PROFESSOR: Today we are going to discuss color vision and adaptation. About 2/3 of it's going to be color vision and one third on adaptation.

Now, I'm going to have several demonstrations on the screen here for you. And I would like to forewarn on you that for some reason, they still haven't fixed the light bulb in this projector. And this, you see this is a bluish color to it, speaking of color vision? And actually, it's supposed to be gray. But there's some loss of balance there in this bulb. And they've promised to replace it some 10 days ago and it still hasn't happened.

So once we come to the demonstrations, they're not going to be perfect. But they will also be available on the internet, as well on Stellar. So you can look at them there and maybe you'll get a better picture of them there than here. But we'll do the best we can.

So anyway, let me first give you a list of things we are going to discuss and the questions we're going to pose. First of all, you're going to ask, what are the basic facts and laws of color vision? Now, one of the nice things about color vision is that their number of laws-- it's a very basic phenomenon. And its in many ways very close to physics.

The second one is, what are the major theories of color vision that we are going to discuss? And then we are going to examine how color is processed in the retina geniculate. Then we're going to move on and examine what happens in the cortex.

And then we are going to discuss what is the nature of colorblindness, which I think will be of interest to most of you because colorblindness is not that uncommon, unfortunately, among humans. And then we're going to look at how adaptation is

achieved in the visual system. That's when we switch from color to adaptation. And then we are going to ask the question, what are afterimages? How are they produced? And what are its effects?

So let's begin, then, with color vision. And the first thing I would like to say about this is that as so often happens in the course of history, often there had been great misconceptions about color. And one of the great misconceptions was that people thought that white light is the pure light. And that was exemplified in the fact that before the 20th century, for example, most nuns were required to wear a white outfit. They were asked to wear the white outfit because it meant that they were pure.

So what happened then in the 1600s, one of the greatest geniuses of our time came along. That was Newton. And at that time-- this is just an interesting coincidence-- it happened that the art of making chandeliers has emerged. And the chandeliers in those cases consisted of little pieces of glass cut in various ways. And people noticed, and so especially did Newton, that when you looked at these chandeliers, you saw all sorts of colors there.

And so Newton said, my god. How can that be? What's going on? And so he began to analyze color, which also came about then for him because that's when they also, in addition to the chandeliers, they came up with prisms.

And so what Sir Isaac Newton did was-- let me skip this for a minute and I'll come back to it. What he did was that he put a little opening in a screen and let the light come through from the sun. White light. And then he put that beam of light through a prism. And he discovered that he got an image much like what you see when you have these chandeliers. Namely, that you get all sorts of colors projecting out of the prism.

And then he performed yet another little experiment. He added another prism, same kind of prism, where the light was separated from the red. And then there was no further separation.

That was a remarkable discovery on his part. And he became interested not only in the physics of it, but he also became very interested in how we organize our color perceptions. And he was the first person to come up with what I will talk a lot about, the so-called color circle.

So this is what Sir Isaac Newton then came up with. And he established that we have a huge range of frequencies. And a very narrow section of it right here is the one that falls into the visible range. And if you break that up like this and enlarge it, much like the colors of a rainbow, you see all of these colors.

And so the conclusion to which he came is something that was quite remarkable. He was at that age just 29 years old. And that was done-- to go back here-- at the age of 29 in 1672. And so he concluded at that time that white light is a mixture of all the colors. It's white because it's an equal mixture of the different wavelengths here. So rather than being pure, white light is a conglomeration of all the little wavelengths in the visible range that the eye can process.

So that was so stunning for him at the time that he delayed publication of it for more than 30 years. And then when he published this, this was extensively debated even 30 years later.

And one of the people who debated it a lot was a famous German poet called Goethe. You probably all of you know who he is. And he said, Newton is a charlatan. He just made this up. It can't possibly be so. White light is pure.

And so what he did, he took a prism just like Newton did. But instead of reflecting the light, he looked into the prism towards the light and he didn't see any colors. And he said, Newton is all full of junk.

And so he asked his associates at the time, Schopenhauer, who is also a very famous philosopher, and said, why don't you do some experiments? Let us prove that Newton is all wrong.

And so Schopenhauer did the experiment right and said, oh my god, Newton is right. What am I going to do? How can I tell Goethe, my boss, that he's wrong and

Newton is right? So that became quite a thorn in his hide at the time. But of course eventually, we all came to recognize indeed that this is the situation, and that white light is a mixture of all colors.

So let me now go back a minute to some of the basic facts, which I will elaborate on as we proceed. First of all, when we talk about color, there are all kinds of systematic things that we are going to discuss. And you're going to become educated about the processing of color as a result because we know a lot of very important basic facts about it. It's solid science.

So when we talk about color, we typically make a distinction between hue, brightness, and saturation. Hue means what is the color. Is it red, green, and blue? Brightness is how intense the impression is. And saturation is that every color can be kind of washed out or it can be very sharp. Can you see a bright red? Or you can see a really washed-out red that's barely different from the background?

This is very important. We have to make a clear distinction between the psychological and physiological attributes, or the physical, actually, attributes of color.

