MSc Computer Games and Entertainment

Maths & Graphics Unit 2011/12

Lecturer: Gareth Edwards

Colour

Part 2: Evolution of Colour Vision

Acknowledgments

- Clive Maxfield and Alvin Brown
- Wikipedia.

Colour Blindness

- Before we proceed, this is probably a good time to note that several forms of colour blindness – which means the inability to distinguish certain colours or hues – are caused by deficiencies in one or more of the cone receptors.

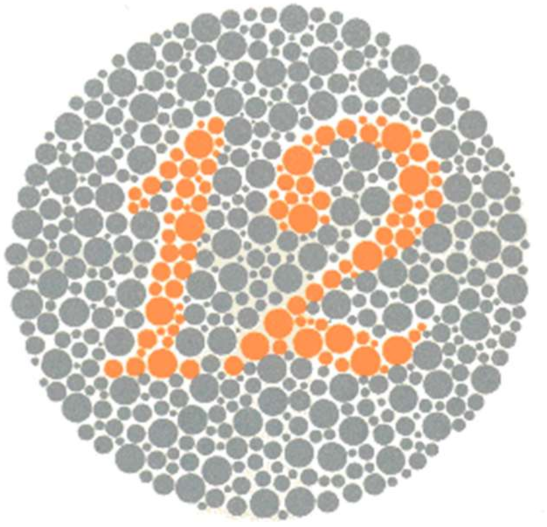
- Colour blindness (also known as "Dyschromatopsia") may also be referred to as "Daltonism," so-named after the English physicist John Dalton (1766-1844) who was one of the first to describe this condition, and who was himself affected (in addition to the purple and blue portions of the spectrum, he could perceive only one other colour – yellow).

- Most of us remember the tests the eye doctor gave us at high school involving cards containing images formed from large numbers of different sized circles of different colours.

- The idea was to determine if you could distinguish a number formed from circles with one selection of colours presented against a background of circles with another selection of colours.

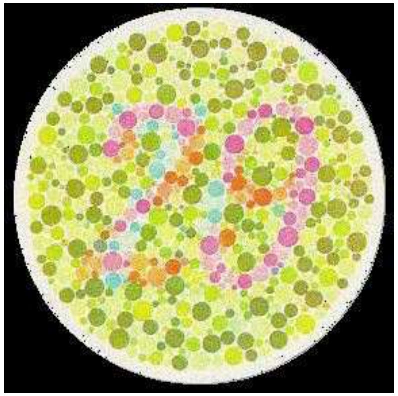
Colour Blindness

- Some websites presenting examples of this sort of test are the Ishihara Test for Colour Blindness, the Colour Blindness Self-Test, and Mike Bennett's Colour Vision Test pages.



- http://www.colour-blindness.com/colour-blindness-tests/ishihara-colour-test-plates/

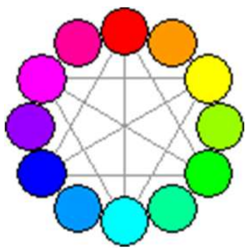
- ttp://www.angelo.edu/faculty/mdixon/HumanBiology/colorblind4.htm



Colour Blindness

- Also, for your interest, there is a really amazing web page on Colour Vision by Microsoft - **Can Colour-Blind Users See Your Site?**

- http://msdn.microsoft.com/en-us/library/ie/bb263953(v=vs.85).aspx



- The Vischeck website presents a tool called *Vischeck that simulates colour-blind vision and another tool called Daltonize that corrects* images for colour-blind viewers.

- http://www.vischeck.com/

Vischeck

Colour Blindness

- And yet another very clever tool is *Visolve from the folks at Ryobi System Solutions.*
- *This is special software that takes colours on a computer display that cannot be* discriminated by people with various forms of colour blindness and transforms them into colours that can be discriminated.
- In addition to a variety of transformations and filters, you can also instruct the software to apply different hatching patterns to different colours.
- http://www.ryobi-sol.co.jp/visolve/en/

Colour Blindness

- Last, but certainly not least, on May 21, 2007, an article on the Science Daily website discussed how gene therapy was used to Restore Cone Cells in blind mice.

- As reported in this article, scientists have used a harmless virus to deliver corrective genes to mice with a genetic impairment that robs them of vision.

- This discovery shows that it is possible to target and rescue cone cells – the most important cells for visual sharpness and colour vision in people.

- In the future, it may be possible to deliver gene therapies targeting a variety of visual problems – such as colour blindness – and degenerative diseases

The Evolution of Colour Vision

- We are primarily interested in following the evolutionary path – as it pertains to colour vision – from the dim-and-distant past to modern humans.

- There are many other paths for other creatures – such as insects – that we don't have the time to discuss here (having said this I will mention in passing the visual systems of a variety of creatures such as mantis shrimp, butterflies, fish, and birds).

The Evolution of Colour Vision

- Just to provide a sense of the time scale with which we're working, it's now generally accepted (check out the US Geological Survey website, for example) that the earth formed around 4.6 billion years ago give or take 100 million years or so (note that we're using the American interpretation of "billion" equating to "one thousand million").

The Evolution of Colour Vision

- The earliest forms of life – possibly based on self-reproducing RNA molecules – are thought to have originated somewhere around 4,000 million years ago (the Wikipedia entry for the Timeline of Evolution provides a useful starting point for this sort of thing).

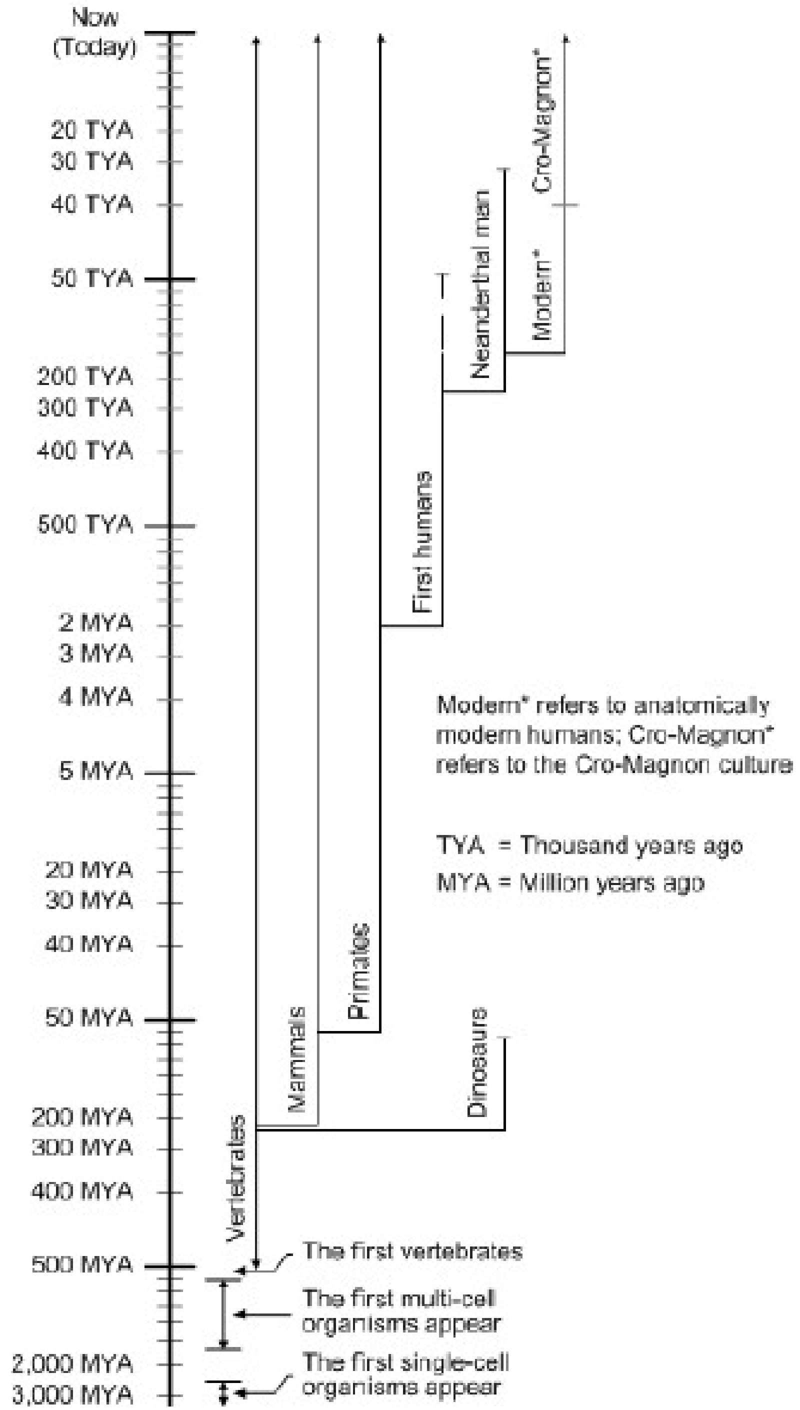
- Proto-cell-type organisms may have arisen as early as 3,900 million years ago, and the first real single cell-like organisms began to appear on the scene sometime between 3,500 and 2,800 million years ago (many folks think this was probably a good deal closer to the older age).

