and it has a very, very large eye because it is sitting around in the depths and it can see the flashes from the bio-luminescence. What it does though is, it does not eat those things, as the sperm-whale dives, the bio-luminesce scatters in the wake, and this can detect it and uses jet-propulsion to squirt out of the way.

Now, these huge eyes can pick up this tiny little speck of light from the other side of a rugby pitch, so very, very sensitive indeed, and they did not just evolve with squids. They evolved in the past. This is an ichthyosaurus. This is Mary Anning, who, in the 1780s, collected fossils and sent them up to what was going to become the Natural History Museum. They also had these colossal eyes as well. Why? Because they had these things, playosaurs, that were their equivalent to sperm-whales, that could dive deep, and they probably scattered light in the same way as the modern animals did, which is why they have the colossal eyes.

Now, it is also used for detecting submarines, because they also scatter bio-luminescence in the deep depths as well.

Terrestrial compound eyes, we will not go into too much detail, except to once again mention Hooke, who was a previous Gresham professor in this College, and here is his drawing of the compound eye of the grey drone fly, whatever that was – probably a domestic fly. They work in a slightly different way, as we have mentioned. They are compound, so there is lots of them, and remember they are in this ice-cream cone shape, with all these little villi, with a light tube that comes down here to guide the light through to the sensing nerve and then out through the nerves to their brain to be processed.

Now, the problem with that is you are only getting individual bits, so you need to have a different form in the night time, and these are night insect eyes that actually pool the resources from different places and you are sampling a much larger part of the world. So, night eyes are functioning very differently.

And flies, even from an Ancient time, use this neural su-position, which, instead of having them scattered over, what they do is pool the light from the various adjacent ice-cream cones and to give very good directional signals and improve their quality of light, of spatial perception.

Now, apart from these eyes, they also have these oscilli as well and they have also got two eyes, eyelets, which they are going to use for circadian rhythm. So, all in all, they have seven eyes, the flies, and wasps.

We have mentioned their temporal vision is very quick because of this mechanism that physically opens this channel rather than the slow mechanism that we have that means that we have got to go through several channels. So, they can also see in colour, and you can measure the colour vision of insects, and it turns out that they have actually got slightly different colour vision from us, and they can see into the UV and, by comparing this, this enables them to have a completely different colour spectrum, and this is needed for their lifestyle – like onion flies need to see little onions when they are in the blue-green, and also flowers, insect-pollinated flowers can do that.

And it is estimated that if we had insect eyes, that is what we would look like. Probably an under-estimation, maybe bigger, and some people calculate they may even have to be the size of a house.

This is what things look like with our eyes if we were to put things in ultraviolet, but remember, they are going to pick up visual clues and colours and see things in a completely different way.

This is the same flower, as it might appear to a bee, except for this would not be red because it does not have a red receptor, and it is going to put all of them together and make a mosaic, and that is probably what a bee sees.

Jumping spiders have evolved this particular beautiful way of using chromatic aberration to see. So they use the ultraviolet here, which is always in focus, this green, four retinas, which is out of focus, and by comparing how out of focus to the in-focus eyes, it knows exactly the distance you are away, and this critter leaps out and gets you – very accurately.

It also scans the retina, as does this funny thing that lives in the Bay of Naples. It has got eyes here. It has got another lens-let here, and the lens-let and the retina move and scan the image.

Finally, we come onto the last group of animals, the birds, which have exceptional visual abilities in different ways because they pack in a lot of receptors, they have got relatively large eyes for their size, and, to give us an idea of what it might do, a kestrel can see a two millimetre insect from the top of a eighteen metre tree, which is astonishing vision really. Night ones have a topetum, they have the reflecting one, as we are going to see in other animals that do night vision. They have tremendous colour vision – they use oil droplets as well to enhance that, and their vision is probably 20/10 or better, even 20/4, much, much better than we can ever hope to achieve.

Now, comparing us to horses, horses have quite good vision, dogs, 20/75, and finally, cats, that have really poor spatial acuity. But what do we mean, that they have got poor vision? Well, it surpasses – they are better than us for functioning in dim light, because they have got this topetum. They have got a rapid retinal response to another image, so they can respond very quickly. They have got better flicker fusion. They have got a better field of view, and they can differentiate many more shades of grey, and they can detect motion in their visual fields much better than we can. But they cannot see colour very well. So, Labradors, the seeing-eye dogs or guide-dogs as we call them in our country, do not see the red and green, but they know where the red and green is, and so they function on position of where the brightness is, and they also know about the speed of traffic.

This is what a dog might see with its colour vision, which is different from a colour-blind human, who has lots and lots of cones. Dogs do not have that many cones, so it is washed out all the way through, lots of shades of grey, and a neutral bit here where we are seeing greens. So, when you buy Lassie the little red ball and you go and take him into the park, you are not doing Lassie any favours because it cannot see it. It cannot differentiate this wonderful red ball against the green grass of your lawn. So when you have your dog and you are buying it a toy, think about what it might see, and it might actually enjoy something that maybe blue-coloured or maybe yellow-coloured rather more than you might expect.

The final animal, of course, to not forget the cat lovers that might be here, also has a topetum because, although it has very poor spatial acuity compared to a human, it is not adapted to live like a human. This is a night predator and they are responsible for the loss of songbirds throughout gardens in Surbiton and beyond to this very day. So, although they are cute and very nice and cuddly, you do not want to cuddle that, otherwise you are not going to be going out at night-time again, and these are animals are very well attuned for the environment that they live in the wild.

So, ladies and gentlemen, I have not been able to include all animals, but hopefully the animals I have included you have enjoyed having a look at how their eyes work. Hopefully it has helped you think a little bit about that fly and why you cannot kill it. Also, understanding how these animals see is going to help us develop much more sophisticated ways for pilot-less aeroplanes and cars, and navigating round a complex environment, we may actually want to use something that has got a fast flicker fusion and maybe a compound eye rather than using camera eyes as we currently think we should be doing.

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