Color blindness, a secret superpower?
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Color blindness is considered to be a disability. Not being able to distinguish certain colors can be very inconvenient in many situations. In the USA it is even possible to receive benefits from the state if color blindness is making it difficult to find a job or provide enough for one's family. But if color blindness were such a devastating disability, it is remarkably prevalent in the modern human population. Color blinds seem to have a terrible disadvantage in life. Would natural selection then not be expected to make quick work of removing alleles that cause such a deficiency from a population? Has this selection just not happened yet? Or is there another reason for color blindness to still be around today? Are the negative effects of color blindness perhaps a bit exaggerated? Or are there actually hidden advantages to being color blind that keep it around?

The workings of color vision

Humans can detect light from their surroundings with the use of photoreceptor cells in the retina inside the eye. Our eyes contain two different types of photoreceptors, cones and rods (Bear et al., 2015). Of these two types, only the cones are capable of distinguishing different colors, and they are only stimulated when there is sufficient light. In low-light conditions only the rods are stimulated and therefore the world is seen only in shades of gray. There are on average over 18 times more rods than cones in the human eye. Humans usually possess three different types of cones that are stimulated by light of differing wavelengths, as can be seen in figure 1. The so-called short wavelength cones are most sensitive to light with a wavelength of about 430 nm. These cones are also called the blue cones because their peak sensitivity is for blue light. The medium wavelength peak sensitivity is at a wavelength of approximately 530 nm, which is close to but not exactly the wavelength for the color green. The third cone type is the long wavelength cone, which is often referred to as the red cone, but its peak sensitivity of approximately 560 is actually closer to orange than to red.

When colored light hits the eye it usually contains not just light of one wavelength activating only one type of cone, but instead a whole spectrum of wavelengths, activating all types of cones to some degree. The ratio of activation of the different types determines what color is actually perceived (as visualized in figure 2). The information gathered by the stimulation of the different kinds of photoreceptor cells travels through the optical nerve into the brain, where the information is integrated into a representation of colour in the surrounding environment. Having three different types of cones is referred to as being trichromatic.
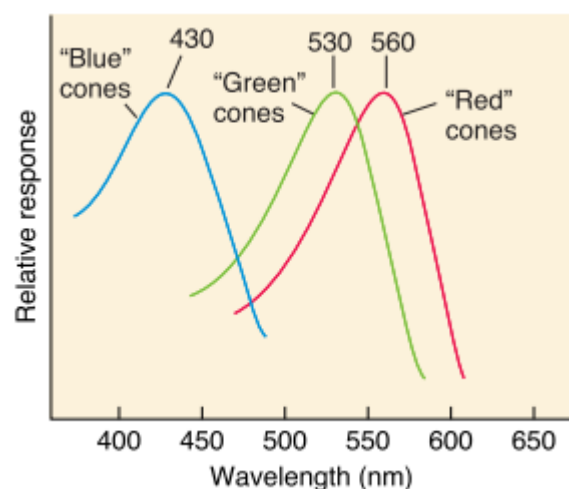

Figure 1 (Bear et al., 2015): The light sensitivity peaks of the short (blue), medium (green) and long (red) wavelength cones.
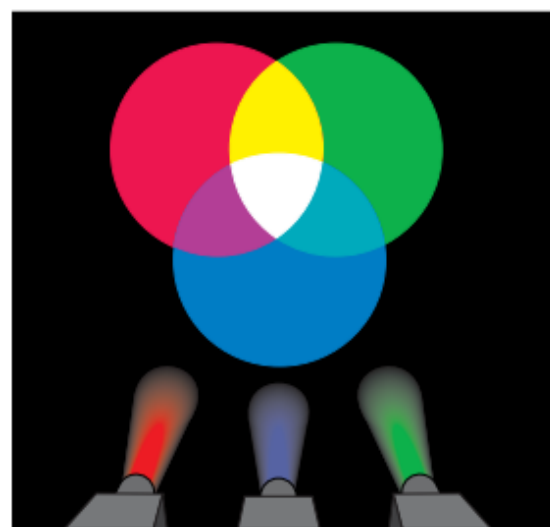

Figure 2 (Bear et al., 2015): light of multiple colors/wavelengths combined creating new colors by activating multiple types of cones simultaneously.