- These were followed by the first multi-cell organisms, which entered the stage sometime between 1,500 and 600 million years ago (recent findings are increasingly pushing us toward the earlier time).

The Evolution of Colour Vision

- Next, *vertebrates (animals with backbones and/or or spinal columns) started to evolve somewhere between 530 and 510 million years ago during the "Cambrian* Explosion" portion of the Cambrian Period.

- The first *tetrapod (an animal that has four limbs, along with hips and shoulders and fingers and toes) crawled out of the Earth's oceans some time between* 375 and 350 million years ago (this event probably occurred relatively soon after the "walking fish" called Tiktaalik roseae took the stage, which happened 375 million years ago in the late Devonian Period.)

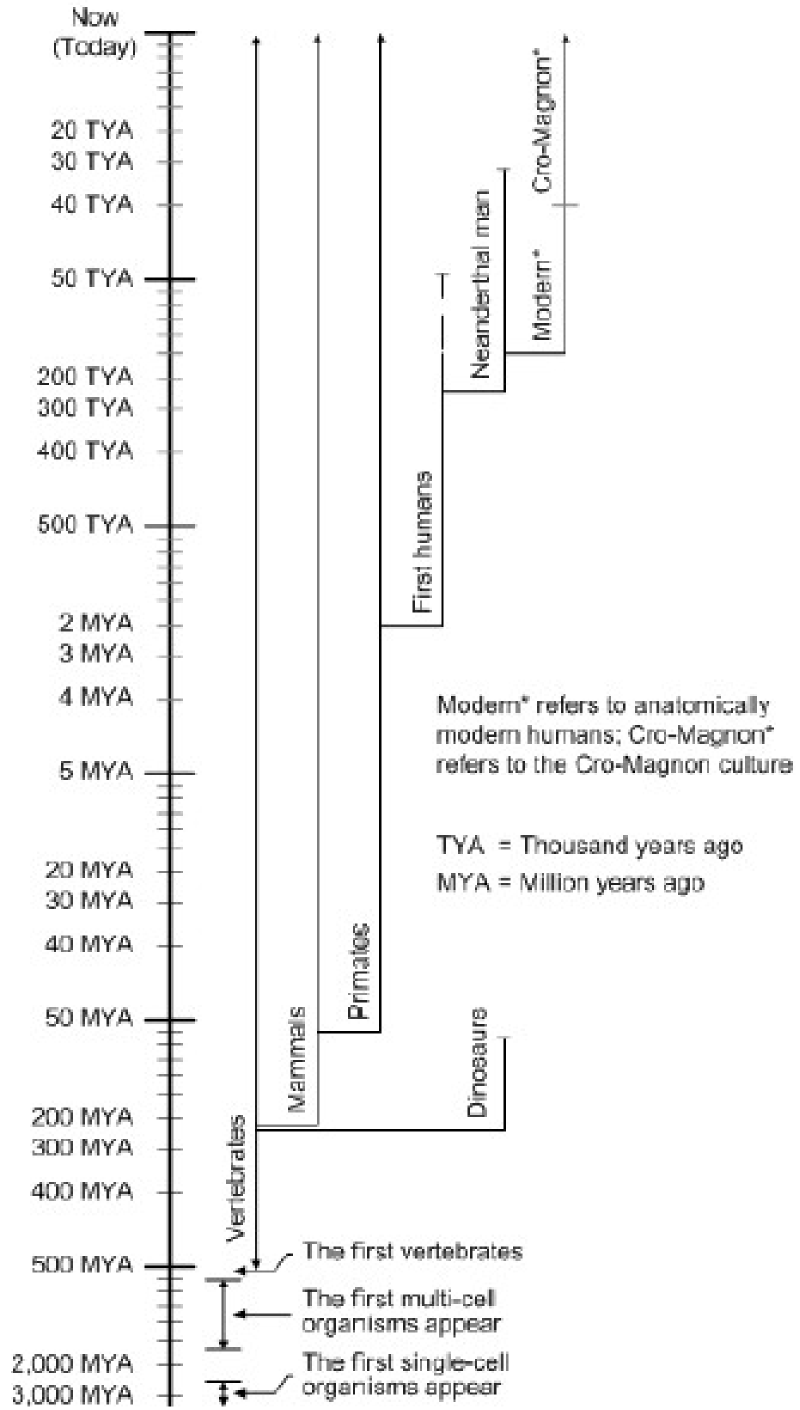


The Evolution of Colour Vision

- Observe that the vertical scale in the above illustration is *logarithmic.*

- *This provides a method for representing a large span of time while maintaining* resolution at the more recent end of the scale.

- Had we used a *linear scale in which 1 mm was used to represent a million years, for example, then our* chart would have been 5 meters long.



The Evolution of Colour Vision

- Even though they aren’t particularly relevant to our story, it would be remiss of us to omit the creatures we commonly think of as *dinosaurs, which were a group of* vertebrates that appeared during the Mesozoic Era (when I say *"...we commonly think of as..." I mean that we're talking about non-avian dinosaurs).*

- *These creatures* had a good run from late in the Triassic Period (about 225 million years ago) until the end of the Cretaceous Period (about 65 million years ago), at which point they exited the stage.

- Meanwhile, the first *mammals (which were small shrew-like animals) evolved in the Late Triassic and Early Jurassic Periods, some 208 million years ago (the term* "mammal" refers to the group of vertebrates having mammary glands, which females of the species use to produce milk to nourish their young).

The Evolution of Colour Vision

- The term *primate refers to the group of mammalian vertebrates that contains all of the species related to lemurs, monkeys, and apes (where "apes" includes humans).*

- Until relatively recently, it used to be thought that the evolution of the primates started in the early part of the Eocene Epoch (this epoch began around 55 million years ago and lasted for around 20 million years).

- However, even though it was only the size of a modern mouse, Purgatorius is arguably a primate – or at least a protoprimate – and this creature lived during the early Paleocene Epoch, so it's probably more accurate to say that primates began to evolve around 60 to 65 million years ago.

The Evolution of Colour Vision

- The first primates of the human genus (that is, to which the honorific "Homo" was applied) were Homo habilis.

- These were users of stone tools who took their turn on the stage from around 2.2 million years ago to 1.6 million years ago.

- The term *hominid used to be popular to describe all of the creatures in the human line since it* diverged from that of the chimpanzees, but the scientific community now favours the term *hominin for this purpose.*

The Evolution of Colour Vision

- Neanderthal man was on the scene from around 250,000 years ago until 30,000 years ago. (It used to be thought that Neanderthals were only on the scene from around 150,000 to 35,000 years ago, but ongoing discoveries keep on pushing the boundaries out in both directions.)

- Meanwhile, the generally accepted date for the arrival of anatomically modern humans is around 100,000 years ago. In this case, however, discoveries by Professor Frank Brown, Dean of the College of Mines and Earth Sciences at the University of Utah, suggest that this could have occurred much earlier – perhaps even as early as 195,000 years ago.

