

Psychology 1XX3 Notes – Colour Perception – Mar 7th, 2010

Evolution of Colour Perception:

Who Has Colour Vision?

- Many birds, fish, reptiles, and insects have excellent colour vision. Among mammals, however, colour vision is limited to primates, including humans.
- This means that your dog and cat, along with the bull, can only see in shades of grey.

The Functions of Colour Vision in Different Species:

- How did primates end up evolving the ability for colour vision? Primate colour vision is especially well suited to distinguish red and yellow against a green background.
- This adaptation helps immensely with foraging for fruit in the bushes and trees.
- In this way, one possible biological advantage of colour vision for primates is the ability to detect colourful objects in the wild.
- Additionally, the ability to perceive colour is an important advantage for detecting predators or prey against a background, determining the ripeness of fruit, the richness of the soil, or even using the colour of sunsets as a means to predict weather.

The Functions of Colour Vision in Different Species:

- Colour vision is also an important part of the lives of many non-mammalian species. Many birds, fish and insects are able to see colours that we don't see at all, including colours at the UV end of the spectrum.
- For birds, the colour of a potential mate's feathers provides signals to other birds about how healthy that bird is, and can influence how likely that bird is chosen as a mate.
- This type of colouration system would help the birds communicate with each other about how sexy and healthy they are, while still remaining inconspicuous in the forest to potential predators that are unable to see this bright colouration.
- Next time you see a bee in a flower garden, don't assume that the beautiful red rose you see must be irresistible to the bee. The bee might be attracted to flowers that look dull to human eyes, because it is responding to specific patterns and colours on the flower that we are unaware of.
- Some flowers have adapted patterns on the petals that are invisible to us, but serve as "nectar maps" to the bee.

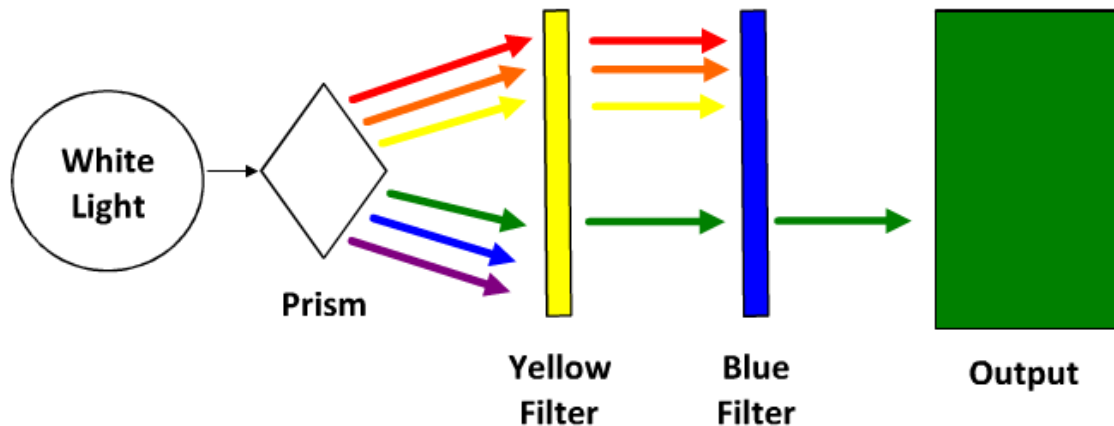
Colour Mixing:

Introduction:

- The human eye processes colour information using principles that have been known to artists for centuries. You don't need to have millions of colour receptors to deal with every conceivable colour out there in the world.
- Instead, you just need a few receptor types whose activity can be combined in various proportions to make every conceivable colour.
- The three primary colours can be combined in various proportions to make every colour in the spectrum. Primary colours are like a base colour, they cannot be reduced into other colours.
- There are actually two different types of colour mixing: additive and subtractive.