While trichromacy is the norm in human beings, it also occurs sometimes that humans are dichromatic (two types of cones), tetrachromatic (four types of cones) or even monochromatic (only one type of cone). Because monochromats have only one (functional) type of cone they are incapable of distinguishing different colors, and perceive the world only in shades of gray. Monochromacy is very rare in humans and only occurs in 0.001% of the world population (Nathans et al., 1989). Tetrachromacy is less rare. It is believed to occur in approximately 12% of women, but rarely, if at all, in men (Jordan et al., 2010). Though it is clear that this group of tetrachromats possess four different functional types of cones, it is still unclear whether this actually improves color vision in this group. Having four different types of cones would theoretically allow someone to perceive colors in an extra dimension of hues, allowing them to distinguish 100 times as many colors as normal trichromats. It remains unclear however whether the optical nerve is able to process the extra information in a way that allows for functional tetrachromacy, or if these tetrachromats, due to the limits of the optical nerve perceive the world the same as any other trichromat (Jordan et al., 2010). Dichromacy is a more commonly known condition, and much easier to detect. As a consequence, the majority of data on colour blindness is derived from studies of dichromatic subjects. The prevalence of dichromacy and the distribution of the condition between the sexes seems to differ between populations. Research has shown that, in Caucasians, dichromacy is regularly found in males (in approximately 8% of the population) and very rarely in females (in approximately 0.4% of the population), while in Asian, African, native American and Polynesian populations the prevalence in men seems to be a bit lower (4 or 5 %) and the prevalence in women a bit higher (between 0.2 and 1.7 %) (Birch, 2012). People are dichromatic when they possess only two different (functional) types of cones. The absence or malfunctioning of a third cone type causes difficulty in distinguishing colors at certain wavelengths, while color perception at other wavelengths remains unchanged compared to trichromats. This color vision deficiency is commonly referred to as color blindness. The most common type of color blindness is red-green color blindness. It can be caused by a defect in either the red or the green pigment cone, and it makes it more difficult to distinguish between red and green light. Blue-yellow color blindness is also quite common, caused by an absent or defective blue pigment cone, making it harder or impossible for someone suffering from this deficiency to distinguish the colors blue and yellow (Bear et al., 2015).

The genetic basis of color vision

The genes that code for the three different types of cones, also called opsins, are found on two different chromosomes. Both the long wavelength (red) and the middle wavelength (green) opsins are found on the X chromosome while the short wavelength (blue) opsin is located on chromosome 7. The long and middle wavelength opsins are very similar. When looking at the nucleotide sequence the two genes are 98% identical. This implies they are the result of a relatively recent gene duplication (Neitz and Neitz, 2011). By comparison the low wavelength opsin shares only 40% of its sequence with the other two opsins. Initially it was believed that all normal trichromats had the exact same opsins and therefore perceived the world exactly the same, but later studies have shown that there is some variation in code between opsins of different people, and that this variation in some cases also caused a slight variation in how colors are perceived (Windericx et al., 1993). Because the two genes on the X-chromosome are so similar the chromosome is very prone to unequal homologous recombination during meiosis (Neitz and Neitz, 2011) resulting in misalignment of the homologous chromatids during crossing over. This can result in daughter chromosomes with one more or one fewer opsin genes than the parent. If an X chromosome bearing only one opsin gene (either middle or long wavelength but not both) is present in male offspring, the son will suffer from red green color-blindness owing to his lack of a compensatory wild-type copy of X (Neitz and Neitz, 2011).

The evolutionary history of color vision

The emergence of color vision seems to have occurred very early in the development of vertebrates. Evidence of a photoreceptor system with cones and rods, as seen in contemporary vertebrates, was already found in the fossil of a fish that lived approximately 300 million years ago (Tanaka et al., 2014). Normally soft tissue of the eye is not preserved in fossils because it decays in about 64 days, but this fossil was extremely well preserved in a layer of river sediment and therefore the cones and rods were still distinguishable (Tanaka et al., 2014). Because almost all birds, reptiles and fish today have tetrachromatic vision, it is believed that the ancestral form of vertebrate color vision was also tetrachromatic. During the early evolution of mammals, tetrachromatic vision appears to have been lost, based on the fact almost all extant mammals are dichromatic. The first mammals were likely small and had nocturnal and/or burrowing lifestyles (which probably helped them survive the mass extinction event that killed off the dinosaurs), and it is believed that for this way of life color vision was less important and the ability to see well at low light conditions was more emphasized. Cones (allowing us to see color) and rods (allowing us to see at dim light conditions) compete for the same space on the retina of the eye, therefore there seems to be a tradeoff between the ability to distinguish colors and the ability to see in dark environments (Gerl and Morris, 2008) Humans and other primates are the only mammals with more than two types of cone, having later evolved trichromacy independently.