So what do we mean by that? When we talk about color, that's an impression we have. That's our own personal psychological experience. But the scientific way to look at it is to call it wavelength. The same thing is true for luminance and brightness.

Now before I go onto this, let me back up for a minute. Here, let me say one more thing about this because it's an interesting way to remember it and also it's relevant to what you are going to hear in the second half of this course, which is going to be on audition.

So here's a classic question people have often been asked, especially when you were still in grammar school or maybe even in high school. It was, when a tree falls in the forest, and there's nobody around, does it make a sound? And so people debate this, and debate this, and debate this.

Well, from my point of view, there's no question there at all. When a tree falls in the forest and there are all these cracks and everything, there is no sound because sound is a psychological attribute that we hear and interpret. There is, of course, the production of wavelengths as a result of the fall. So that's up in the air there. But you need a human being to turn that various frequencies into what we call sound.

So now the next thing I would like to briefly approach-- I'm going to talk about it in much more detail in a minute-- is that it's been established by now, but initially there was quite a debate-- I'll come back to it-- that we have three major kinds of cone receptors in humans and in many primates. And actually, in some animals and some birds, there are actually four of them.

And these three are the short, middle, and long wavelength cones. Of course, we can call those-- for short, we mean blue, for medium, we mean green, and for long, we mean red.

And then we have the rods. And these numbers here-- this one is misspelled. bb? I don't know what bb is. At any rate, these are nanometers at which they peak. And we'll come back to that in a minute.

But before I go on with that, let's imagine for a minute-- and we can skip this. Suppose that you are the emperor of the universe since the beginnings of time 1,500 million years ago. And you decided that you're going to create animals. And once you've created animals, you have decided that they're going to have to see things. And so they have to have an eye with which to see.

And then you have to decide, well, if that's the case, color is very important. You looked around in the world and said, oh, all these beautiful colors. How are we going to have these animals and these humans see all the colors?

And then you said, well, there are hundreds of colors. So what are we going to do? Are we going to create the receptor for every one of these colors and put them in the eye? And you said, oh dear, that's a problem because then we would need a gigantic eye. And so the question became, of course, how else would you come

around this?

And so here the idea, that here you have sensitivity, and then here you have wavelength. And so the idea was that you could create hundreds of very sharply tuned photoreceptors like that so you could get all the colors.

Well, that did not seem to be a very good way of doing things. And so getting more back to the present time-- still a long ways off from the present, actually-- people began to hypothesize about, they say, well, what can we do to minimize the number of receptors with different sensitivities color and still be able to see well?

And so one theory that came up before they knew anything about the eye and the three cone photoreceptors, Young and Helmholtz came up with the idea that if you had just three types of cones that are broadly tuned, they could take care of most of the ability to see various colors.

And so that became a very interesting, very, very powerful theory. And actually, speaking of theories and models, it still is in my mind probably the greatest model or theory that has ever been developed about how the brain works because it subsequently did turn out that indeed, there were three of these receptors that are broadly tuned that can provide all that information for you. And that actually, as you will see, became a huge issue.

Sorry. Let me go back for a minute to this. And let me just reiterate. These are the nanometers for the three types of cones. And at the end here, we have the nanometers for the rods. Then as a result of analyzing all this stuff, people have come up with all sorts of rules and laws. And that's what is one of the nice things about color vision.

And one of the rules is called-- actually, laws in this case-- is called Grassmann's laws. And he said every color has a complimentary which, when mixed properly, yields gray. And I will explain this to you in just a few minutes. And the other is that non-complementary colors yield intermediates. Just keep that in your head for me until I fully explain it. And the other law, which I'm not going to talk too much about,

is that the luminance of a mixture of differently colored lights is equal to the sum of the luminance of its components.

So these are very, very basic rules-- laws.

So here we go again, and move on. Here is what is called the CIE chromaticity diagram. And it was initially devised in 1931.

And let me explain to you how this came about. This became an international undertaking. And it came about because it was highly desirable to be able to communicate throughout the world your particular color desire or experience.

So for example, if you had a particular hat you had bought, say a blue hat of some sort, and then said now I would like to get a dress that fits it. How can I do that?

Well, what you can do now as a result of this chromaticity diagram, there's a scale here. You can see the vertical values and the horizontal values going from 0 to close to 100. And then, if you can specify a particular color, say you want this color here, you simply can state what that color is by giving it the number.

And then you can send that number to China or to, I don't know, to South Africa or something, to a particular company, and say I want to have a dress like that with that color. And then because this is international, they were able to produce that color as you specified on this diagram.

So that was a very powerful undertaking. And this arrangement is such that actually, the colors go from the center outward, become more saturated. Think, for example, we're going to here to here. And the center of this, which is about 333 333 on the chromaticity diagram, is white, which is not that obvious here, partly because of the colors of the background.

So that is the famous 1931 chromaticity diagram. And what one can do with this is to superimpose on this some rules about the human or, say, the primate color vision abilities.

And the person who came up with this, as I've mentioned, was Newton. He came up

with the so-called famous color circle. Now, the color circle is described here. And I'll show it to you in just a minute head-on.