Def'n of Subtractive Colour Mixing: When coloured pigments selectively absorb some wavelengths and reflect others

- Subtractive colour mixing applies to the mixing of pigments, dyes, or paints, and it is called 'subtractive' because every reflective surface absorbs (or subtracts) the colours that it does not reflect. Adding other pigments to that surface alters the combination wavelengths subtracted.
- So a blue object looks blue to us because all wavelengths are being absorbed by the object except short, blue waves, which are being reflected back to our eye and making the object look blue.
- So when we mix two pigments, all wavelengths are being absorbed except those that the two pigments jointly reflect.
- It may help to think about what would happen if we shine a white light through both a yellow filter and then a blue filter and look at the remaining light on a white screen. You would see that it looks green.



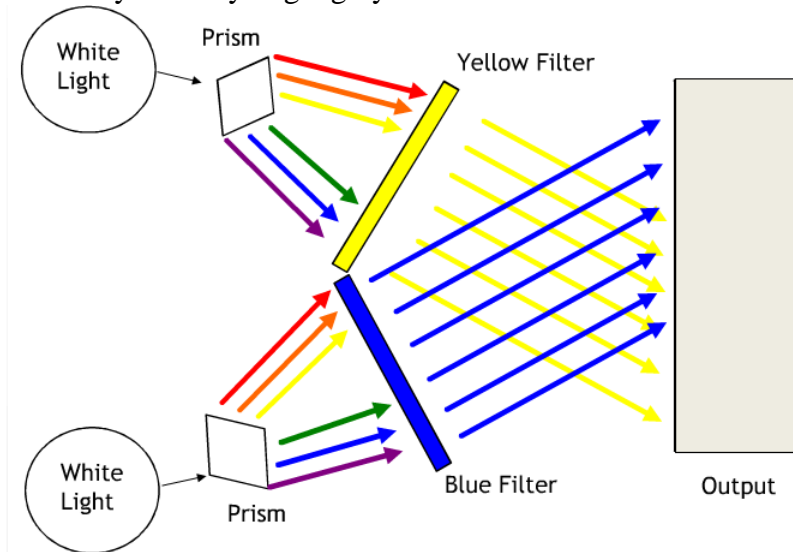
- This is because when the light hits the yellow filter all the short waves (the blues and purples) are being absorbed, or subtracted out, and only the longer (green, yellow, orange and red) waves are allowed to pass through. When these longer waves hit the blue filter, it absorbs the longest waves (yellow, orange and red) and what is left over is a middle band of wavelengths that is transmitted by both pigments. This middle band that is left over is green.
- With subtractive colour mixing the primary colours are red, yellow and blue, because these three colours can be mixed in various proportions to make all colours in the rainbow.
- The complementary colour of red was green, for yellow it was purple, and for blue it was orange. If you mixed a primary colour with its complementary colour, you always got brown.

Def'n of Additive Colour Mixing: When coloured lights add their dominant colour to the mixture.

- The coloured lights add their dominant wavelength to the mixture as opposed to subtracting wavelengths out.
- This is how our visual system processes colour; by adding the effects of different wavelengths together in our nervous system. With additive colour mixing, the primary colours are red, green and blue, because these three colours can be added together in various proportions to make all the different colours that we see.
- If you made a colour circle using additive colour mixing, you'd find that the complementary colours are also different: the complementary colour of blue is

yellow, for red the complementary colour is a bluish-green, and for green the complementary colour is a reddish-purple.

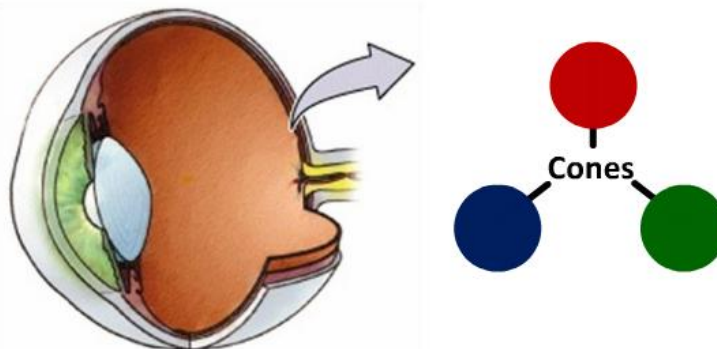
- With additive colour mixing, whenever you mix a primary colour with its complementary colour you get grey or white.