- Last but not least (for the purpose of these discussions), the first appearance of the Cro-Magnon culture occurred around 40,000 years ago.

- This leaves us with the current peak in human evolution, which would be me (and you, I suppose).

The Evolution of Colour Vision

- So, how does the evolution of colour vision map onto the above? Ah, ha! That's the million dollar question, isn’t it?

- Until relatively recently, many folks worked under the incorrect assumption that the path from the original life forms to humans was largely one of monotonic improvement.

- In the case of colour vision, for example, many folks assumed that the evolutionary path started with black-and-white vision and progressed first to dichromatic colour vision and then to trichromatic colour vision.

- However, more recent developments in our understanding of the paleontological record – coupled with new tools and techniques in molecular biology – have revealed that the picture is far more complex.

The Evolution of Colour Vision

- Let's take things one step at a time. First, even as a "thought experiment," it would seem unlikely that rod cells preceded the earliest cone cells.

- This is because rod cells are so much more sensitive to light than are cone cells, which makes it logical that at least one type of cone cell evolved first. In fact, several lines of evidence now point to the fact that rod cells are derived from cone cells.

- So when did the first cone cell evolve? Well, the ancestor of all animals with bilateral symmetry may have evolved anywhere from 550 million to 1,000 million years ago, so this is the age range during which photoreceptors first evolved.

The Evolution of Colour Vision

- Furthermore, photoreceptors may have evolved twice or even more times, although this was probably from the same precursor cell population.

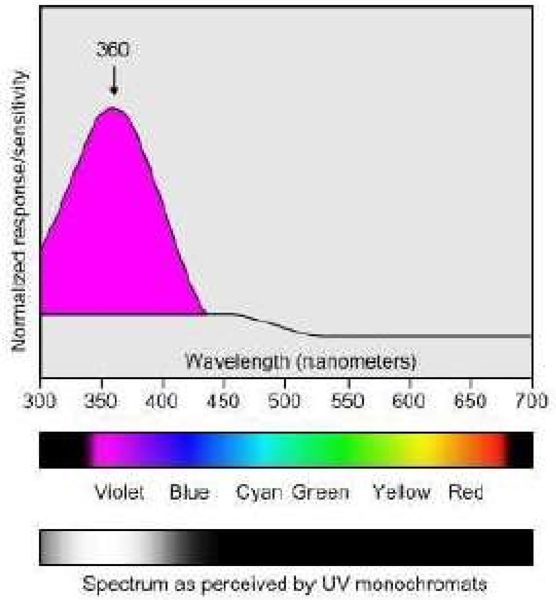
- Either that, or there was a very early split into two very different types after the emergence of the first photoreceptor.

- Note that we aren't talking about rods and cones here; instead we're referring to the difference between *ciliated photoreceptors (like the ones we use for vision) and rhabdomeric photoreceptors (like the ones arthropods use for vision).*

The Evolution of Colour Vision

- Be this is it may, at some stage along the path – say 800 million years ago on a Wednesday afternoon following a small lunch – some multi-cell organisms managed to develop photoreceptors that gave them the ability to detect and respond to some form of light.

- Purely for the sake of discussion, let's begin by assuming that these first photoreceptors were cones that were primarily sensitive to ultraviolet (UV) light.

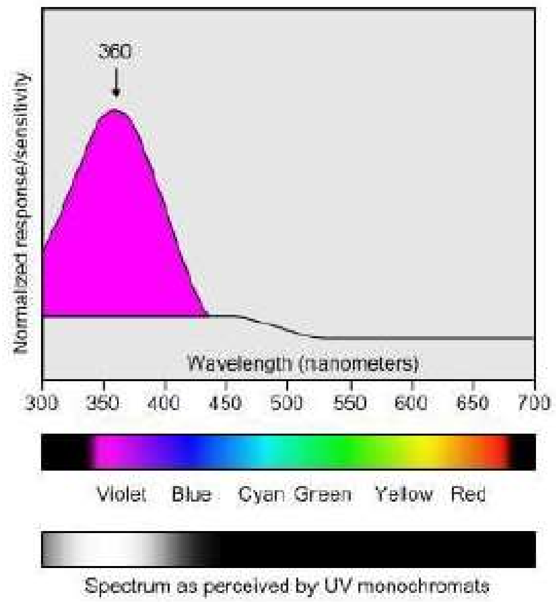


Evolution of visual systems: monochromats with UV cones

The Evolution of Colour Vision

- Observe that the spectrum as perceived by these creatures would have been monochromatic, which – in this context – means *"having or appearing to have only one colour." The point is that they would have had the ability to perceive only differences in the intensity of the band of wavelengths to which these cones were sensitive.*

- *This* is why we've represented their "perceived" spectrum as being gradations of black-and-white.

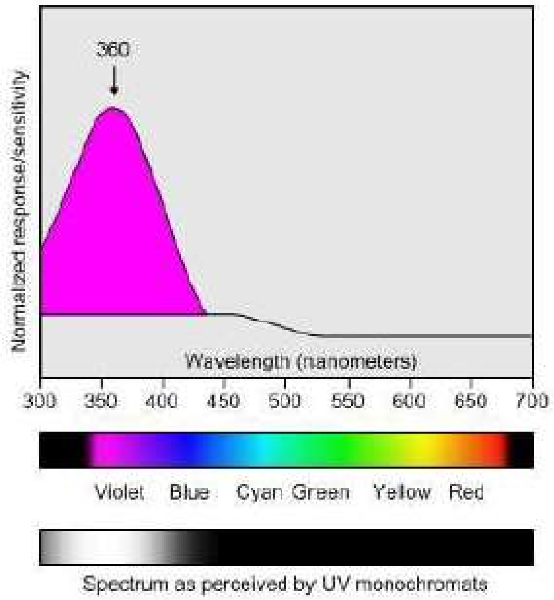


Evolution of visual systems: monochromats with UV cones

The Evolution of Colour Vision

- Also, the fact that these creatures had only one type of cone means that they would be classified as *monochromats.*

- *Note that the 360 nanometer peak sensitivity associated with these cone is an educated guess based on the capabilities of* existing life forms.



Evolution of visual systems: monochromats with UV cones

The Evolution of Colour Vision

- It's important to remember that the idea that the first cones were primarily sensitive to ultraviolet light is purely conjectural (an alternative scenario is presented a little later in this topic).

- So why would ultraviolet light make a good candidate?

- Well, ultraviolet radiation is more energetic than what we now consider to be the visible portion of the spectrum, which would make it "easier" for a biological system to evolve to detect it.

The Evolution of Colour Vision

- Another possibility is that the first photoreceptors were used for *negative phototaxis (where "phototaxis" refers to the influence of light on the movements of primitive* organisms). Ultraviolet light is harmful (this is what gives us skin cancer).

- Early in the earth's history, the ozone layer didn't protect us like it does now. Initially this may not have presented too much of a problem, because the first animals probably lived in water deep enough to protect them from harmful radiation.

- As animals began to come closer to the surface, however, they faced new challenges, including slow death caused by overexposure to ultraviolet radiation.

- Thus, the ability to detect ultraviolet and move away from it would have provided an evolutionary advantage

The Evolution of Colour Vision

- Before we proceed, this is probably a good time to briefly consider the way in which cones are actually formed and the way in which they perform their magic.

- One way to think about this is to visualize an "antenna" formed from a molecule of *retinal, which is a derivative of vitamin A (our bodies produce vitamin A from the beta carotene* found in many of the foods we eat, including – of course – carrots).

- The role of the retinal molecule is to convert incoming light rays (photons) into corresponding electrical signals that can be processed by other structures in the eye and – ultimately – by the brain.

- Each cone is formed from a large number of these "antennas“ (say 100 million or more).

The Evolution of Colour Vision

- Each retinal molecule is surrounded by an associated "pigment" molecule.