Genetic polymorphism amongst trichromatic and dichromatic individuals, as seen in humans , can also be found in primates, especially in new world monkeys (see figure 3, which shows a phylogenetic tree of modern primates with their colour vision systems mapped onto the branches). In many new world monkey species, most females are trichromatic while some females and all males are dichromatic (Jacobs, 1998). But while dichromatic polymorphism is observed in many new world monkey species, a study looking at old world monkeys and apes, genetically much closer to ourselves, found no instances of dichromacy at all and instead observed only trichromacy (Jacobs and Williams, 2001). This is an unexpected finding because humans are more closely related to old world monkeys and apes than to new world monkeys, but seem to be more similar to new world monkeys in this regard. This would imply that either the genetic variation giving rise to dichromatic individuals evolved twice, both in (an ancestor of) humans and in an ancestor of the new world monkeys, or
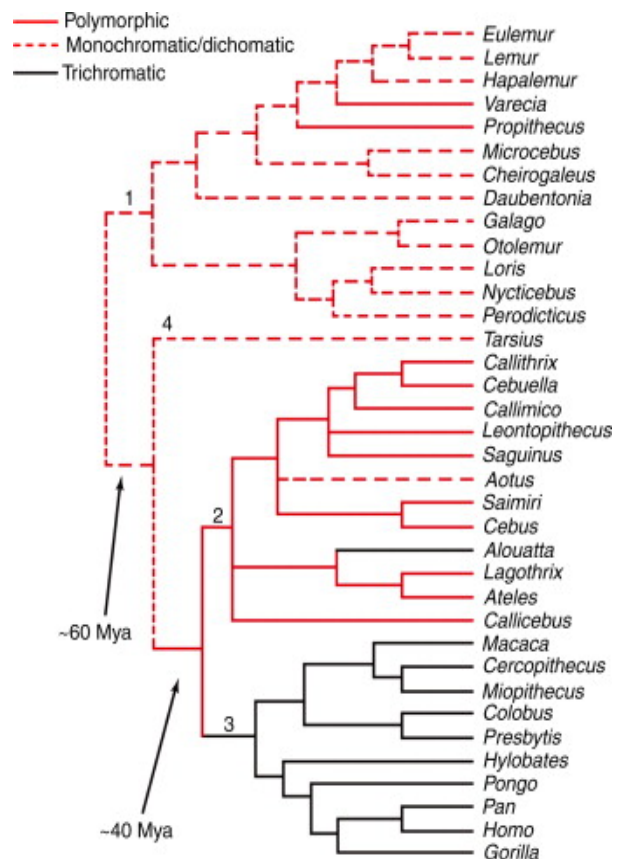

Figure 3 (Jacobs, 2007): An overview of the prevalence of trichromacy and dichromacy in primates. The black lines indicate lineages where individuals are (almost) all trichromatic. The solid red lines indicate lineages of species with both dichromats and trichromats being present. The dotted red lines indicate lineages where trichromacy is not present at all, but only dichromatic or monochromatic individuals are found. Branche number 2 represents the new world monkeys, while branch number 3 represents the old world monkeys and apes, including humans.

that dichromatic polymorphism evolved in an ancestor of all primates and this genetic variation was lost (perhaps by purifying selection) along the branches leading to apes and old world monkeys. One thing to note here is that the study of old world monkeys and apes has only 107 test subjects of 12

different species. This means very few subjects per species and also not that many in total. Therefore the conclusion that dichromatic polymorphism is not present at all, or at least very rare, is unreliable.

One study identified a single functionally dichromatic chimpanzee (so in possession of genes coding for three different types of cone, but only two types actually beeing expressed). Though no real dichromatic individuals existed in the group of 58 chimpanzees that were tested, this is the first time a color vision deficiency was observed in non-human apes (Terao et al., 2005). Due to the sample size of the research, in my opinion no firm conclusions can be drawn about the frequency of color vision deficiency in apes. But this study, along with a whole list of previous studies that found no color deficiencies whatsoever in chimpanzees (Essock, 1977, Grether, 1940a, Grether, 1940b, Jacobs et al., 1996, Matsuzawa, 1985, Yerkes, 1935, Yerkes and Petrunkivitsch, 1925), does suggest that color blindness is at least quite rare amongst non-human apes.