- Take a blue and yellow filter, but instead of passing the light through each filter successively, overlap the coloured lights from each one onto the reflective surface.
- Because each coloured light adds its dominant wavelength to the mixture, you find that now blue and yellow do not make green when added together; but instead they make grey.
- This is because grey light is the sum of complementary colours (in this case, blue and yellow).

Theories of Colour Vision:

- Def'n of Trichromatic theory: Proposes that the retina contains three different kinds of cones.
- The trichromatic theory of colour vision is based on the proposal that the retina contains three different kinds of receptors that are each maximally sensitive to different wavelengths of light.
- This very influential theory has a long history, first proposed by Thomas Young in 1802, and later modified by Hermann von Helmholtz in 1866. Sometimes it's referred to as the Young-Helmholtz theory.
- This theory follows from empirical observations about primary colours and colour mixing; namely, that it's possible to match all of the colours of the visible spectrum by the appropriate mixing of 3 primary colours.



- Thus, the trichromatic theory postulated that you only need three different types of receptors to discriminate all the colours of the visible spectrum. Although this theory was developed purely from behavioural data, we now know that the human retina is indeed equipped with three types of cones which contain spectrally selective photopigments that are maximally responsive to wavelengths of light that correspond to the primary colours red, green and blue.
- ‘maximally responsive’: this means that a given receptor will respond to other wavelengths, just not as much as it would to its peak wavelength.
- When you perceive yellow, this is because the red and green cones are equally stimulated. White is what you see when all three receptor types are stimulated.
- However, some things didn't quite fit the theory. First, yellow seemed to be a primary colour and not a mixture of red and green. When people were asked to describe the most basic colours, yellow was usually included as one of them, even by young children.
- Furthermore, the trichromatic theory could not explain the law of complementarity, that certain pairs of wavelengths produce the experience of white.
- Finally, there was the phenomenon of the complementarity of afterimages: why do you see a yellow afterimage when you stare at a blue stimulus?

The Opponent-Process Theory:

Def'n: Each colour receptor is made up of a pair of opponent colour processes.

- In 1920, Hering formulated the opponent-process theory of colour vision. Like the trichromatic theory, the opponent- process theory argues that there are three classes of receptors, but unlike the trichromatic theory, the opponent-process theory posits that each of these receptors is made up of a pair of opponent processes.
- Each receptor is capable of being in one of two opponent states and it can only be in one of those states at a time. The ability to see blues and yellows is mediated by a blue-yellow opponent receptors, greens and reds are mediated by green-red opponent receptors, and 3rd type of opponent receptor distinguished bright from dim light; these brightness detectors are excited by lights of any wavelength.
- The new opponent- process was very successful at explaining how a mixture of wavelengths from complementary colours (like blue and yellow or red and green) appear white; it also explained why the afterimage of a visual stimulus is the complementary colour.
- It also fit logically with the fact that most people can easily imagine a yellowish-red or a bluish-green colour; but it's more difficult to imagine a reddish-green or a bluish- yellow colour.
- According to the opponent-process theory, these colour pairs are opposite and occur from differential activation of the same receptor type; accordingly, it would be impossible for a single red-green receptor to be active in both the red and green states simultaneously.

Both Theories Needed to Explain Colour Perception:

- Both of these theories are needed to explain colour perception. Hurvich and Jameson elaborated the theories in 1955 and proposed that there are three component receptors or cones in the retina that are each maximally responsive to light of a certain wavelength, just as the trichromatic theory suggested.