This is green, this is red, this is yellow, this is blue. And of course, the question is, why do we have them set up in this fashion? And we'll explain that in just a minute.

So here is the color circle, the two-dimensional color circle, where things are pretty much equiluminant across it. Now, if you go from the center out, you increase saturation, as I had already said. And as you go around, you change hue. So those are the basic attributes.

Now to anticipate the issues here, let me tell you this-- this is yellow, this is blue, this is green, and this is red. These are called the cardinal axes. As long as a line goes through the center, that's a cardinal axis. These are the ones which are best known, the red/green and blue/yellow.

And the fascinating fact about this is that this explains a number of very interesting facts about our ability to see colors. So let me tell you this-- if you mix yellow and blue, as we have talked about the law, if you mix them in equal luminances, you get what's in the center here. You get white.

Furthermore, and because of this, there is no such experience in our existence that's called yellowish blue. And there's no such existence in our minds, as far as color's concerned, that's reddish green.

On the other hand, if you don't go across the center, but you say you had yellow here and you have green here, there is yellowish green. There is yellowish red. There is bluish red. And there's bluish green. So we can process those and see those in-between colors, but we cannot do that along the cardinal axes.

So this incredible color circle essentially explains the very essence of how we can see color.

Now, there's one more factor here, is that we also have to take into account luminance values. And so people turn this color circle for some purposes into a

three-dimensional entity that's shown here. Here's a color circle. And the third dimension going up and down here, as you go from white to black, if you will, in the center. So here, things are brighter and here, things are darker.

So that is sort of a complete, then, arrangement for your color impressions. But what we are going to do, we are going to concentrate on the color circle itself as we move along.

So now let's next turn to the outgrowth of this, starting with Newton's color circle, which has been somewhat modified in the manner that I had just shown you. And as a result of all this, a number of competing theories have emerged. And I'm going to talk about two of them.

The first one is the famous Young-Helmholtz theory. Young initially, and he collaborated with him many years later, with Helmholtz, came up with the idea that you could experience colors by just having three types of cones that are broadly tuned. And so he said there are three types of broadly tuned color receptors. The color experience is the product of the relative degree of activation.

Now, that's a fantastic theory. But there's a big problem with it. The big problem with that theory is that he doesn't explain Grassmann's laws. Remember what Grassmann's law is? That if you mix things along the cardinal axes, you get white. And you only get other colors when you mix them not along the axes.

So that became a problem. And because of that, another famous person, Herring, came up with an alternate theory. He came up with a theory which said that color opponency is based on the observation that red and green, as well as blue and yellow, are mutually exclusive, just as I had said. The nervous system probably treats red/green and blue/yellow as antagonistic pairs, with a third pair being black and white. That's where the third dimension comes in. So therefore he argued that we need something like color opponency to be able to see colors right.

Now, the interesting thing about this is that he became very famous coming up with this incredible theory. But then if you go back in history, you find that Leonardo da

Vinci had this same idea many, many, many years before that.

And this is from his autobiography, with a very poor translation. It says, "Of different colors equally perfect, that will appear most excellent, which is seen near its direct contrary, blue near yellow, green near red, because each color is seen, when opposed to its contrary, than any other similar to it." It's not written in English really, but you get the idea.

So we have a major two theories. And then numerous experiments subsequently emerge, especially when it became possible to record the neural activity of cells to determine to what degree these theories are correct.

And of course, the first correct aspect of both theories was that indeed, we have three types of cones that are selected to red, green, and blue, and that they are broadly tuned.

So to now understand better how it really happens in the nervous system, let's take a look at the basic physiology of color processing.

I showed you this slide once before. I pointed out to you that contrary to red and green cones, blue cones are much less numerous. Only one out of eight are blue. And furthermore, if you look at this in the retinal surfaces in the fovea area, there appear to be very few blue ones in the fovea itself.

So the blue cones are less numerous. And consequently, it became a puzzle of how do they contribute to color vision.

Now, to exemplify this further, let me show you a slide here. Here what we vary is a spatial frequency. And what you can see is-- I think most of you probably don't see anything here. But most of you probably still see this. This is the same spatial frequency as this. But this activates the blue cones mostly. And this activates your red cones.

And you can see that your acuity is much, much lower when you only have your blue cones available. And that's because only one out of eight blue cones exist in

the retina. So there's this very, very clear distinction.

So now let's talk about the photoreceptors. Here we have an absorption spectrum, or I should say a series of absorption spectra, for the four kinds of photoreceptors. And the fourth one is your rods.

So what you see here-- and each of them are fairly broadly tuned. Here we have nanometers. And I'm sure all of you know this already, that 1 nanometer is a billionth of a meter. So we're talking about incredibly, incredibly high frequencies.

So that the important thing to remember here is that each of these cones is fairly broadly tuned. And so consequently, any light that comes into the eye tends to activate all of the cones unless they're at the very extremes. .

And so indeed, as Young and Helmholtz had proposed, somehow we have to derive our color experience from the relative amount of activity from these different cone types.