- The purpose of this pigment molecule – which is actually an incarnation of the protein *iodopsin – is to "tune" the sensitivity of the cone to a particular band of frequencies.*

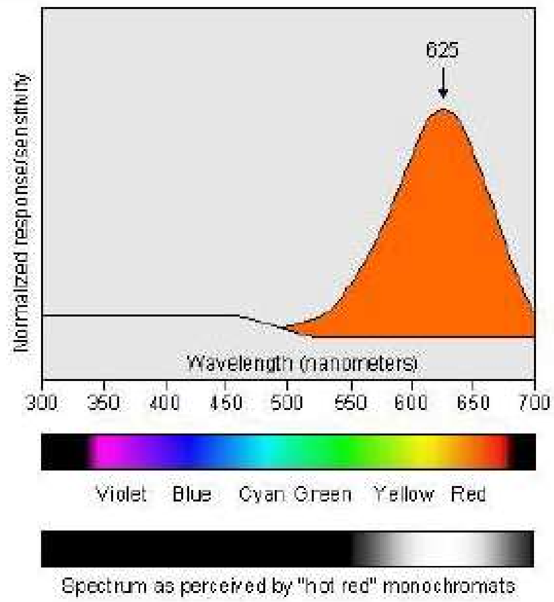
- *The pigment molecules for the ultraviolet cones (introduced above) and the blue,* yellow, orange-red, blue-green, and yellow-green cones (discussed below) are all formed from different "flavors" of iodopsin – only a few of the amino acids located near the site where the iodopsin binds to the retinal molecule are varied in each of the proteins.

- Collectively, these pigment molecules are referred to as the *opsins.*

The Evolution of Colour Vision

- Now, remember that the idea that UV cones came first is purely speculative. In fact, here's another hypothesis that, given the data, is equally plausible.

- One of the things we consider to be "noise" in vision is the thermal isomerization of pigments (where *isomerization is what normally happens when a photopigment absorbs a* photon of light).



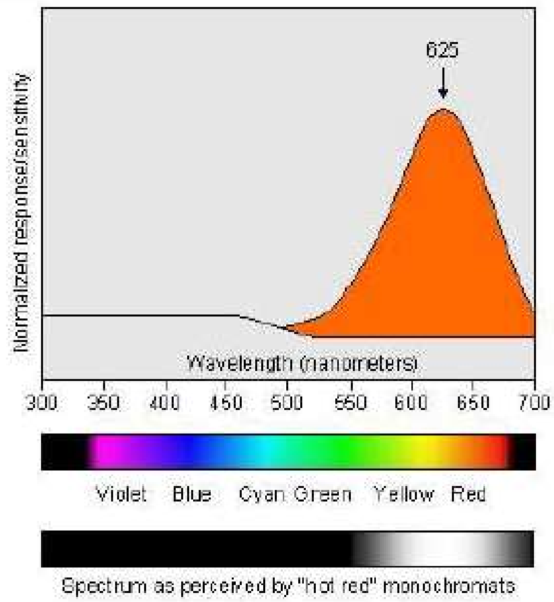
Evolution of visual systems: monochromats with orange-red cones

The Evolution of Colour Vision

- This can also occur when the pigment gets jostled or absorbs a very long-wavelength photon.

- There are more of these long-wavelength photons and more jostling at higher temperatures, so photoreceptor signals are noisier at higher temperatures.

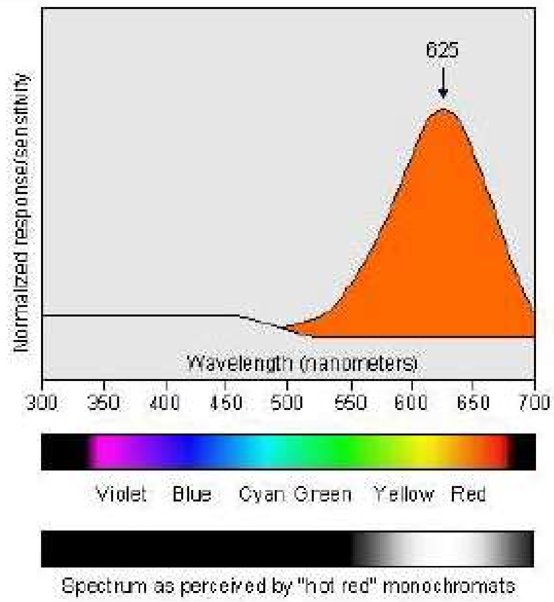
- But one cell's trash is another cell's treasure. Thus, it may very well be that the first photoreceptors were not visual at all.



Evolution of visual systems: monochromats with orange-red cones

The Evolution of Colour Vision

- It could be that the first photoreceptor was a "temperature sensor."
- Therma isomerizations are more likely in pigments with peak absorptions at longer wavelengths, so the first photoreceptor may have been an orange-red cone with a peak sensitivity of say 625 nanometers as opposed to an ultraviolet cone with a peak sensitivity of 360 nanometers.
- The 625 nanometer peak sensitivity associated with the orange-red cone is an educated guess based on existing life forms.



Evolution of visual systems: monochromats with orange-red cones

The Evolution of Colour Vision

- So the UV cone may have been first, or the orange-red cone, or even one of the blue, green, or yellow cones discussed below.

- Any of these scenarios are consistent with existing data.

- The point is that having even a rudimentary form of vision obviously conveyed a tremendous evolutionary advantage, such as the ability to sneak up on your visionless contemporaries and eat them!

The Evolution of Colour Vision

- On the downside, having only only one type of cone cell means that you're limited to seeing only a small portion of the electromagnetic spectrum.
- If you can extend your visual capabilities to encompass additional portions of the spectrum, this will obviously convey an even greater evolutionary advantage.
- Thus, during the course of the next several hundred million years (sometime before 450 million years ago), our ancestors evolved four different types of cone pigments.
- When we use the term "ancestors" in this context, we are referring to the creatures that were to evolve into vertebrates, dinosaurs, mammals, primates and – ultimately – humans.

The Evolution of Colour Vision

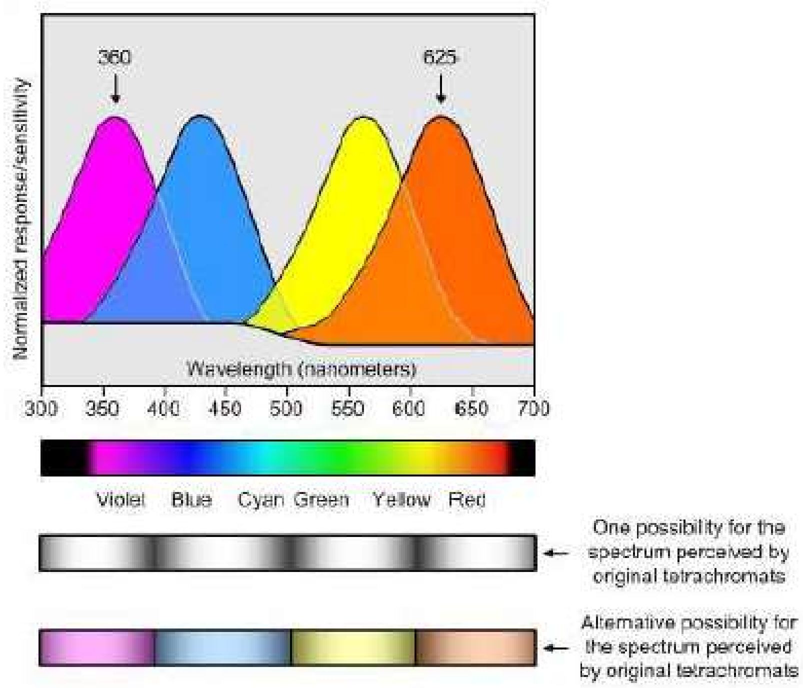
- How good is this date?

- Well, we know that diversification of ciliary photoreceptors into four spectral cone types occurred some time before the emergence of the most recent common ancestor of parakeets and goldfish, and this is generally taken to be around 450 million years ago.