The evolution of trichromacy

As mentioned above, our early vertebrate ancestors appear to have been tetrachromatic, because most groups of vertebrates like fish and reptiles still are tetrachromatic, but the ancestral mammals seem to have evolved dichromatic vision with only a short and a long wavelength opsin (Bompas et al., 2013). Primate trichromacy seems to be the result of a duplication of the ancestral M/L opsin gene resulting in separate M and L opsin genes. It is highly unlikely that this duplicated genotype would have become fixed in the ancestral primate as it did, if there was no positive selection for it (Surridge et al., 2003). There are multiple hypotheses for what selective benefits of trichromacy may have driven its fixation.

First, trichromacy may have evolved for the purpose of intraspecific communication. It is argued that trichromatic vision plays an important role in primate discrimination of emotions, in socio-sexual signaling and in threat displays (Changizi et al., 2006). The argument that is presented to support this theory is that, though skin color and reflection differs a lot within humans and between primate species, the degree that the face can change color is universal throughout all primate species. The face can either turn more red because of more hemoglobin oxygen saturation or turn more green because of more hemoglobin skin concentration. The wavelength sensitivities of the L and M opsins seem to be absolutely perfectly adapted to detecting this red-green difference. Changizi et al. argue this would be unlikely if trichromacy was not developed exactly for this purpose. A further argument for their case is that all monkeys who possess regular trichromacy also have a bare face (Changizi et al., 2006). This is of course a necessity if perception of skin coloration is of social importance. But statistical work by Fernandez and Morris (2007) suggests that trichromacy evolved before red skin and that red skin is far more likely to evolve with the presence of trichromatic color vision. They think it more likely that trichromacy initially evolved for a reason other than intraspecific communication.

An alternative hypothesis was originally proposed in 1879 by Allen. His suggestion that being trichromatic offered an advantage while foraging, and therefore natural selection favored trichromatic individuals, is still widely accepted today. There is however still debate on the foraging of what food source trichromacy evolved for. Initially trichromacy was believed to have evolved to make it easier to find fruit on trees, but while trichromacy really does help with finding food (Bompas et al., 2013), it has been recently proposed that the selective advantages of trichromacy may be related to the foraging of young leaves rather than ripe fruits (Lucas et al., 1998). It is difficult to say what exactly caused a trait to evolve in the past because circumstances change all the time. Traits that evolved because they were advantageous in the past might no longer be advantageous in the environment today, meaning that there may be no straightforward test that can be carried out in extant species to test evolutionary hypotheses. And traits that are advantageous today might have evolved for entirely different purposes in the past. Particularly in humans it is very difficult to trace back the reason for an adaptation, because our environment changed so much and so fast in the past few millennia (a relatively short time on the scale of evolution). So, we might never know exactly

what purpose trichromatic color vision had when it first emerged, but nevertheless studying the advantages that trichromacy has for humans and primates today may give important insights.

First, let us consider the potential advantage of trichromacy while foraging. Trichromatic vision is very useful when trying to find fruits (or young leaves) against a background of (other) leaves. Ripe fruits usually have more reddish or yellowish colors, and the same goes for young leaves, making it difficult for dichromats to distinguish them from a green-colored background. It has been found that trichromatic vision is most effective when foraging for fruits nearby, however the advantage of trichromats over dichromats is the largest when foraging from a distance (Bompas et al., 2013). Trichromatic people had significantly faster responses and made less mistakes than dichromatic people in a visual search task where the participants had to spot fake fruits made of paper in a real bush. And the difference only increased when the distance of the search task increased (Bompas et al., 2013).

Another advantage trichromats seem to have over dichromats is an increased ability to recognize faces. A 2020 study by Brosseau et al. shows that dichromats perform significantly poorer in a face recognition task. Especially when the facial features were less distinct because the pixels of the images were more and more scrambled, the dichromats were at a disadvantage (Brosseau et al., 2020). This indicates that color plays a crucial role in face recognition, in particular when faces are seen less clearly because they are for example partially obscured or seen from an unusual angle. It is furthermore suggested that color blind people have more difficulty recognizing the gender of faces and that especially red-green discrimination is important for face recognition (Nestor and Tarr, 2008). These studies lend support to the notion that trichromacy may have been of social importance during primate evolution.