- The three cones are maximally responsive to red, green and blue. The response of these receptors differentially affect what is happening further down the line in the brain, where things are organized as the opponent-process theory would have predicted. The opponent pairs are red-green, blue- yellow, and light-dark.
- The combination of the two theories says that the output of the cones is input for the next layer of colour processing in the retina, which is organized in an opponent fashion.
- Colour coding continues in this opponent arrangement up to the brain's visual processing systems.
- For example, a red light would stimulate a red cone in the retina, which would then excite the red-green ganglion cells that are organized in an opponent fashion, and this excitation of the red-green ganglion cell would signal the brain that the stimulus is red.
- A green light, however, would stimulate a green cone, which would then inhibit the red-green ganglion cell. This inhibition of the red-green cell would signal to the brain that the stimulus is green.
- A blue stimulus, would activate the blue cone, which would send an inhibitory signal to the yellow-blue ganglion cell, signalling to the brain that the stimulus was blue.
- With yellow, it's a little bit more complicated. Remember that yellow is a mixture of red and green, so yellow light would cause equal activation of the red and green cones. Activation of the red cone would send an excitatory signal to the red-green ganglion cell as well as the yellow-blue ganglion cell, and activation of the green cone would send an inhibitory signal to the red-green cell and an excitatory signal to the yellow-blue cell. The red-green ganglion cell, having received an excitatory message from the red cone and an inhibitory message from the green cone, would send no change in signal since the two effects would cancel each other out. The yellow-blue ganglion cell, however, would have received an excitatory message from the red and green cones, which would excite the yellow-blue ganglion cell. This excitation would then signal to the brain that the original stimulus was yellow.

Colour Processing in the Brain:

- If you stare at this black and white panda for 30 seconds while fixating on the dot, and then look at this white surface, you'll see that all the white areas are now dark grey and all the black areas are whitish.

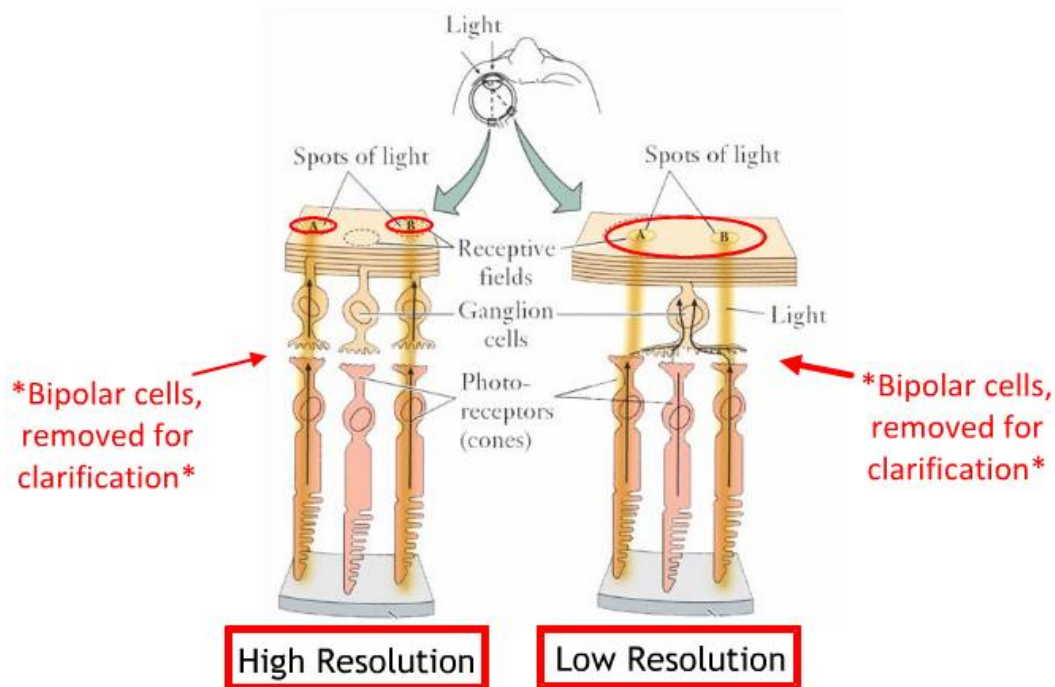
What Afterimages Have Taught Us About Colour Processing:

- The rate of firing of the colour receptor signals to the brain what colour is being seen, so that a receptor that fires at a rate that is faster than baseline means one colour, but if that same receptor fires at a rate that is slower than baseline, meaning it is inhibited, then this signals to the brain that you are looking at the complementary colour.
- The same colour receptor has two different channels, and the colour you perceive depends on what channel you're on, or how fast the cell is firing.
- The reason afterimages occur is because when a colour receptor is excited (or inhibited) for a prolonged period of time, you get a rebound effect when you stare at a neutral colour like white, and that same colour receptor will go into the opposite state, causing you to perceive the complementary colour.
- For example, when you stare at a green square, all your green-red colour receptors are excited, firing at a rate that is much faster than baseline. When you then stare

- at a neutral surface, all those cells that have been firing so fast for so long go into the opposite state and actually fire less than baseline, possibly because the pigments are partly bleached out by the prolonged exposure to the stimulus.
- Firing below baseline levels in these receptors is perceived as red, so you'll see the afterimage of a red square after staring at a green square.
 - Red/green cells would show the opposite response to the green/red cell. The same is true for blue/yellow and yellow/blue cells.

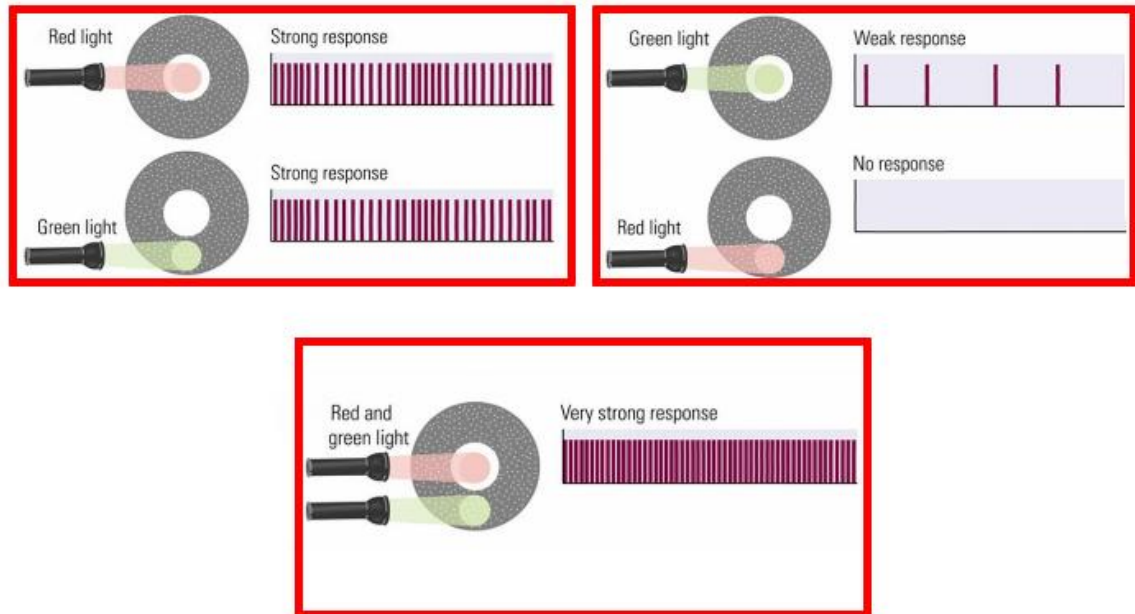
Colour Coding in the Retina:

- In high-resolution channels, one cone is transmitting information to one ganglion cell. But with lower resolution channels (away from the fovea) many cones are transmitting information to a single ganglion cell. (See image below.)
- In both cases, the ganglion cells are said to have a receptive field, or a region on the retina that, when stimulated, will cause the ganglion cell to increase or decrease its firing rate.
- In high-resolution cells, these fields are small, while in low-resolution fields, they are large.