The Evolution of Colour Vision

- Creatures with only two types of cones are called *dichromats; those with three types of cones are called trichromats; and those with four types of cones are called tetrachromats.*

- *Observe that we've illustrated the spectrum as perceived by these early creatures in two different ways.*

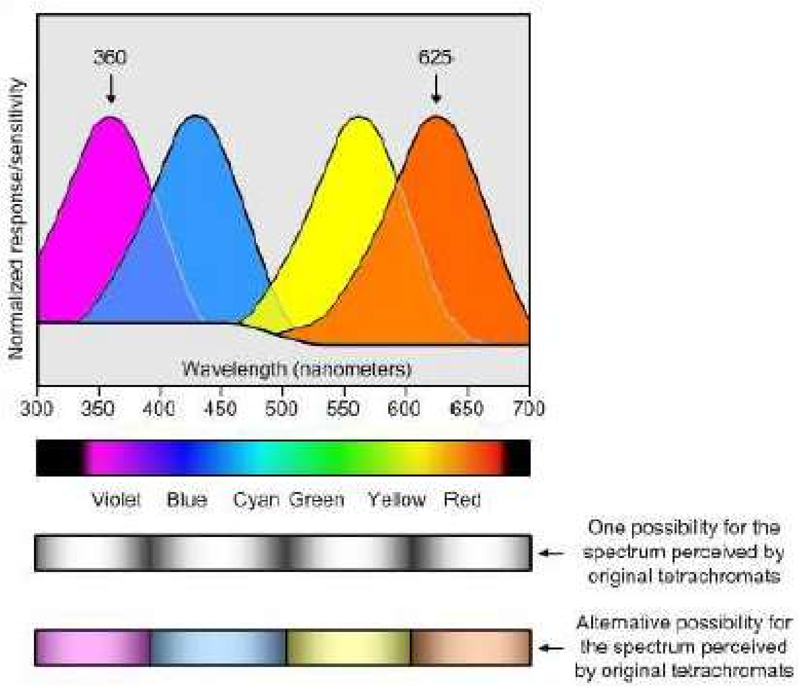


Evolution of visual systems: original tetrachromats (UV, blue, yellow, and orange/red cones)

The Evolution of Colour Vision

- The reason for this is that, at the time the second type of cone cell evolved, it seems likely that the signals being output from both types of cone cells were fed directly to the creature's nervous system and/or brain.

- One representation shows multiple bands of black-and-white intensity.

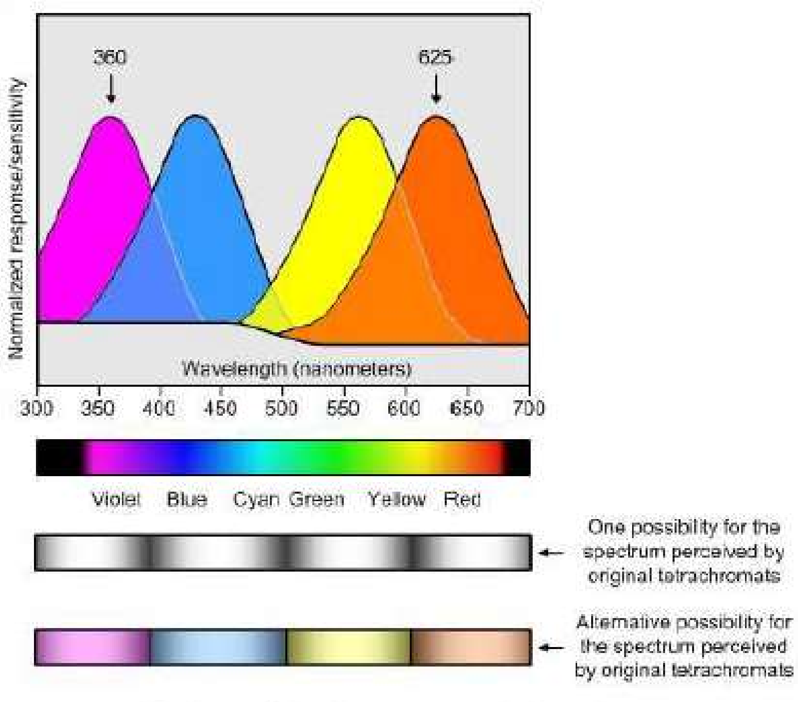


Evolution of visual systems: original tetrachromats
(UV, blue, yellow, and orange/red cones)

The Evolution of Colour Vision

- That is, there is a strong possibility that the "comparator" cells we now use to compare the relative outputs from different cone cells had not yet evolved in those early years.

- Similarly, it's more than possible that the "comparator" cells were still not present when the third and fourth cone cells evolved.



Evolution of visual systems: original tetrachromats (UV, blue, yellow, and orange/red cones)

The Evolution of Colour Vision

- Having said this, it may be that these monochromatic representations paint a somewhat bleaker picture than was actually the case (again, you'll have to forgive the pun).

- This is because – even without the presence of special "comparator" cells – each type of cone cell would respond to different intensities in its own portion of the spectrum.

- For this reason, perhaps we should visualize the spectrum perceived by these creatures as being more like the "alternate possibility" portion of the preceding illustration.

- And, of course, there is always the possibility that these creatures *had evolved the special "comparator" cells used to compare the relative outputs from* different cone cells, in which case they might have perceived the spectrum in a similar manner to the way we do now.

The Evolution of Colour Vision

- As clever as they are, one problem with cone cells is that they function only in bright light. For this reason, rod cells appeared at some stage in the game.

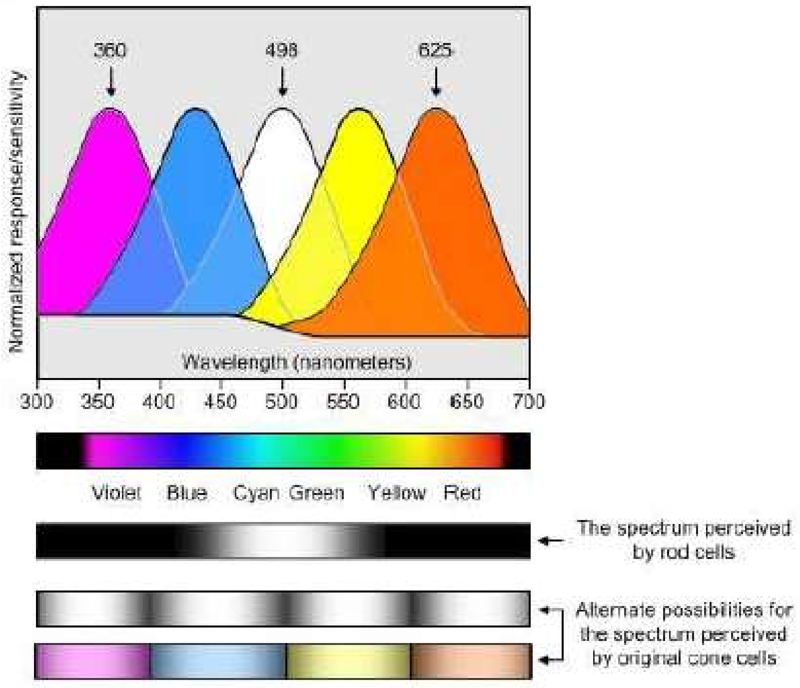
- As we discussed in the previous topic, rod cells are much more sensitive than cone cells and they give their owners the ability to see at night (assuming some level of moonlight and/or starlight).

- We can visualize rod cells as having large numbers of "antennas" (say 100 million) formed from the same retinal molecule we find in cones.

- In this case, however, the retinal is surrounded by a pigment molecule formed from the protein *rhodopsin.*

The Evolution of Colour Vision

- We aren't sure exactly when rod cells appeared on the scene, but our rods (the ones that eventually ended up in human eyes) probably evolved after the split between jawless and jawed vertebrates; let's say somewhere around 450 to 500 million years ago just to give round numbers. As we mentioned in the previous topic, some references state that the peak sensitivity of rod cells is close to the main spectral component of moonlight.