Other studies assessed the impact of color blindness on life in general. One study by Bastos et al. (2015) assessed this by interviewing participants and letting them undergo psychophysical color vision assessment. They found that 27% of the participants encountered direct negative effects of color blindness on the quality of life and that 29% relied on somebody else during daily activities (Bastos et al., 2015). Unfortunately, no examples of such situations and activities were provided by the authors. 60% of participants were however of the opinion that life would be no different if their color vision was normal, and only 30% would want to undergo treatment for color blindness if it was available (Bastos et al., 2015). Though the sample size for this research is rather small (only 12 participants with dichromacy were interviewed) and therefore the results are less reliable, this study does show that the impact dichromacy has on daily life differs a lot between individuals. What profession an individual is in also seems to have an effect on how much difficulty a dichromatic individual experiences (Bastos et al., 2015), but the sample size of this research is not sufficient to say anything meaningful about this effect.

Another study investigating the effect of dichromacy on daily life was a literature review by Stoianov et al. (2019) covering 20 recent relevant papers about the impact of color blindness. Similar to Bastos et al., they concluded that the impact of color blindness varies markedly for each individual, and that every case is unique (Stoianov et al., 2019). They also concluded that color blindness can affect almost every aspect of daily life, for example performance at work or school, personal care and access to information and entertainment (Stoianov et al., 2019).

The evolution of a trichromatic and dichromatic polymorphism

If trichromacy is indeed so advantageous to an individual, it is a remarkable finding that in many new world monkeys there remains genetic polymorphism that results in dichromatic and trichromatic individuals within each species. A 2003 study by Surridge et al. discussed the observation that both trichromacy and dichromacy regularly occurs in many new world monkey species and theorized about the cause of this phenomenon. They proposed three different theories that could explain how this polymorphism could be maintained in a population. The one least likely to be true is that

selection might not be acting on dichromacy or trichromacy here at all. Instead, balancing selection might act on an adjacent locus on the chromosome, and dichromacy might only be maintained because it is linked to that locus (Surridge et al., 2003). It is very unlikely however that such a link is maintained in so many different species over such a long period of time, especially since the chromosomal organization of the primate genome has evolved substantially, so the reason why dichromacy still persists is more likely to be found in one of the next two theories.

The second theory explored is that of heterozygote advantage. This theory implies that in a perfect world all X-chromosomes in a species gene pool would contain the duplicated M and L opsin, leading to the entire population being trichromatic. But if such a duplication rarely happens, all X-chromosomes in a population would have only one opsin, either M or L. If this is the case, trichromacy can still be achieved in some females if they have different types of opsin on each X-chromosome and thus with both chromosomes combined does have both an M and an L opsin (Surridge et al., 2003). This would also mean that dichromacy is not something that is selected for, but instead is still there in the population because the duplication to have two different opsins on one X-chromosome has not yet happened. If such a duplication were to happen it would likely spread through the population quickly because there would be strong selection for it, so over time dichromacy would disappear from the population entirely.

The third suggestion is that there might actually be an advantage to being dichromatic in some situations, and that this would lead to frequency dependent selection (Surridge et al., 2003). Back in 2003 Surridge et al. were only able to speculate about situations where it would be beneficial to be dichromatic. But the matter has been investigated further in the time since, and now some actual evidence can be presented of circumstances where it pays to be dichromatic.