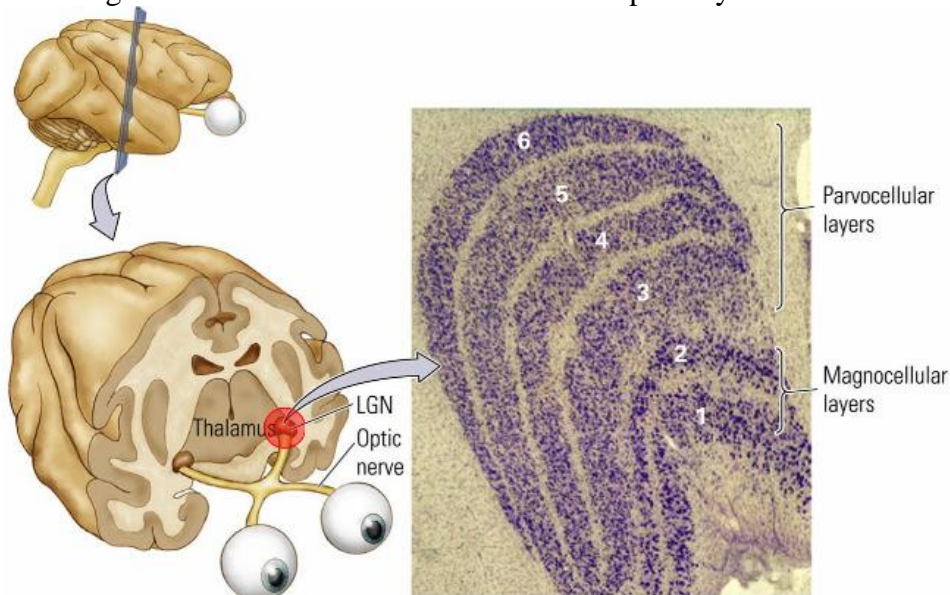
- The receptive fields of the ganglion cells are donut-shaped and respond to colour in the center-surround fashion that we discussed in our lecture on vision.
- These are colour-sensitive receptive fields that are responsive to yellow-blue and red-green, with one colour increasing the rate of firing of the ganglion cell if it strikes the middle portion of the donut, and decreasing the rate of firing if it strikes the outer ring of the donut.

- So, for example, this ganglion cell is excited if the colour red strikes its middle region or if green strikes the surrounding portion, but that same cell is inhibited if the opposite were true, with red striking the surrounding region or green reaching the middle portion. (See image below.)
- The strongest response is seen, when both conditions are true and you have red striking the middle and green on the surround.

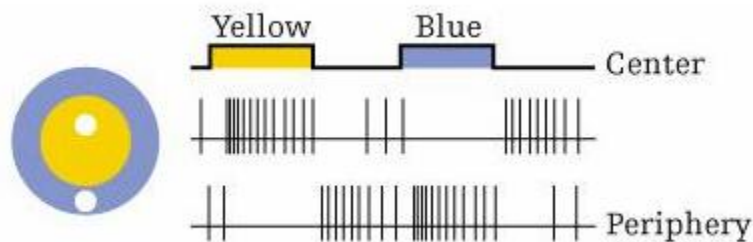


Colour Processing in the LGN:

- From the retinal ganglion cells, colour information is sent to the lateral geniculate nucleus, or the LGN.
- Recall that the LGN has six layers, with 2 layers, called the magnocellular layers, processing form, movement, and depth.
- The remaining four layers, called the parvocellular layers, are where colour information from the red and green cones and information about fine detail is processed.
- In addition to these six layers, there is also a sublayer to each of the six layers, called the koniocellular sublayers. These sublayers are especially important for transmitting information from the blue cones to the primary visual cortex.