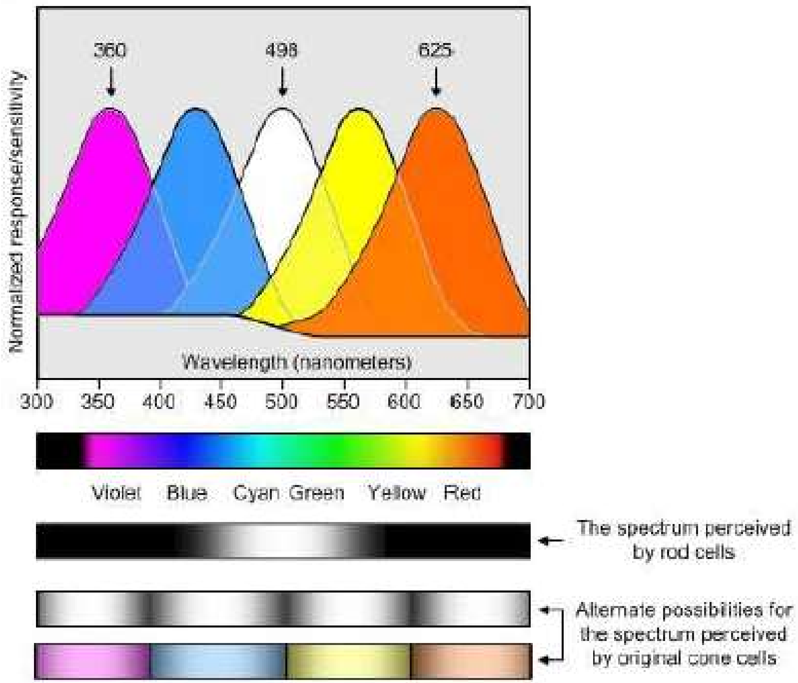


Evolution of visual systems: original tetrachromats
(UV, blue, yellow, and orange/red cones – plus rod cells)

The Evolution of Colour Vision

- Based on this, some folks hypothesize that rod cells first evolved in nocturnal animals.

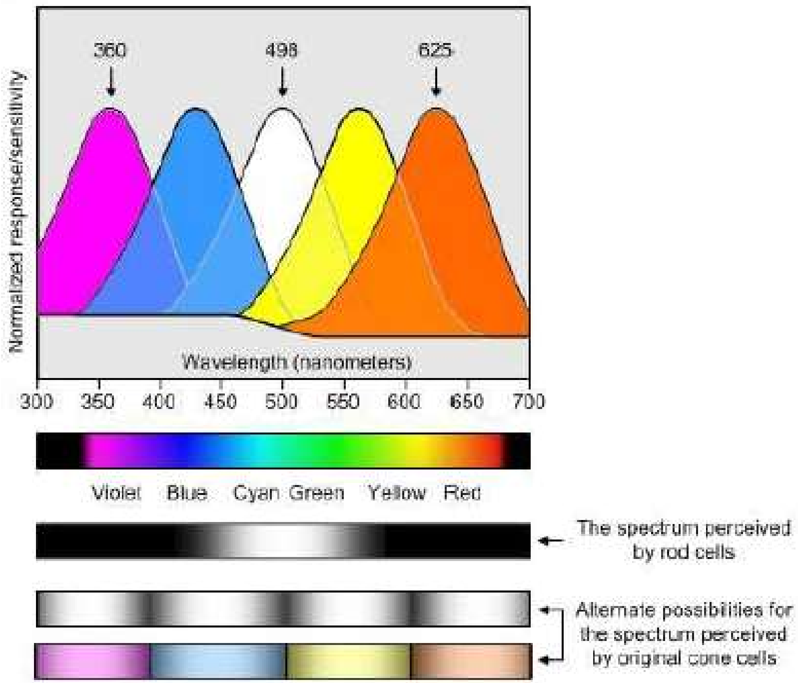
- However, we also noted that – in fact – the peak absorption of rod cells (498 nm) is not particularly close to the main spectral component of moonlight, which actually occurs at anywhere between 548nm and 575nm depending on your source of data.



Evolution of visual systems: original tetrachromats (UV, blue, yellow, and orange/red cones – plus rod cells)

The Evolution of Colour Vision

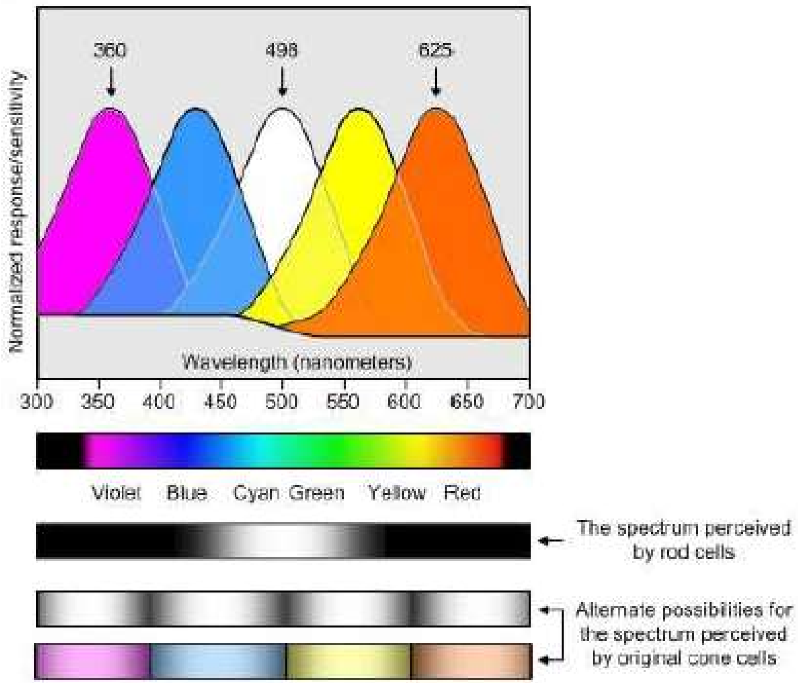
- In reality, we really don't know why rod cells peak where they do. In a classic paper published in the *Quarterly Review o f Biology back in 1990, author Tim Goldsmith* goes through several possible explanations for the position of the peak of vertebrate rod pigments (virtually all such pigments have a peak near 500nm in terrestrial animals).



Evolution of visual systems: original tetrachromats (UV, blue, yellow, and orange/red cones – plus rod cells)

The Evolution of Colour Vision

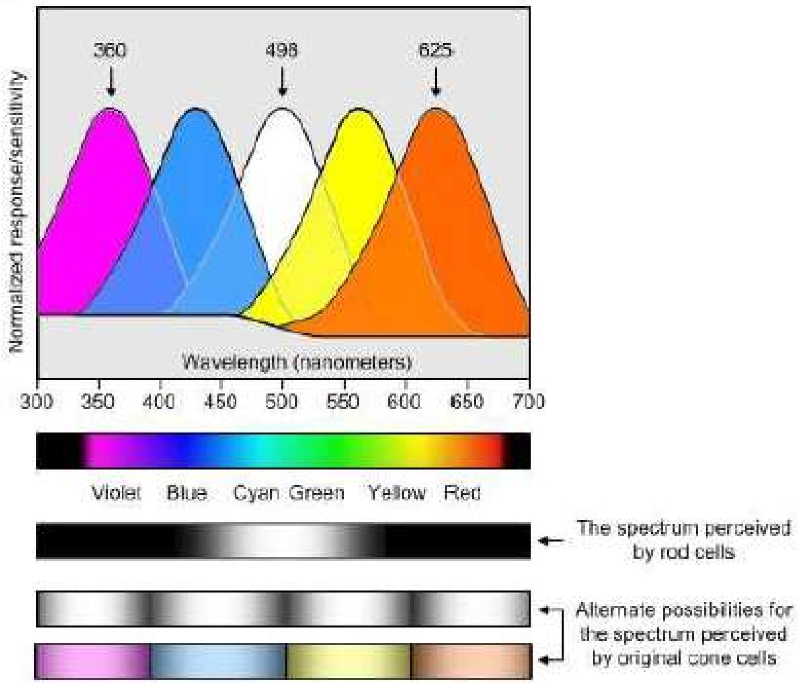
- The bottom line is that Goldsmith found none of the common explanations – including any relationship to the main spectral component of moonlight – to be plausible.