Since the turn of the century, multiple methods for assessing whether a monkey has dichromatic or trichromatic color vision have been developed that can be used by researchers wanting to study and compare the behaviour of dichromatic and trichromatic individuals. A study by Saito et al. (2005a) investigated three of these methods on the same group of capuchin monkeys and compared the results to test the reliability of these methods. They conducted a genetic analysis, an electrophotometry test and a behavioral test. The genetic analysis consisted of DNA sequencing the visual pigment genes to determine if an individual is dichromatic or trichromatic. This could be done with no discomfort to the monkeys because the DNA needed could be collected from hairs or fecal matter. For the electrophotometry test, the monkeys had to be sedated and were then placed in a holder to support their head. The retinal sensitivity of the monkeys was measured for medium and long wavelength light by flashing red and green LEDs in one eye and recording the retinal response. This can be used to determine whether the monkey was dichromatic or trichromatic. The behavioral test was conducted with Ishihara plates (see figure 4), a method very similar to the one used to detect color blindness in humans. In a learning exercise the monkeys were presented with a pair of plates (as in figure 4) and were rewarded with food if they touched the plate with a circle first. Their ability to recognize the plate with the circle was measured. It was found that the individuals who struggled to recognize the circle were the same individuals who were suspected to be dichromats on the basis of both the genetic analysis and the electrophotometry test (Saito et al., 2005a). Therefore it was concluded that all three methods were reliable methods to determine if a monkey is dichromatic. Most of the research discussed in the subsequent text uses only the genetic analysis method to discriminate their monkeys (except for the other work of Saito et al. (2005b) who used the same monkeys for their subsequent research). This is probably because it is more comfortable for the monkeys than the electrophotometry test, and because it is less time consuming than the behavioral test.
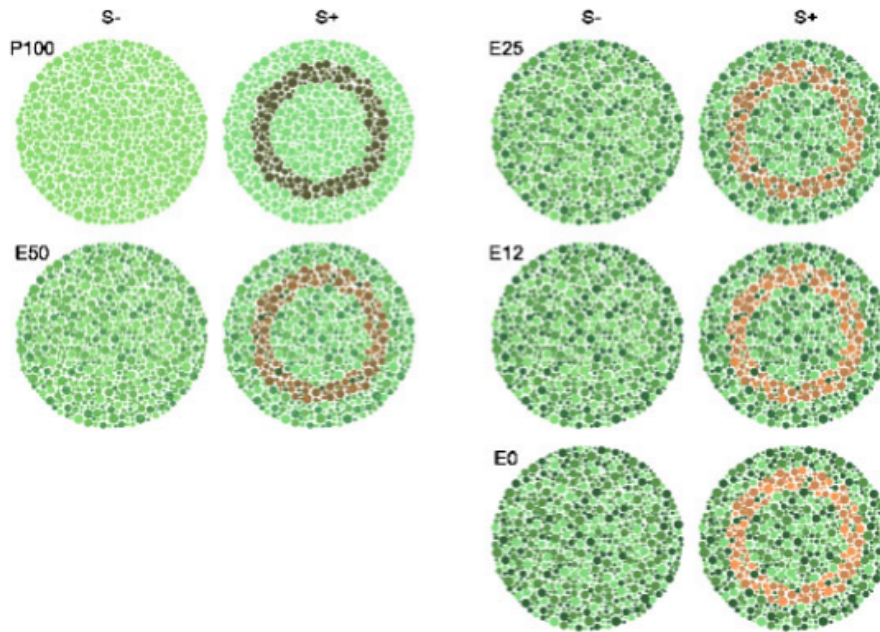
Figure 4 (Saito et al., 2005a): the Ishihara plates that were used to determine if the capuchin monkeys were dichromatic or trichromatic.

A 2012 study by Smith et al. (which Surridge and both her coauthors of the 2003 study also contributed to) presented evidence that dichromatic tamarins (a genus of squirrel-sized new world monkeys) where better at finding camouflaged insects than their trichromatic peers (Smith et al., 2012). They observed the monkeys both in captivity and in the field and found the same pattern: trichromats catch more insects overall, but dichromats catch relatively more insects that are camouflaged (Smith et al., 2012). The same pattern had already been found in a 2003 study by Caine et al. (also co authored by Surridge) with a more experimental setup in which they found that trichromatic Geoffroy's marmosets found significantly less cereal when it was camouflaged, while dichromatic peers were unaffected by the camouflage (Caine et al., 2003). If dichromats are able to exploit a different food source (in this case camouflaged insects) than the trichromats, that could explain why the polymorphism is maintained in a population.

Another study, also on Geoffroy's marmosets, also by Caine et al., found that dichromatic individuals outperform trichromatic individuals when foraging in the shade (Caine et al., 2010). The trichromatic individuals found significantly more cereal in the sunlight than in the shade, while the dichromatic individuals foraged just as well in the sun as in the shade. There was no significant difference between trichromats and dichromats in the sun, but the trichromats performed significantly worse than the dichromats in the shade. This would be another way for dichromats to exploit a different food source than trichromats, and thus another possible reason why the relative fitness of dichromacy and trichromacy can be the same (if they occur in the right frequency). So an advantage in foraging in the shade could give rise to frequency-dependent selection that helps maintain the polymorphism of dichromacy and trichromacy in a population.