But then as I've mentioned to you, Herring felt that that was not sufficient to explain our color abilities. And so what he did then is to move on and had people, especially much more recently, examine more closely what the center-surround organization is of the different midget cells in the retina.

And if you remember, initially I told you that the prime theory was that the center comes up, is comprised in the central retina of just a single cone and the surround of its color opponent cone.

But then, when people began to study this very carefully using a combination of recordings and anatomy, they found that actually the surround is not specific to one type of cone input. It's mixed. And so then people began to model that. And they found that this arrangement is almost as good as this arrangement. And this is the truth, actually. That's how it is.

And so then, just to remind you, the parasol cells have a mixture of these inputs, both in the center and the surround. And as we had discussed, the parasol system

cannot tell you about colors. This I mentioned to you before. The midget system gives a more sustained response than the parasol system.

So now I also showed you this diagram. And we established that the green and the red cones each give rise to an on and off system at the level of the bipolar cells, and then give rise to the on and off ganglion cells. The red and green on and off ganglion cells.

Now, the blue system is more complicated because if you would have had four different kinds of cones, meaning a blue one and a yellow one, then probably would have had a similar arrangement. But nature somehow had failed to create a yellow cone because it felt it was not necessary-- because if you have an equal mix of red and green, you get yellow, because remember, they're not on opposites.

Sorry. They're opposite. But if you mix them, you can create an impression of yellow because they're not along the exact axes for the colors themselves.

So the argument was therefore that you must have blue on and blue/yellow on ganglion cells. But whether this is really the case is still to some degree debated. People have done a lot of recordings. And much of this was done not only in the retina, but also your lateral geniculate nucleus.

And so the question was, let's just find out what is the color tuning of cells in the lateral geniculate nucleus to understand this. And to do this, when we went back to the color circle and presented stimuli along the color circle through the receptive fields of these cells to see how they responded.

And here's an example of a so-called blue ON cell. It shows here you [INAUDIBLE] the cell is tuned. Sharply tuned, mostly to 90 degrees. The yellow cell is the opposite. And green OFF cell here and a green ON cell here.

So what happens then is when you take a lot of sample of these, huge sample of them, what you find is that in the lateral geniculate nucleus, you don't get any cells that are at the diagonals. All the cells fall into these major four categories along your cardinal axes.

And then if you take a big huge sample, you come up with the following summary-- that you have red ON cells, red OFF cells. You have green ON cells and you have green OFF cells. And at least some people claim that you only have blue ON and Yellow ONs. You don't have blue OFFs and yellow OFFs. That is still under debate. But certainly, if you do extensive recordings, if you find any OFF blue and yellow OFFs, they're extremely rare if they exist at all.

So now to try to gain yet further understanding of the role various areas play in color vision, is that one can make lesions. And I've already told you what happens when you make either parvocellular or magnocellular lesion. That blocks the parasol or the midget systems. And that the midget system is essential for color vision.

And then I showed you this. Here is a geniculate. If you take out this area, you block the midget system. And if you take out this area, you block the parasol system. So if you do that-- here is an overall view of the monkey brain. Here's area V1 Here's the V2. And here's area V4, which I've mentioned to you before had been believed to play a central role in color.

So then it becomes important to see just what happens when you make lesions in these areas. In this case, you can make a lesion V4. And then we can examine color discrimination. And I told you in a monkey, what you do is you use an oddity task. After fixation, you can present the odd stimulus either in the intact parts of the visual field or those that had been lesions.

This is a high contrast. And if you do that experiment-- I showed you part of this data before. I showed you that after lesion of the parvocellular geniculate, which blocks the midget system, you totally lose the ability to discriminate even these high colors, red, green, and blue. But no deficit arises when you make a lesion in the magnocellular portion of the geniculate.

And then the big question became what happens in V4, since that had for decades been declared to be a color area. And what was surprising about that is that after V4 lesion, there was only a small deficit in color for this high-contrast stimuli.

So therefore people have to go on and do a more careful detailed study to see what happens if you use less saturated colors. Remember that the degree of saturation is one of the important factors for analyzing color.

And here we have an example of a very low saturation. And here we have a somewhat high saturation. And you can vary that systematically and see what happens after V4 lesion and after other kinds of lesions.

And here's an example of what happens in a V4 lesion. And this is what happens in an MT lesion. It shows no deficit at all with an MT lesion, indicating that MT does not play a crucial role in analyzing color. We do get this significant deficit here, but it's a small one.

So even at low saturations, the monkey still can do colors reasonably well. So it's not like V4 is the color area. There apparently are several areas in the brain that can process color. And V4 does that in addition to performing several other analyses that we will discuss in a couple of sessions from now.

So now we're going to turn to another very interesting phenomenon, which is what is called isoluminance. What is isoluminance? Isoluminance is the presentation of different colors that have the same illumination level. So I'm going to give you a few examples of this.

If you look at this-- how many of you can read those words there? Pretty tough, isn't it? This can be set up in such a way that it's even worse. But because of the light bulb in there, it's not really perfect. But just to give you a sense of it obviously goes to a lot easier to read. So that's because this is close to isoluminance, at which our ability to see objects is much impeded. Not eliminated, but impeded.