Evolution of visual systems: original tetrachromats
(UV, blue, yellow, and orange/red cones – plus rod cells)

The Evolution of Colour Vision

- Now, after pondering the previous illustration for a while, you are probably saying to yourself: *"Just a moment; as rod cells primarily respond to the wavelengths we now regard as being in the cyan-green portion of the spectrum, why would they not perceive some form of colour, and therefore why would we not class these creatures as being pentachromats?"*



Evolution of visual systems: original tetrachromats
(UV, blue, yellow, and orange/red cones – plus rod cells)

The Evolution of Colour Vision

Well, there are a number of answers to this as follows:

1. All of our previous cone-and-rod response curve illustrations have sported the words *"Normalized response/sensitivity" on the vertical axis. In simple terms, this* means that we've artificially drawn the curves such that they have the same maximum height.

- As we noted earlier, however, rod cells are MUCH more sensitive than cone cells. The next illustration – which is NOT to scale – is intended to provide a "feel" for this difference in sensitivity.

- The bottom line here is that rods and cones simply don’t play together in the same lighting conditions.

The Evolution of Colour Vision

- Cones require bright light to function, but rods are saturated in a bright light environment and aren’t in a position to generate any useful data.

- By comparison, in the dim lighting conditions when rods some into their own, cones shut down and provide little or no useful information.

2. In the case of modern animals (and we are probably safe in assuming that this was also the case with the creatures of yesteryear), the only information used from rod cells is intensity, which is passed through the eye's luminosity channels; that is, signals from rod cells do not make any contribution to the eye's color channels.

The Evolution of Colour Vision

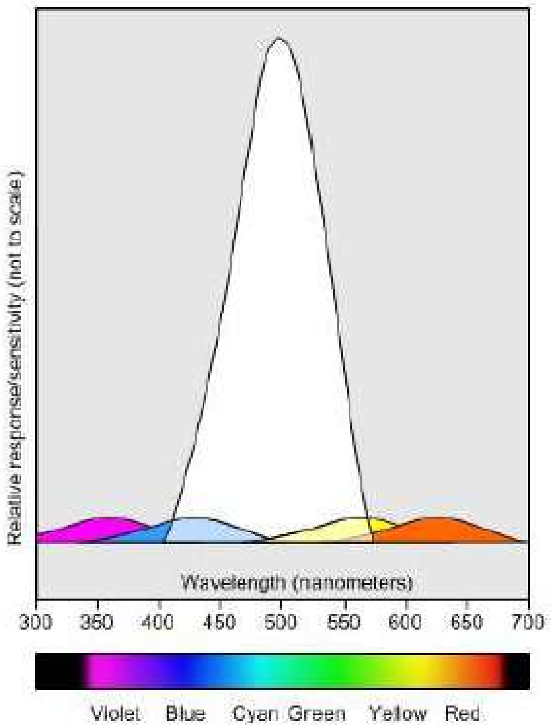
3. The terms *pentachromat, tetrachromat, trichromat, and dichromat are generally associated with having five, four, three, or two types of cone cells, respectively.*

- Similarly, creatures like Owl Monkeys that have only one type of cone cell (along with their rod cells) are known as *monochromats (as the only nocturnal* monkeys, Owl Monkeys are also known as "Night Monkeys").

- Furthermore, in the case of modern creatures like the skate (small cousins of the giant rays that have roamed the earth's oceans for around 400 million years) that have only rod cells and no cone cells – and in the case of humans whose cone cells don't function – the term *rod monochromat is used to distinguish this type of monochromat from creatures sporting only a single type of cone cell.*

The Evolution of Colour Vision

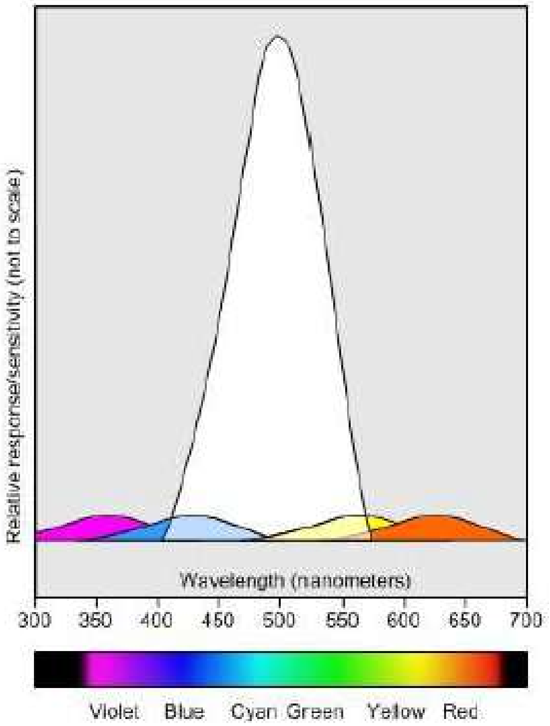
- Sad to relate, however, sometime between 310 and 125 million years ago our ancestors lost first one and then two of these pigments. We don't know exactly when or why, although one possibility is because these creatures became nocturnal.



Evolution of visual systems: original tetrachromats plus rod cells
(four types of cone cells plus rod cells – rod cells are much more sensitive)

The Evolution of Colour Vision

- Sad to relate, however, sometime between 310 and 125 million years ago our ancestors lost first one and then two of these pigments. We don't know exactly when or why, although one possibility is because these creatures became nocturnal.



Evolution of visual systems: original tetrachromats plus rod cells
(four types of cone cells plus rod cells – rod cells are much more sensitive)

The Evolution of Colour Vision

- So, how did we arrive at the dates noted in the preceding paragraph.

- Well, the first loss had to occur after the divergence between mammals and reptiles, which is generally taken to have occurred somewhere between 288 and 338 million years (we averaged and rounded this out to 310 million years ago).

- Next, all living mammals are divided into three groups: *monotremes (those who lay eggs), placentals (those who give birth to live and more mature young), and marsupials (those who give birth* to live, less mature young that they subsequently nurse in pouches).

- The point is that we also know that the first cone loss had to have occurred before the split between placentals and marsupials, which is thought to have been some time in the range of 130 to 175 million years ago.

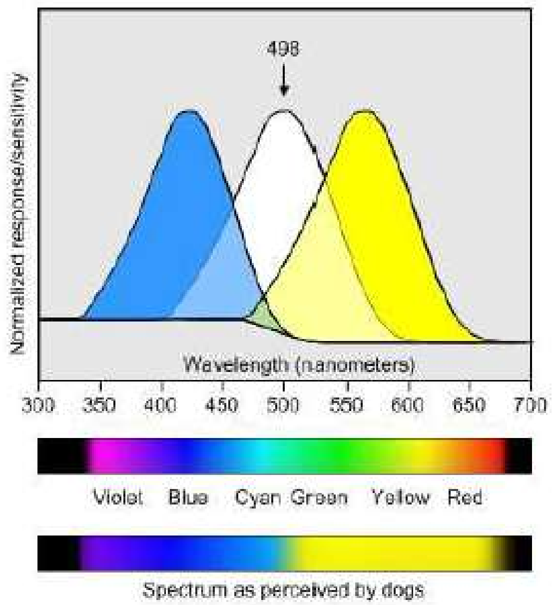
The Evolution of Colour Vision

- The earliest known placental mammal is Eomaia scansoria, while the most primitive and oldest known relative of all marsupial mammals is Sinodelphys szalayi.
- Both of these creatures lived around 125 million years ago during the early Cretaceous period.
- The second cone loss most likely occurred shortly after the marsupial/placental split, which occurred prior to the emergence of the most recent common ancestor of all placentals.
- The most recent common ancestor of all placental mammals appears to have had only two cone pigments. Creatures that still use this system – such as dogs – are known as dichromats.