If there would be a difference between the foraging success of the different groups under different circumstances, one would also expect to find specialization of foraging behavior, with dichromats and trichromats exhibiting strategies adapted to the strengths and weaknesses of each group. But the researchers also measured the amount of time both groups spent foraging in the sun and In the shade and, quite unexpectedly, found no difference between the dichromats and the trichromats here. Both groups spent approximately one third of their time foraging in the shade (Caine et al., 2010). And in another study, on insect foraging in wild tamarins, a similar pattern was found. The dichromats perform better than trichromats at low light conditions, but do not seem to have a relative preference for foraging in the shade compared to trichromats (Melin et al., 2007). Because of

these contradicting findings it remains unclear what exact mechanism does maintain the polymorphism in new world monkeys, but that there are certain mechanisms that can cause polymorphism to persist has been made abundantly clear.

Do these selective benefits of dichromacy also apply to (early) humans?

It is important to consider that, though monkeys are an excellent model for human ancestors and early humans, they, and their lifestyle, are not exactly the same. Advantages for foraging only translate to (early) humans if the humans in question were also foraging the same source of food as the monkeys studied. It is difficult to say with absolute certainty what food our ancestors were eating, but by investigating the teeth of fossilized humanoids and by looking at the diet of societies still living a hunter gatherer lifestyle today an estimation can be made of the diet of our ancestors. It is thought that the diet of our ancestors, when they still lived in rainforests, was very similar to that of monkeys today, who still mostly live in rainforests. This is a diet containing mostly fruit and leaves. But 8 million years ago the early hominid species are thought to have developed in more savannah-like conditions, and this was associated with a transformation of the human diet to include more roots and tubers (Gowlett, 2003). The ancestors of our species are believed to have evolved only 200,000 years ago from tropical regions in Africa, and it would seem that their diet was still 70% plant based (Gowlett, 2003). Only when they started coming to colder Europe, about 40,000 years ago, was it necessary to start eating higher proportions of meat (Gowlett, 2003). About 10,000 years ago agriculture started to emerge and cereals and dairy products steadily became a larger part of the modern diet (Gowlett, 2003). These changes in diet should be considered when comparing humans to monkeys, since different diets mean different selective pressures. But it should also be noted that many of the largest changes in diet happened relatively recently, giving natural selection little time to adapt us to these new diets. Therefore it would seem reasonable to assume that the circumstances our visual system was originally adapted to were very similar to the circumstances of monkeys today, and that therefore advantages observed in monkeys today translate well to early humans but are less relevant to modern humans.

To compare dichromacy in monkeys with dichromacy in humans it is very useful to take a look at the work of Saito et al. They performed two different experiments, published in 2005 and 2006, investigating the difference between dichromats and trichromats in the discrimination of color camouflaged stimuli in primates and humans respectively. The first study concluded that the dichromatic new world monkeys and the one protanomalous (having a not properly functioning L cone) chimpanzee they included all performed significantly better than their (functionally) trichromatic peers in an exercise for the discrimination of color-camouflaged textures (Saito et al., 2005b), an observation very much in line with the studies discussed before (Caine et al., 2003, Smith et al., 2012). Interestingly, the next year they published another paper about an experiment with the exact same color camouflaged stimuli, but this time designed for human test subjects. They recorded the time it took twelve dichromatic and twelve trichromatic individuals to recognize specific textures under single-color and color-camouflage conditions. Though they found no significant difference between dichromats and trichromats under either condition, they did find that the trichromats performed significantly worse under color camouflaged conditions compared to single-color conditions, while this was not the case for the dichromats (Saito et al., 2006).

An experiment that is more biologically relevant was conducted by Troscianko et al. (2017). In a citizen science experiment, participants were asked to spot birds and nests in nature pictures. The pictures of half the participants were digitally edited to simulate dichromatic vision. They found that trichromatic vision was beneficial under all conditions, however the performance of the simulated dichromats improved faster during the exercise (Troscianko et al., 2017). In the egg-searching tasks the simulated dichromats were on the same level as the normal trichromats at the end of the exercise, and they were still improving. The exercise was not long enough (only 20 slides) to determine if the simulated dichromats would have eventually overtaken the trichromats and

outperformed them, but this is a possibility. Two possible explanations for this finding are discussed. The first is that the dichromats, upon the loss of color information, learn to use other cues to identify the targets. This would suggest that the dichromats can only reach the same level of visual discrimination as the trichromats, but not surpass them. The second possibility is that the loss of (potentially distracting) color information allows the dichromats to adopt a different search strategy than the trichromats. Such an alternative strategy might be a more efficient way to find the targets and might thus allow the dichromats to actually outperform the trichromats. This study was only on simulated dichromacy, no actual dichromats were involved. Therefore this study can only draw inferences about how trichromats can process different images and different color information.