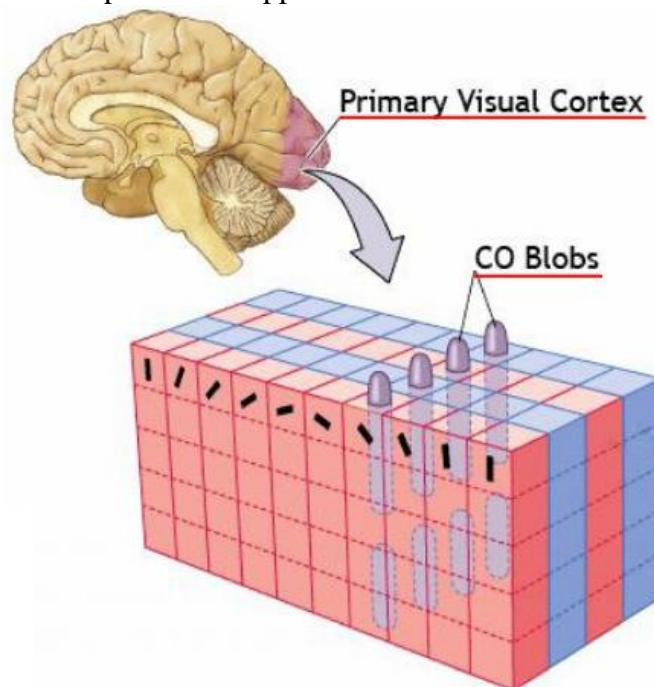


- Evidence from single- cell recordings in the LGN of monkeys shows that cells here still respond in the same opponent fashion that the retinal ganglion cells do. So, if a researcher presented the monkey with a spot of yellow light onto the center of the receptive field or blue in the periphery, the LGN cell would fire more rapidly, but if the monkey was shown a blue light in the center or a yellow light in the surround, that same cell would now fire less than it did at baseline. (See image below.)

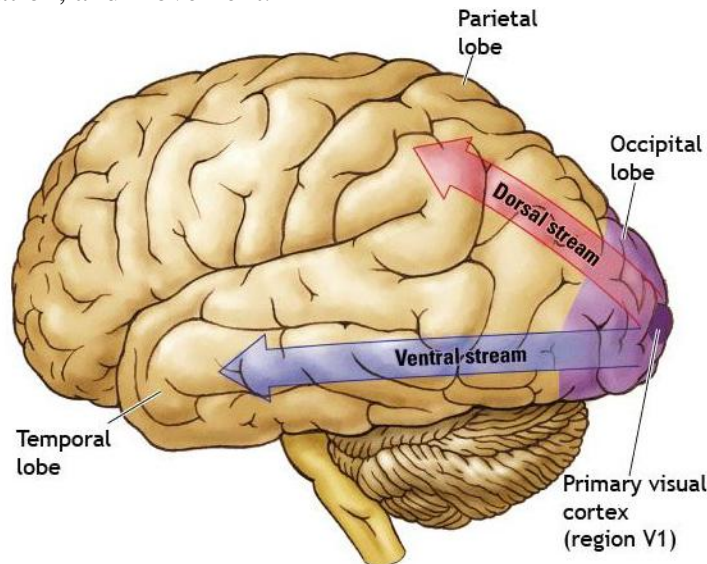


CO Blobs and the Visual Cortex:

- From the four parvocellular layers of the LGN, as well as the koniocellular sublayers, colour information is passed on to the primary visual cortex in the occipital lobe at the back of the brain.
- In 1984, Livingstone and Hubel discovered what are called cytochrome oxidase blobs, also known as CO blobs, which are regions of cytochrome oxidase containing neurons that are distributed at roughly equal intervals over the primary visual cortex.
- The neurons in the CO blob respond exclusively to colour information, and show little or no response to shape, orientation, or movement.
- These CO blobs look oval in shape if you're looking at them from the surface of the primary visual cortex.
- Depth wise, they're arranged in columns that project down into layers 2 and 3 (and less so into layers 5 and 6) of the primary visual cortex. Again, the neurons in the CO blobs respond in an opponent fashion.



- Recordings from neurons in the CO blobs show that they have a roughly donut-shaped receptive field, where one colour presented to the centre of the receptive field increases the firing rate of the cell and the complementary colour decreases the rate.
- Colour information is then passed from the CO blobs of the primary visual cortex to the visual association areas or the extrastriate cortex, where it is analyzed further in the ventral stream.
- Here, information from colour is finally integrated with other information, like shape, orientation, and movement.



