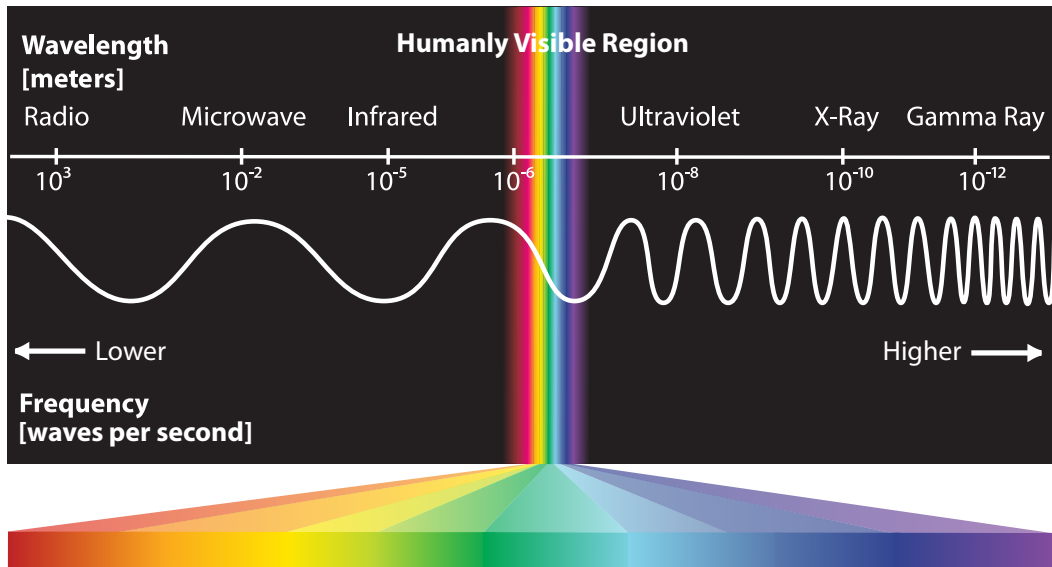


# Human Potential for Tetrachromacy

by Kimberly A. Jameson



**Figure 1.** The Sun's electromagnetic spectrum with the small portion that is visible to humans highlighted by pseudo-coloring. Scale shown is approximate, created based on information from The U.S. Department of Energy Lawrence Berkeley National Laboratory website ([www.lbl.gov/MicroWorlds/ALSTool/EMSpec/EMSpec2.html](http://www.lbl.gov/MicroWorlds/ALSTool/EMSpec/EMSpec2.html)).

Nature's color palette—the changing sky, autumn leaves, the tinted irises of beloved eyes—has allured human interest since time immemorial. Scientific advances over the past twenty years have led to a far better understanding of the relevance and physiological basis of color experience than ever before. Recent research in molecular genetics, color perception and cognitive psychology is clarifying the underpinnings of human color sensations, how color experience has evolved, and along which perceptual paths we might be headed as a species of color-experiencing individuals. Together, such advances suggest that extensions of color perception theory are needed to account for retinal photopigment diversity unanticipated by accepted models of color vision trichromacy.

## Why do we experience color?

The ability to perceive color is so natural that we rarely consider its origin. Color perception, like

perception of texture or motion, occurs when our visual system encounters illuminated objects. This ability to detect surface variation by sampling the light, or spectra, reflected off environmental objects is widespread across species. Humans enjoy color by processing reflected spectra within a narrow (~380 nm to ~780 nm) “visible” range of electromagnetic wavelengths (Figure 1). Color requires both (i) photon capture by photoreceptors and (ii) encoding of photoreceptor excitation ratios.

The number of colors humans can distinguish varies across individuals, and is generally estimated to be between one and ten million. Perceived color variation is due to the ways our available photoreceptors react to reflected light. Photoreceptor response sensitivities also underlie *metameric* color equivalence classes (object reflectance spectra that have different physical forms but produce the same color percept) (Figure 2). The existence of natural and man-made metameric

classes of reflectance spectra, and their variation *vis-à-vis* observer's photopigments, give strong evidence that profiles of light reflected off objects are not uniquely colored. Indeed, object reflectance spectra are only electrical and magnetic pulses of photon energy waves, which do not *contain* any color, or even have any visual features. Thus, color is an internal construction.

### What is color vision for?

**D**espite the non-unique mapping from color to reflected light, color cues are used in detecting targets against dappled backgrounds, perceptual segregation and object identification or categorization by color.<sup>1</sup> During non-human primate evolution, an ability to detect color differences from surface reflectances was likely selected for because it provided a means of signaling for the species. Perhaps color permitted the identification of carbohydrate rich fruit or tender leaves,<sup>1, 2, 3, 4, 5</sup> or aided social interaction through detecting physiological states of conspecifics.<sup>6, 7, 8</sup> The benefits of such color vision capabilities may have played an important role in the evolution of non-human primates into humans. Thus, although color is not a physical property of the world, and considerable color perception variation exists among humans, the ability to perceive color in the environment seems evolutionarily important.