But it is also possible that people who are actually dichromatic not only see the information differently, but also process the information differently. This possibility was investigated in multiple studies. A 2006 study by Jägle et al. found that dichromats have higher visual acuity (sharpness) than trichromats. This is only true however for dichromats that do have multiple copies of their one L/M opsin gene. Dichromats with only one gene coding for an opsin were found to have similar acuity to trichromats (Jägle et al., 2006). It is assumed that this ability to see sharper is the result of seeing less colors leading to less chromatic noise (the inability of the lens to converge differently wavelengths to the same point on the retina of the eye). This does not explain why there should be a difference between single gene and multiple gene dichromats, but two other explanations are proposed for that issue. Having only a single gene for the L/M opsin can either lead to a different spatial pattern of the opsins on the retina of the eye or lead to different 'wiring' from the eye to the brain. Both options could lead to reduced acuity (Jägle et al., 2006). Furthermore a 2013 study by Jánaky et al. found that the achromatic processing of dichromats is superior to that of trichromats, because their contrast sensitivity was significantly better. The contrast sensitivity also determines the sharpness of the image perceived by the eye. It is assumed that this advantage is again due to less chromatic noise (Jánaky et al., 2003).

Conclusion

All things considered, what do I think is the reason that color blindness is so prevalent in human populations today? I think the idea of frequency dependent selection being the reason for dichromacy to persist is very interesting, but I am not convinced that it is the explanation for human dichromacy. Though there are some examples of circumstances where it might be advantageous to be dichromatic, both in primates (Caine et al., 2003, Caine et al., 2010, Melin et al., 2007, Saito et al., 2005, Smith et al., 2012) and in humans (Saito et al., 2006, Troscianko et al., 2017, Jägle et al., 2006, Jánaky et al., 2003), I am not sure if it is enough to compensate for the major advantages trichromacy seems to have, especially in overall foraging success (Bompas et al., 2013, Brosseau et al., 2020, Smith et al., 2012). This belief is further backed by the fact that multiple studies found dichromatic primates to show no preference for foraging under the circumstances where they would have an advantage (Caine et al., 2010, Melin et al., 2007). I find it far more plausible that dichromacy is so prevalent in new world monkeys because the mutation that is required for males to also be trichromatic, the duplication of the L/M opsin on the X chromosome allowing men to have two different opsins while only one X chromosome, has not happened for them yet. This point is further backed by the fact that in old world monkeys and apes, where this duplication did happen, dichromacy seems to be virtually nonexistent.

It seems unlikely that there is still selection pressure for or against dichromacy in modern society. Many people with minor color vision deficiencies only find out about their deficiency later in life, sometimes not until they first encounter a color blindness test (Birch, 2012), and a majority of interviewed dichromats thinks life would be no different with normal color vision and less than one third of dichromats would like to undergo a treatment to cure color blindness, if it was invented (Bastos et al., 2015). Color blindness nowadays seems to be no more than a minor inconvenience, except for cases of monochromy but this is extremely rare. Furthermore, all the advantages of

dichromacy found in primate studies, while they may have also been advantageous for early humans and our ancestors, are much less relevant in modern society. Though there are still scenarios imaginable nowadays where seeing a little sharper and being better at finding camouflaged objects could make the difference between life and death, these situations are increasingly rare.

Because of the reduced negative effects and the negligible positive effects of dichromacy in modern society I think the main cause for the high prevalence of color vision deficiency nowadays is relaxed selection. This existing theory implies that in early humans there was selection against dichromacy, and therefore dichromacy was very rare. But because the selection pressures were reduced, other evolutionary processes, like the founder effect or genetic drift, caused the rise of dichromacy (Adam et al., 1967). The previously discussed literature study by Birch (2012) supports this conclusion. From the collection data on the prevalence of dichromacy from studies concerning populations all over the world it was learned that dichromacy is most prevalent in Europe and Asia, the areas of the world that have developed away from a hunter-gatherer society the earliest (Birch, 2012). The small number of studies conducted on primitive societies who still live like hunter gatherers today seem to confirm this pattern (Garth, 1933, Mann and Turner, 1956). Both studies found very low instances of dichromacy in the primitive populations they investigated, as would be expected if there would still be selection against dichromacy. But this could also be because the studies are quite small and therefore very susceptible to chance. Further research should be conducted to rule out this option and confirm the theory that high prevalence of dichromacy in modern humans is caused by relaxed selection.

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