Human colour vision can most often be described as trichromatic. Having trichromatic colour vision entails having three types of wavelength specific cones in the retina, each of which are maximally responsive to short, medium or long wavelengths of light in the colour spectrum. Short, medium and long wavelength cones maximally respond to blue, green and red light respectively (Goldstein, 2002). Trichromacy is not a uniform feature of human physiology however. Because colour vision is inherited genetically, with medium and long wavelength specific genes being located on the x chromosome, mutations can occur. These mutations can cause a type of colour blindness called anomalous trichromacy, in which the red photopsin becomes slightly shifted (Sanocki, Shevell, Winderickx, 1993). If a woman inherits the three cones for normal trichromacy on one x chromosome, and the three cones for anomalous trichromacy on the other x chromosomes, she will possess two types of red photopsin and therefore have the possibility of four wavelength specific cones. If having four different wavelength specific cones defines tetrachromacy it is highly likely that there are tetrachromats (Jameson, Highnote and Wasserman, 2001). If, however, tetrachromacy is defined by the visual system acting upon this extra cone and creating the neural mechanisms to allow visual experience to be derived from it, then evidence for tetrachromacy is not so forthcoming (Jordan and Mollen, 1993). It is likely that even if the visual system can derive information from this extra cone containing the shifted red photopsin, this is not going to result in a considerably different visual experience to that of trichromats because the shifted red photopsin is only six nanometres (nm) away from the original red photopsin (Winderickx, Lindsey, Sanocki, Teller, Motulsky, Deeb,1992). The theory of trichromacy is often referred to as the Young-Helmholtz hypothesis. This assumes that colour vision is subsumed by three photosensitive pigments in the retina (Ingler, 1968), where short wavelength specific cones have a peak absorption maxima of 419nm, medium wavelength specific cones of 531nm and long wavelength specific cones of 558nm (Bruce, Green and Georgeson, 2004). Colour vision is inherited genetically with short wavelength specific genes being transmitted on chromosome number seven, and medium and long wavelength specific genes being transmitted on the x chromosome (Bowmaker, 1998). Medium and long wavelength specific genes are highly homologous and it is polymorphism of these which cause variation in colour vision. Winderickx et al (1992) found that a common polymorphism occurs at point 180 on the red opsin, and that this results in the general population having two different types of red opsin, one being alanine, and one being serine. Serine has a peak absorption maxima of 557nm and alanine has a peak absorption maxima of 552nm (Winderickx et al, 1992). This means that if alanine is substituted for serine at point 180 on the red opsin of the long wavelength specific cone, it's peak sensitivity will fall below that expected for a long wavelength sensitive photopsin and the carrier will have a reduced sensitivity to red light (Bowmaker, 1998). The implication of Winderickx et al's (1992) evidence is that if a female inherits the genetic code for alanine on one x chromosome, and the genetic code for serine on the other x chromosome, she is heterozygous and has the propensity to have four different wavelength specific cone cells. The female would have the short, medium and long wavelength sensitive cones required for trichromatic colour vision, and also an extra cone which has been shifted between the medium and long wavelength sensitive cones. Males only have one x chromosome and therefore will only ever inherit alanine or serine, they will not be able to have both types of the red photopsin and therefore cannot become tetrachromatic. Typically however, even if the female inherits both types the shifted red opsin (alanine in the case of long wavelength sensitive cones), will not be expressed, so even if the female is heterozygous she will not be tetrachromatic. There is however a physiological mechanism called x inactivation which acts upon the x chromosome and results in both types of red opsin being expressed. It is this that gives females the propensity to be tetrachromatic. X inactivation is the process by which one or another x chromosome becomes inactivated (Jordan and Mollen, 1993). If x inactivation occurs in heterozygous females, the allelic properties will be separated so some cells will express alanine and some will express serine and the female will have in total, four wavelength specific cones (Jordan and Mollen, 1993). To support this it was predicted by Lyon (1961) (as cited in Cohn, Emmerich and Carlson, 1989) that if a woman had the propensity to express both types of red opsin, some cells should have normal colour vision, and some cells should have below level colour vision as a result of expressing the shifted gene. Cohn et al, (1989) found that when they asked heterozygous carriers with x inactivation to identify the colour of a green light shone on certain patches of the retina, on certain patches they often made mistakes and saw yellow or white light. Significantly more mistakes were made by heterozygous females. This suggests that there is a mosaic pattern of cells on the retina (Cohn et al, 1989), some of which express the three cones for trichromacy. The other cells express two normal trichromatic cones for green and blue and the