So what can you do to do this kind of experiment systematically? What you can do here is you can use various capabilities. Stereopsis, motion parallax-- just motion-- and texture. And if you do that, and you vary the red/green luminance ratio, you can see that there's a dramatic drop off at around very close to a luminous ratio of one and one. So indeed, our ability to process information in the absence of luminance

information is greatly compromised.

So then the question came up-- I mean, we're talking about here such things as motion perception, texture perception, and stereopsis. And as we had discussed before, we have already established that texture and stereopsis are processed to a large extent by the midget system. And that motion to a large extent is processed by the parasol system. But all three of these types of capabilities are compromised isoluminance

So a series of experiments had been carried out in which people argued that when you present stimuli at isoluminance, you render the parasol system unresponsive because it gets equal input in the center-surround, some red and green cones and blue cones. So therefore, they concluded, that if there's a deficit in performance like this, that must reflect the fact that the parasol system plays an important role in the analysis.

But as I told you before, stereopsis is processed predominantly by the midget system and so is texture. So that raised quite a problem. And so people began to run experiments in which they recorded from the parasol system to see what happens actually to unit responses when you are at isoluminance. And that resulted in quite a surprise.

So here is an example of a magnocellular cell, meaning a cell that gets input from the parasol system of the retina. And you alternate between red and green here repeatedly, collect the data, and you vary the red/green ratio. And you can see here that throughout the whole thing, the cell continues to respond. So that became quite a puzzle. We were not able to silence the magnocellular system at isoluminance.

So the question is, how come? Well, the answer is, as you had seen before, that the parasol system is extremely sensitive. It gets input even in the center of the receptive field of each cell for many of-- I should maybe say several-- different cones. And because of that, there's much more information and excitation coming into those cells than into those that are in the midget system that most of which only get input from a single cone for the center.

So that being the case then, we can move on and ask a question of what about if you do the same kind of experiment in area MT. Now, who remembers? Area MT gets most of its input from which system? Good. Mostly from the parasol system going through the magnocellular layers. So now you can record in the area MT and do the same kind of experiment I just described to you the retina in the lateral geniculate nucleus.

And so what you can do here is you have a monkey. The monkey fixates. And you move a bar of light across the receptor field back and forth which is isoluminant-- red/green in this case. And then you see how well the cell responds.

And then for comparison what you can do is you can use a luminance grading, bright and dark in the background, to which we know that the parasol cells and the cells in the area MT respond vigorously. So now we are going to compare what the difference is between these two conditions, meaning luminance grading as opposed to an isoluminant color grading.

So if you do that experiment, you're in for surprise. Here's an example of one cell in which there's a much more vigorous response to luminance. Here are the various luminance contrasts. And here is a chrominance one. And the cell doesn't respond as well here, but it still responds reasonably well.

Then you take another cell and you get the opposite. And this particular cell, still in area MT, responds a bit more vigorously to chrominance than to luminance. And so if you add this all up and record for many, many cells, you find that the cells in area MT, just like in the lateral geniculate nucleus and in the retina, respond quite well at isoluminance-- the parasol cells and the same cells, of course, in the lateral geniculate nucleus, and in area MT.

So this area MT is one that responds surprisingly well to anything that's out there that results in a change, whether the change is produced by virtue of chrominance or by virtue of luminance. And that, in fact, is one of the very important attributes of the parasol system. Namely, and that's so numerous in the periphery, is to be able

to detect just about anything that happens-- motion, flicker, just the onset of a single stimulus, whatever.

But that system is very sensitive and can tell something has happened there. That's what that system is very good for. It's not that good, obviously, for seeing very, very fine detail. But it's very sensitive. And it's very, very good for detecting motion and appearances.

So now we're going to move on and talk about a topic that I'm sure many of you have an interest in. And that has to do with deficiencies in color, often referred to as color blindness.

And the first fact is that if you look at the incidence of color deficits in humans, 8 out of 100 males among Caucasians, 5 in a 100 in Asians, 3 in a 100 in Africans. In females, it's much, much less. It's 10 times less frequent. But still overall, that's quite a number of people who have some sort of deficiency in color.

So now that we know that, we can ask the next question-- what kinds of color deficits can we denote? And the type, these are given fancy names, which are called protanopes, deuteranopes, and tritanopes. And that simply refers to the fact that protanopes lack long-wavelength cones, which are of course the red cones. The deuteranopes lack medium-wavelength cones, if you talk green ones. And the tritanopes lack the short-wavelength cones, which are the blue ones. So that is the basic types of deficits.

Now, some people have a combination of these. Some people have no color vision at all, but that's very rare. Quite common are these three types. You somehow don't have one particular kind of cone or you have very few of them, or you have them, but they don't function right.

So now, how do we establish our ability to see colors and whether we have normal color vision? Now, that's very interesting. A number of tests have been developed. And the most famous of those, the oldest one-- let me go back, sorry-- are the so-called Ishihara plates. And the next one's the Farnsworth-Munsell Hue Test. And

the third one I was going to tell you about is the dynamic computer test.