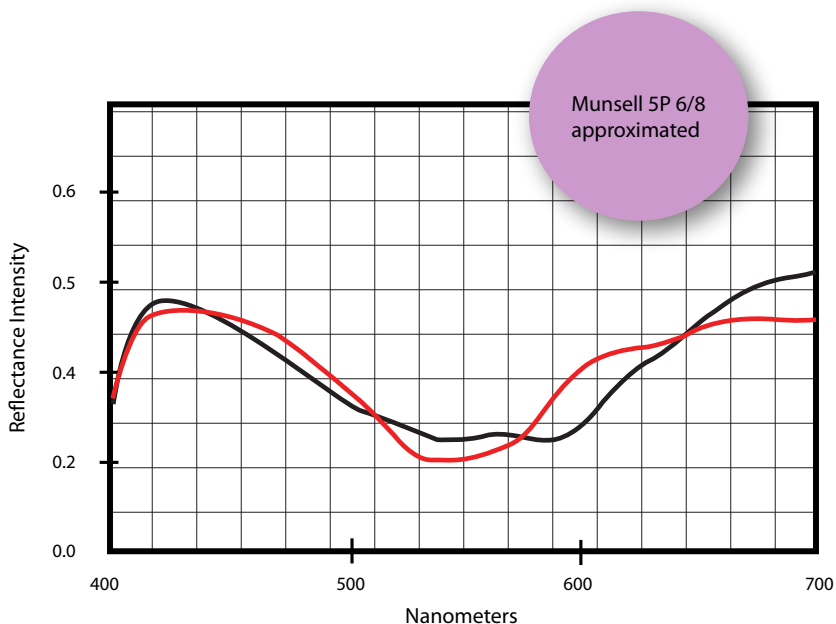
### The genetic basis of color vision.

**A**s mentioned, color stems from object reflectance spectra, through comparisons of different photoreceptor class signals that arise from the probabilistic capture of reflected photons from a usable portion of the electro-

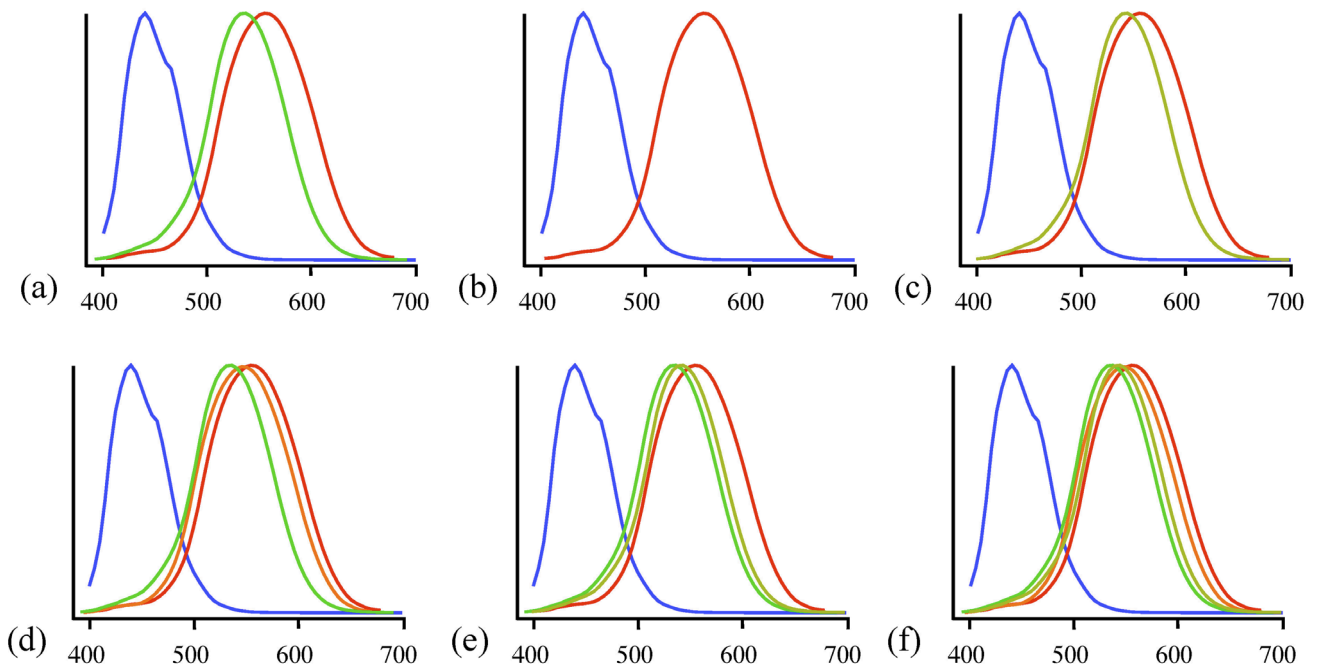
magnetic spectrum. The contrast encoding of receptor excitation is essential because a photoreceptor whose sensitivity distribution peaks around 540 nm only communicates the varying presence stimulating light to the brain, not its wavelength. It only says "I'm responding, I'm responding!" it does not communicate "I'm responding and I'm greenish!" The "greenish" part of the message comes when signals from different photoreceptor types are subsequently compared, beyond the retina.