abnormal slightly shifted red cone, which results in anomalous trichromacy in these cells (Jameson et al, 2001). Cohn et al did find however that the heterozygous carrier can compensate for this as when they were allowed to scan the stimuli, and use the whole of their retina (the fully functional as well as the shifted cones), they had no colour deficiency. The importance of Cohn et al's results is that it demonstrates the expression of two different types of cell, those containing one type of photopigment and those containing a slightly shifted variant. Although the results were gained in contrived laboratory conditions, these results are extremely valuable in demonstrating the process of x inactivation and how it can lead to four different types of wavelength specific cones. Although Cohn et al (1989) found that this can limit the female's colour vision in some respects, it has been shown that the woman can compensate for this by scanning. This evidence can be linked with Winderickx et al's (1992) finding that as well as having short, medium and long wavelength specific cones responding to an absorption maxima of 419nm, 531nm and 558 nm respectively (Bruce et al, 2004), heterozygous females can also demonstrate a fourth wavelength specific cone with an absorption maxima of 552nm (Winderickx et al, 1992). Winderickx et al (1992) and Cohn et al (1989) both show that it is possible for a woman to be a tetrachromat. An important distinction has to be made however between being a tetrachromat and having tetrachromatic vision. The requirement for tetrachromatic vision is not as simple as having four different wavelength specific cones. The brain has to be plastic enough to adapt to the extra cones and create post receptoral neural channels to process the information and interpret it(Jordan and Mollen, 1993). Simply having four wavelength specific cones available is known as weak tetrachromacy, but being able to use them is strong tetrachromacy (Jordan and Mollen, 1993). This however is very difficult to test whilst the person is alive, and behavioural tests do not appear to be sensitive enough to accurately discriminate between tetrachromatic vision and trichromatic vision (Jameson et al, 2001).A problem regarding the sensitivity of behavioural tests is that the shifted fourth cones are possibly too close to original trichromatic cones to be able to accurately distinguish between them. There is only a maximum of a six nanometre difference between alanine an serine, and whereas this may be enough to produce a more detailed, complex vision of the world in females who are tetrachromatic, it may be that it is not enough to always be detected in contrived, laboratory, behavioural tests. There is some evidence however that heterozygous females may not only be tetrachromats, but have tetrachromatic vision (Jameson et al, 2001). The fact that Cohn et al (1989) found that there are normal and defective cells operating in the retina implies that the fourth, shifted opsin is operating and that the brain has adapted to receive the input because if it had not, Cohn et al (1989) would not have found defective patches on the retina. This strongly suggests that as well as having four different cones responding to different wavelengths of light, they are also all being utilised. The notion that humans may possess the ability, not only to be tetrachromats, but to use their tetrachromatic vision can initially be investigated by looking at new world monkeys. Mollen, Bowmaker and Jacobs (1984) found that in a species of typically dichromatic squirrel monkeys, there were the occasional females who showed trichromatic behaviour after training on Rayleigh colour matches. They also found using microspectrophotometer techniques, that squirrel monkeys who displayed trichromatic behaviour could draw two pigments corresponding to medium and long wavelengths as well as pigments corresponding to short wavelengths, illustrating trichromacy physiologically (Mollen et al, 1984). The relevance of this shows how females in a predominantly dichromatic species can develop the ability to enhance their colour vision by developing, and critically using, an extra photopsin. It has also been found that the coding sequences of red and green photopigment genes of certain species of monkey are highly homologous to human coding sequences of red and green photopigment genes (Deeb, Jorgensen, Battisti, Iwanski and Motulsky, 1994). This suggests that if monkeys, who have coding sequences which are highly homologous to human coding sequences, can develop and use extra portions of the visual system. It may be possible to generalise this to humans and anticipate a similar ability. We know humans can develop a fourth type of photopsin (Windericks et al, 1992), and this evidence suggests that if monkeys can do the same (albeit with a third photopsin) and develop the capacity to use their extra photopsin, humans may be able to. Evidence of human ability to create neural mechanisms in order to use the information from the fourth photopsin is not as conclusive as evidence from new world monkeys as it is not possible to use microspectrophotometer techniques. Behavioural evidence has illustrated some possible cases of full tetrachromacy however. Jordan and Mollen (1993) asked heterozygous carries of anomalous trichromacy and trichromatic controls to adjust a mixture of green and orange light, and yellow and red light, to obtain a match. They found no significant difference in behaviour between the two groups, suggesting either that this is not a sensitive enough