Colour Blindness:

Introduction:

- Many people who are colour blind don't know it until they realize that others see colours that they don't. They have learned to label grass as 'green' and ketchup as 'red', and assume that everyone else sees these items to be the same colour just as they do.
- Then one day, they may comment on someone's grey pants, only to have a friend point out that the pants are in fact green.
- If we can't be sure that others perceive colours in the same manner as we do, it seems even more difficult to figure out how exactly a colour blind person perceives the world. However a unique case study was conducted on a woman who was colour blind in only one eye, with her other eye being normal.

Case Study:

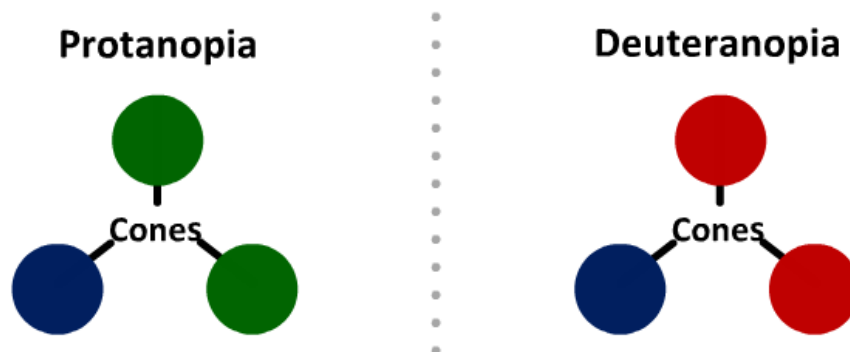
- So she was shown wavelengths of light between 400 nm and 700 nm to her colour blind eye, and asked to match the colour that she perceived to a range of colours that she looked at with her normal eye.
- For the colour blind eye, all wavelengths between 500 nm and 700 nm appeared to be the same shade of yellow, or roughly 570 nm, in her normal eye.
- When her colour blind eye was presented with wavelengths between 400 nm and 500 nm, her normal eye perceived them as the same bluish colour of around 470 nm.
- So this woman was red-green colour blind in one eye and only able to see blues, yellow, and shades of grey.

Types of Colour Blindness:

- Although colour blindness is sometimes caused by an injury to the colour detecting regions of the visual cortex by a stroke, tumour, or head trauma, it is usually an inherited condition.
- We will focus on the genetic case since this is much more frequent, affecting one in 20 males, though much less so for females.
- Total colour blindness, where a person sees everything in shades of grey, is very rare. Usually, if a person is colour blind, they are unable to see specific colours, but they can still see some colours.
- Most often, a person with colour blindness will see red and green as greys, and they are commonly referred to as red-green colour blind.
- Very rarely do you find someone who will see yellow and blue as greys.
- There are three types of colour blindness that we're going to go over: **protanopia**, **deutanopia**, and **tritanopia**.

Protanopia and Deutanopia:

- Both protanopia and deutanopia occur when someone confuses red and green, and they see the world in shades of yellows, blues, and greys. These people have normal visual acuity, suggesting that their problem is not that they are lacking a number of cones, but that they are lacking the colour photo pigment in the cones.
- People with protanopia have red cones that are filled with the photo pigments for green, while people with deutanopia have green cones that are filled with the photo pigment for red.
- Either way, these individuals do not have any way of responding differently to red and green.
- If, however, there is even a slight difference in the way each cone's photo pigment absorbs light, that person will be able to tell green from red, even if these colours would look different than the reds or greens than a person with normal colour vision would see. (See image below.)



Tritanopia:

- Tritanopia involves the yellow-blue system, and occurs very rarely in less than one in 10,000 individuals.
- Since the faulty gene for tritanopia is not carried on the X chromosome, it is equally prevalent in males and females. It is thought to occur because the blue cones, which are much less frequent in the retina to begin with, are either lacking or defective. So these people see the world in shades of reds, greens, and greys. To them, the sky looks bright green and a banana would look pink.