The Evolution of Colour Vision

- Also, at some stage along the way, creatures evolved the "comparator" cells in their eyes that allowed them to compare the output signals from different cone cells and to perceive the results as being a range of different colors.

- This means that modern dichromats like dogs probably enjoy a far richer visual experience than did their antediluvian counterparts.

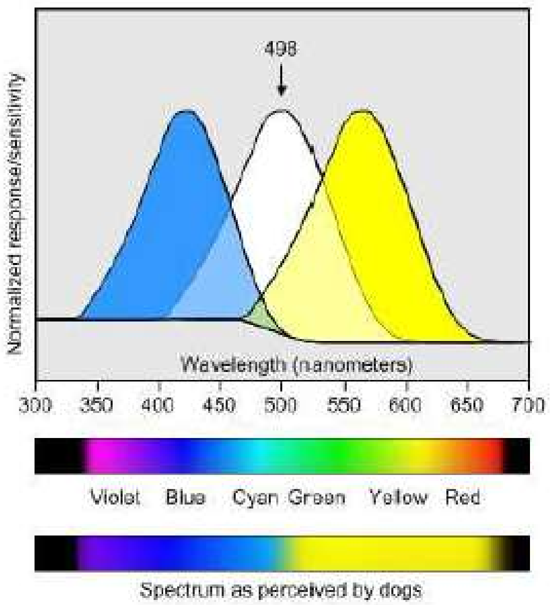


Evolution of visual systems: modern mammalian dichromats (blue and yellow cones – plus rod cells)

The Evolution of Colour Vision

- Sometime between 45 and 30 million years ago, the primates that were to evolve into humans "split" their yellow cones into two new types: blue-green and yellow-green.

- Actually, the situation with regard to primates is complicated because the majority of New World monkeys are so unusual.

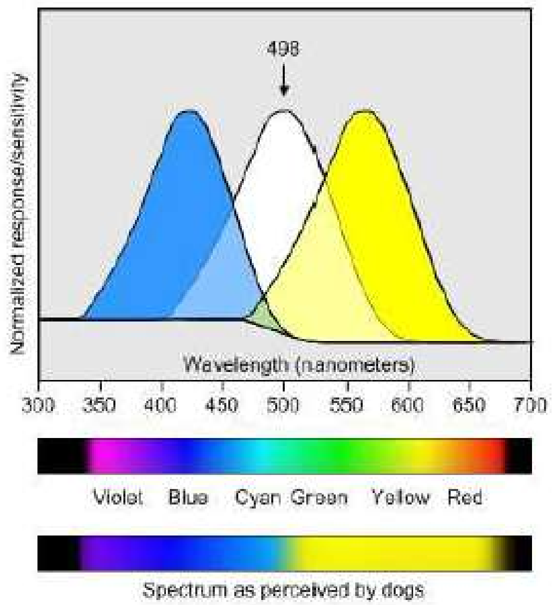


Evolution of visual systems: modern mammalian dichromats (blue and yellow cones – plus rod cells)

The Evolution of Colour Vision

- But sticking with the lineage to us, it's almost certainly true that the duplication event that gave us back a third photopigment occurred shortly after the split between New and Old world monkeys

- That would have been some time after Eosimias, which was an early primate that lived about 40-45 million years ago in China.



Evolution of visual systems: modern mammalian dichromats (blue and yellow cones – plus rod cells)

The Evolution of Colour Vision

- Furthermore, analysis of the skull bones of a bunch of primates suggests that the cone split occurred some time around the appearance of **Aegyptopithecus zeuxis.**

- Such analysis involves comparing fossil skulls of ancient creatures with those of modern animals whose visual ability we know and understand, and using any similarities or differences as the basis to hypothesize different evolutionary scenarios.

- Also known as the *Dawn Ape, Aegyptopithecus was a small, tree-dwelling, fruiteating* animal that lived some 35 to 33 million years ago in the early part of the Oligocene epoch.

- So, taking all of this into account, 34 million years ago is probably a good estimate for the time of the cone split.

The Evolution of Colour Vision

- Last but not least, we also have the "comparator" cells that allow us to use these cones to perceive the entire visual spectrum. This leaves us in our current situation in which normal humans have three types of cones and are therefore known as *trichromats.*

The Evolution of Colour Vision

- And there you have it!

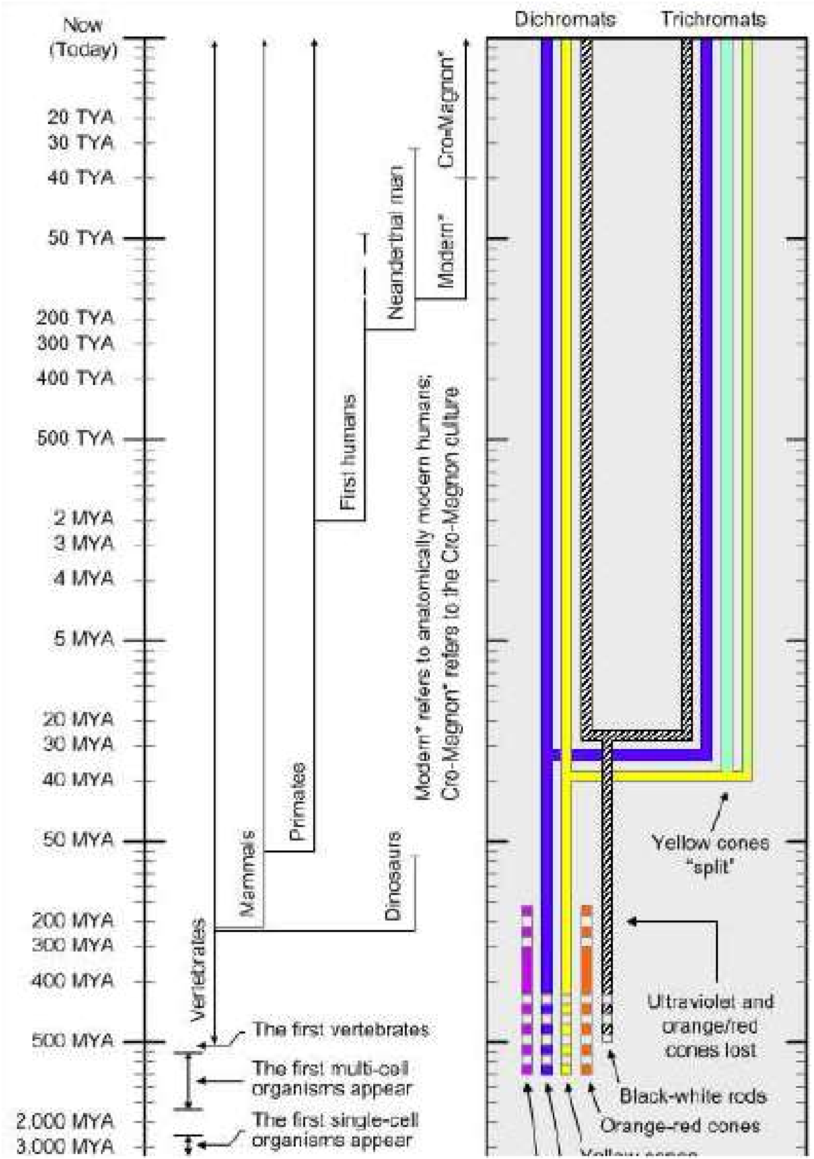
- As you can see, getting to our present state of colour vision has been something of a roller coaster ride, but the final results are rather spectacular, aren't they?

- Having said this, different creatures have evolved their visual systems in different ways, and – as we'll discover in the next topic on Tetrachromats, Pentachromats, Etc. – some of these developments put us to shame.

- Some creatures have rods but no cones, and some creatures have cones but no rods, and...

The Evolution of Colour Vision

- So let's pull all of the above into a timeline diagram that combines our original representation of evolution in general with the evolution of colour vision.



END of Part 2