So let's look at the Ishihara plates If you look at that, how many of you can see what is written there? What is it?

AUDIENCE: Eight.

PROFESSOR: Eight. Very good. Anybody who doesn't see it? OK, you don't see that. We'll get back to you in a minute.

So now another test is a dynamic one. The reason for using a dynamic test is that the so-called isoluminant point of individuals is not the same. Expect a lot of variations from person to person.

And so this test is the dynamic one. They presented for the background, as you can see here, different luminance levels in gray. And when the computer starts running, these keep exchanging each other in randomized fashions. It's the dynamic view.

And then you have a central area here. Everybody can read this, right? What's the word?

AUDIENCE: Lite.

PROFESSOR: Lite. Very good. So now instead of presenting these letters here in a high brightness overall, we can present them in color.

So I'm now going to show you an easy test. Anybody can read this? Anybody who cannot read it? Can you read it?

AUDIENCE: Ish.

PROFESSOR: Ish. So what's the word?

AUDIENCE: MIT.

PROFESSOR: MIT. What's that? So now I'm going to make it more difficult. You guys ready? What is this one?

AUDIENCE: Fit.

PROFESSOR: Are you having a--

AUDIENCE: Yeah, it's a little harder.

PROFESSOR: You're having a fit, huh? Can you read that one?

AUDIENCE: No, I can't.

PROFESSOR: No. So now it seems like we do have one person here who has perhaps a mild color deficiency. And so now the question comes up, even if all of you want to do this, what can you do to test yourself? Well, so let me tell you about that.

There is a so-called Farnsworth-Munsell color test. So what you want to do here is-- can you read this down here? Get on Google and just type in Farnsworth-Munsell color test online. If you type that in, all kinds of things come up. Click on the topmost one.

And then what you see here is a set of colors. Actually, there are four sets. And each of these has 20. And I just drew a few of them in. And your task is then-- each of these can be moved-- to arrange them in an order, going from this color to that color in order. So you do that for all four of them.

And after did that, you can click on the bottom. And it will tell you what your score is for each of these. And so if your color vision is very good, it gives you sort of a set of histograms. And if the histogram is very, very low, then you're good. And if it's high, then you're not.

What you can actually do is when this first comes on, these are in random order. Your task is to put them in order. But at the bottom here, it says score. So if you click on score, it will give you the histograms uncorrected. And they're all going to be high. Then you do this work. And then you click on it again and see how good your color vision is based on that.

It's a bit time-consuming. But if you are interested in getting a sense of just how

good your color vision is, this is a rather good test, which is readily available on the internet.

Does anybody have any questions about this portion? Good.

So now as a result of this, we're going to move on and spend the remainder of our time talking about adaptation because that is pretty closely relevant, as we shall see, to color vision as well. So I'm going to talk about adaptation.

First of all, again we come up with a number of basic facts. Now let me at this point interject and just tell you that all the material I'm talking about today will be posted on Stellar. What's on Stellar now is not an updated version. But what I'm talking about today will be on Stellar I think by tomorrow.

So basic facts. We talk about overall levels of illumination. That's what's so remarkable about the visual system. It's actually unbelievable. 10 log units overall. But the reflected light varies over much smaller range. In other words, you don't want to look at directly at light. The reflected light varies only about 20 fold.

So now the question is, how do we handle this? Well, it turns out that the pupil, which does play a role in this, can only adjust over a range of 16 to 1. So that's a long cry from 10 log units. And so much of the adaptation I would say, even more so the adaptation that takes place, occurs in your photoreceptors.

So here I'm saying this again-- most light adaptation takes place in the photoreceptors. Now, how does it take place? Well, the way it takes place is that-- I mentioned this to you before-- the photoreceptor molecules, like rhodopsin in the rods, comes in two basic forms. You don't need to know the chemistry of it, but you make two or simply that it comes in two forms. We can call it bleached and unbleached. Some people call it open and closed. But let's call it bleached and unbleached.

This is very dynamic process. At any level of illumination a certain percentage of molecules is bleached in each receptor and a certain number is not bleached. And the brighter the illumination, the more are bleached. It's dynamic, which I mean is

that the molecules constantly keep changing. So it's the overall percentage of the ratios between the beached and the unbleached.

So that means that any increase in the rate of which quanta is delivered to the eye results in a proportional decrease in the number of pigment molecules available to absorb those quanta because they are bleached.

Now, this arrangement happens to be extremely clever. And this is reflected in the fact that the retinal ganglion cells are sensitive to local contrast differences. Remember, I told you there's a center-surround organization. This is one of the prime reasons we have that. The overwhelming majority, like 95% of the cells in the retina, the retinal ganglion cells, respond to contrast differences, not to absolute levels of illumination.

And that's how we often talk about contrast. And if you remember what the contrast formula is, it's the contrast level of the stimulus itself and the contrast level of the background. You subtract one from the other, divided by the sum of the two, multiplied by 100. I showed that to you before.