measure of tetrachromacy, or that people may carry four wavelength sensitive cones, but cannot actually use them due to the structure of the brain. Jordan and Mollen (1993) did find one person however, who they label as cDa7, who found only one combination of the two mixtures that would give a match. The other trichromatic controls and the heterozygous carriers had a greater variability in the repeated responses they gave on the ratio matching tasks, whereas cDa7 repeatedly gave the same response. This implies that she had greater ability to distinguish between the colours to gain a precise match and therefore her visual system was using tetrachromatic vision as opposed to the extra, shifted cone not being utilised. It may be that all the heterozygous carriers used in the study did have tetrachromatic vision, it was just that cDa7 had shifted opsins far enough away from the original cones required from trichromacy, to be detected by such behavioural techniques. Overall however, it suggests that even if all the heterozygous carriers do have tetrachromatic vision which has not been picked up by the tests, their vision cannot be considerably different to that of a trichromatic's vision. To further research this area, Jameson et al, (2001) tried to investigate tetrachromacy using techniques that they considered to be more reliable, and found a far higher incidence rate of tetrachromacy. Jameson et al, (2001) propose that ratio matching is not a reliable technique to measure tetrachromacy because it does not take into consideration real world viewing situations, such as surfaces, textures and surround contexts variations. It was suggested that many colour vision mechanisms only become active when there is sufficient variation and context in the light, which cannot be captured by ratio matches. Instead Jameson et al, (2001) asked participants to identify spectral delineations for a diffracted spectral stimulus. Although this is not entirely reflective of real world viewing conditions, it does offer more variability to the retina than simple ratio matching techniques. It was found from this that heterozygous carriers of the two types of red opsin, delineated more bands of colour in the diffracted spectrum than a control group of non heterozygous trichromatic females. This removes any differences that may be attributed to gender (Jameson et al, 2001) and also implies that the two groups of females are experiencing different perceptions of colour. This also suggests that the heterozygous carriers are experiencing strong tetrachromacy and that their visual system is utilising the fourth photopsin. This evidence demonstrates a stronger tendency for heterozygous females to exhibit tetrachromatic colour vision than Jordan and Mollen (1993) found, and it is likely that this is a more sensitive measure of colour perception. It also suggests that the viewing experiences of women who have the propensity to be tetrachromatic, in this case, is more advanced than women who are not heterozygous than expected by Jordan and Mollen (1993). Further evidence that the human visual system should be able to accommodate a fourth wavelength specific cone comes indirectly from Neitz, Carroll, Youmauchi, Neitz and Williams, (2002). They demonstrated that the visual system is plastic and can adapt to environmental stimuli after it is fully developed. Neitz et al, (2002) asked people to wear coloured filters to alter their chromatic experience. They found that as a result of this there was a shift in colour perception which lasted for nearly two weeks after the filters had been removed. This shows the nervous system's ability to use experience gained from the environment and adjust the inputs to the red and green channel to accommodate this. The implication of this is that if the visual system can adapt and change inputs to the red and green system to external stimuli, it should also be able to do the same to internal stimuli, such as receiving input from an extra photopsin. The majority of the evidence discussed suggests that there are tetrachromats. It has been shown by Winderickx et al, (1992) and Cohn et al, (1989) that physiologically a woman can posses four different types of wavelength specific cones. Whether women in this position have the neural mechanisms to utilise an extra cone is more controversial. It has been shown behaviourally that women with four cones can be distinguished from women who have three, particularly by Jameson et al, (2001), and as this can be demonstrated behaviourally it implies that the women are having a different perceptual experience of colour than women who have three cones. It would also make sense for the visual system to adapt to an extra photopsin because the nervous system can change and update itself, and this has been demonstrated by Neitz et al, (2002). The fact that the extra photopsin is only six nanometres (Winderickx et al, 1992) away from the long wavelength specific cone suggests that if there are tetrachromats, as there appear to be, their colour vision is not likely to be much superior to a trichromats. As it has been shown by Jordan and Mollen, on simple behavioural tasks such as ratio matches there does not appear to be much difference at all. It is likely that cDa7 had a larger shift than the expected six nanometres to show tetrachromatic behaviour on these assessments. It appears conclusive that women can have four different wavelength specific cones, although the extent to which the extra is utilised and an advantage to colour vision still requires further investigation.