So now here we are. If you talk about light and dark adaptation, this is the basic outline of the retinal connections that we have talked about. We have presented this several times before. And then if you are light adapted, you essentially have non-functional rods, so I took them off here. But then when you darken that, the opposite happens. And you have the rods active.

But they all fit into the same ganglion cells. And that's why at night, the receptor fields are bigger. And you don't see color at night because this is what the picture is.

Now what you can do is let's ask the question, how do the neurons, like the cells in the retina, the retinal ganglion cells how do they fire at different levels of illumination? And that's quite an interesting story and a very straightforward one.

Here we have a cell that had been adapted to these different levels of background illumination. At minus 5, your rods are functional. And what is important to see here is that as you change quite dramatically the background level, the eye adapts. And I

should say that it's the photoreceptors predominately that do so.

And what they look at are local differences. And so each of these then sees a fresh, the contrast that is created, rather than looking at absolute illumination levels. And that's what you want, of course. You want to be able to drive well at night. You want to be able to drive well in the daytime. And by having this system, you can look at predominantly at contrast differences rather than absolute levels of contrast. So that's the arrangement here.

And now what we are going to do is to move on and talk about the so-called after-effects of adaptation. So let me tell you how this initially was done.

People ask the question, what happens if I fix something on your retina for a period of time? If that previous set of data that I've shown you is correct, if I present something to the retina and leave it there, pretty soon you won't see anything.

A famous series of experiments was done, by now many, many years ago, in which they-- very clever experiment-- had subjects lie down. And they put a contact lens in the eye. And in the contact lens, they put a miniature projector on, which meant that when you turn that projector light on, it went to a fixed position on the retinal surface.

Why was this necessary? Well, the reason it happened is because it was discovered that your eye actually is not really stable on purpose. Your eye ha a so-called eye tremor. And of course, you move your eyes all the time. So this procedure of having a contact lens with a projector attached to it kind of got rid of the eye tremor.

So when they did that, they found that, depending on the contrast, in a matter of a minute or less, maybe even 30 seconds, you would stop seeing what was presented to the eye because you then change the adaptation level in your photoreceptors.

So then subsequently, people had a clever idea. Said, we don't need to go through this incredible trouble of having to have people with contact lenses and a projector, and having them lie down because that's the only way it would work. We can do this

much more simply. And so to do that, I'm going to have a demonstration here.

What I would like each of you to do is to-- you see it's a light spot here and dark spot there. So I want you to fixate here and count to about 30. And be very relaxed about it. This is a Gaussian. Therefore there's no sharp edge and the eye tremor doesn't matter. Then after you counted to 30, shift your gaze to the bottom one.

The first thing that happens if you keep looking at it, the two on the top here disappear if you fixate very tightly. And once they disappear, then you can look down.

Everybody see it disappear? Good. And what happened when you looked at the bottom?

AUDIENCE: [INAUDIBLE].

PROFESSOR: You got a reversal, right? You got a dark spot here and a light spot here. And you say oh my god, what's going on here?

So now let's do another experiment. I want you to do this again. But what I want you to do is to cover one eye up and then do it again. Count to 30. And after you did so, make [INAUDIBLE] down the bottom, but switch your eye. And if you switch the eye, cover the one that you looked at and uncover the one that you didn't look at. And if you do that, you won't get any effect.

So what does that prove? That prove that this is happening in the retina. Everybody agree? Very clear cut.

So what's going on here? So let's diagram this. Here we have the situation. You turned on these two stimuli. And then when we turn it down, initially their sensitivity of your photoreceptors is pretty much the same because it was a homogeneous background.

Then after you looked at this for awhile-- no, one more thing. In this case, the ON cells fired, and in this case, the OFF cells fired, saying, oh, dark spot, oh, light spot.

Now, if you keep looking at this for awhile, what happens is it begins to disappear. When it does, what happens is you don't see anything and what happens also is that the sensitivity here decreases for white light and [INAUDIBLE] increases here for white light. So therefore, what happens is once you adapted to this, there is no response in the ganglion cells.

Then for the third step. When you've made yourself look down, there were homogeneous background. But this region is less and this region's more sensitive. And so therefore the photons come into your eye from those two regions hit more and less sensitive regions on the rental surface, thereby activating the opposite cells-- here activating the OFF cells, here activating the ON cells. Sorry-- right, yeah. We got a reversal. So that explains why you see the after image.

So now we're going to continue and get back to the question of the color circle, see what happens with after images with color. So this color circle is unbelievably powerful because it explains the after images that you see with color. And I will come back to this circle.

But what I want you to do now again is to fixate here, count until, again, about 30, and then fixate on the bottom. So if you do that, I think most of you should see, again, a reversal. Here you would see some reddish. Here you would see something greenish.

Does everybody see that? Do you see that too? Good. So you have a very minor color deficit. So that's the case here.

So now let me show you another one. And again, do the same experiment. And what you see here at the after images you get-- whoops. Sorry. Let me go back. The after images you get here are not going to be the complimentaries here.

So what's going on? So let me explain it to you. Here again is a color circle. And here the prime axes. It turns out that if you adapt to this level here, the rule of the color circle says if you go across, this is the after image you're going to see. And if you adapt to here, this is the after image you're going to see. So let me draw that

up. It looks like that.

And that is true everywhere, as long as you go across the axis. You could do this horizontally or even diagonally, and you get this reversal.

So it says that an after image can be perfectly predicted by the rules of the color circle. It's on the opposite side of the image that you look at, going across the center along the cardinal axis.

But now if you do the diagonals, which I showed you before, when it didn't match, what we have here, you have this and this. Then the after image is this and that. And so we don't have a correspondence, of course, because you're not along the axes that would predict this. This one gives you that and this one give you that. So if I did this and this to begin with, it would be the same as that, but rotated.

So that then clearly enables us to use the color circle to predict not only some of the basic effects of what colors we see, but also to tell you exactly what kinds of after images you get. Quite remarkable.

So now to drive this home once more. This doesn't work too well because the colors are crummy here, but we can try it. Everybody agree this is sort of a more or less black and white display-- a little bluish, unfortunately, here-- of a beautiful castle?

See that fixation point here? What I want you to do here is to fixate here, again, count to 30, and then I'll switch back to it. And if this were to work right, you would see the original black and white image in color. Keep fixating. Count to 20 more. And then I'll switch back.

Did you see the colors? Yeah. So this is a very clever demo I found. I'm afraid I don't remember the person's name who came up with this one. But the essence of it is, again, that indeed what is happening is that you're creating an after effect due to adaptation in the retina. And when you do this very cleverly, like this particular castle picture, you can actually create an artificial impression of colors which are in consonance with what the real colors would look like in a black and white picture.

So that then is the essence of what I wanted to cover about adaptation. And we can now come and summarize what I had covered today.

So first of all, I told you that there are three qualities of color-- hue, brightness, and saturation. And just to go back-- hang on for a minute. I want to go back once more to make this clear, which I forgot to mention.

If you go around the circle, you change hue. And if you go from the periphery to the center, you change saturation. And the center here, if this color circle were 100% correct, this would be a white area.

Now, the basic rules of color vision are explained by the color circle, as we have amply seen. There's something probably-- I have a color circle up on my wall in my office because I'm always fascinated by this, even though I've been doing it for years.

So the three photoreceptors we talked about in humans and in primates, the red, green, and blue, which shouldn't be called that. People get mad when you do that, even though that's the way I call it. But people want to call them short, medium, and long-wavelength cones. They are broadly tuned, as I had shown you in those spectrograms.

The color-opponent midget retinal ganglion cells form two cardinal axes, the red/green and the blue/yellow. And those, if you remember I told you at the level of the retinal ganglion cells and at the level of the lateral geniculate nucleus, fall into these two major categories. We won't have any under diagonals. So for us to be properly able to see diagonals, that's done somewhere in the cortex. It's not done at the level of the retina or the lateral geniculate nucleus.

Now, I also pointed out to you several times already that the midget system's essential for color discrimination. And the parasol cells can see stimuli even at isoluminance. They just cannot say what the color is. They don't, quotes, "perceive" different colors. But they can see any kind of change that occurs in the environment, even when it occurs at isoluminance.

Color is processed in many cortical areas, lesions to any single extrastriate area fails to eliminate the processing of chrominance information. It can reduce it, but it doesn't block it out. That's true for many things. So the cortical areas are very, very complex. And they do interactive analysis for many different attributes, including color.

However, I can add here that does not apply to area MT because MT does not seem to be specializing in color because lesions there, you [INAUDIBLE] any deficit. But there's several other visual areas. We went through that, V3, and [INAUDIBLE] cortex, and so on. These areas contribute to the processing of color.

Now, the perception of isoluminance is categorized for all categories of vision. It's not selected to only those that are processed by the midget or the parasol systems. All aspects of vision-- and the three I showed you was, stereopsis, motion, and what was the third one?

AUDIENCE: Texture.

PROFESSOR: Texture, right. So all three of those are compromised when stimuli are presented at isoluminance.

The most significant aspect of luminance adaptation occurs in the photoreceptors. And it's explainable by the relative number at any given level of adaptation of bleached and unbleached photoreceptor molecules, as in the case of rhodopsin.

Lastly, after images are a product of photoreceptor adaptation and their subsequent response to the incoming light.

So that then is the essence of what you wanted to cover today. And I hope you did find this interesting, because certainly our ability to see color is quite a remarkable thing. It's amazing to get a sense of how the nervous system does that, even though at this stage, we are still at a fairly early level of having gained full understanding of it.

Now the next time, we are going to move on to another fascinating topic, at least for

me fascinating, which is depth perception, which I had mentioned before is a remarkable achievement because images fall on a two-dimensional retinal surface. And from that, the third dimension has to be reconstructed. And how that is done, we are going to discuss the next time.

Now let's make sure that all of you had signed attendance. And the next thing is if any of you have any questions, I will be happy to try to answer them. So once again, I'm crystal clear, huh?

Well, thank you very much for attending. And I do hope that your knowledge has increased a bit about how we process color information.