Humans derive color information from responses of typically three cone classes containing different photopigments, distributed by the millions across the retina. These different cone classes are generated through expression of different opsin genes. Opsin genes with different amino acid sequences and a light-absorbing chromophore can produce photoreceptor classes with drastically different absorption spectra.

Genetic sequences identified for human light-sensitive pigments include: (a) the chromosome-3 linked rod rhodopsin pigment<sup>9</sup> that interacts with color vision at low



**Figure 2.** Two curves showing metamerically equivalent reflectance spectra under a standard observer model. Both reflectances produce the same lavender color appearance (Munsell color chip 5P 6/8) shown approximated by the inset circle. The lavender screen sample of Munsell 5P 6/8 was rendered Aug. 26, 2009 at [www.myperfectcolor.com/Match-of-Munsell-5p-6-8-p/mpc0110461.htm](http://www.myperfectcolor.com/Match-of-Munsell-5p-6-8-p/mpc0110461.htm). Special thanks to Professor A. Kimball Romney for providing the reflectance spectra for use here



**Figure 3** (above). Several known and estimated variations in human retinal phenotypes linked to variation in photopigment opsin genes. Curves illustrate the responsivity of different photoreceptor classes to the electromagnetic spectrum.[46] Top row depicts known observer models, bottom row depicts estimated observer models. Panel (a) shows a normal trichromat observer with short- (SWS), medium- (MWS) and long- (LWS) wavelength sensitive photopigment classes; (b) a deficient dichromat, a form classically known as “Daltonism” (a Deuteranope-type missing MWS photopigment)[19]; (c) an anomalous trichromat (Deuteranomalous with shifted MWS photopigment); (d) a retinal tetrachromat with two LWS pigment classes in addition to the usual SWS and MWS photopigment classes; (e) a retinal tetrachromat with two MWS in addition to SWS and LWS photopigment classes; and (f) a retinal pentachromat with two MWS and two LWS photopigment classes in addition to the SWS photopigment. Uncertainty and debate exist regarding the phenotype expression of forms (e) and (f).

light levels; (b) the chromosome-7 linked short-wave sensitive cone photopigment; and (c) the X-chromosome linked middle- and long-wave sensitive cone photopigments.<sup>10</sup> Genes for the X-chromosome linked photopigments are the basis for our color sensitivity at the mid- and long-wave portions of the visible spectrum, M-opsins and L-opsins, respectively, and share 98% gene sequence similarity.<sup>11, 12, 13</sup> The structure and function of X-linked opsin genes reveal much about their evolutionary purpose as a highly adaptive component of the visual system. Several genetic features support this idea. First, considering naturally occurring genetic variations, the ability to differentiate appearances of predominantly long-wavelength frequencies from medium-wavelength frequencies arose in our primate ancestors via straightforward X-linked *gene duplication* – a key process in evolving new gene functions. Second, a single missing or different amino acid (called “SNP” for single-nucleotide polymorphism) in certain portions of the opsin gene sequence produces dramatic shifts in the visual response to light.<sup>14, 15</sup> And third, duplication, divergence, intra- and inter-genic cross-overs and unequal recombination are all normal operating procedures for M- and L-cone opsin genes.

These opsin gene features contribute to differences in retinal photopigment response properties. Figure 3 shows typical retinal photopigment responses (a), compared to several variations (b-f).

The initial identification of opsin gene sequences yielded unexpected M- and L-opsin gene variation.<sup>16</sup> Subsequent research found many M- and L-opsin gene sequence variants are systematically linked to the peak responses of photopigment absorption curves.

Measuring spectral response properties of different photopigment variants *in vivo* is complicated by varying optical density of pigments, cell “wave-guiding” morphology, and ocular media filtering. Nevertheless, variations in color vision phenotypes are traceable to genetic variation, so it’s viable to use individual opsin genotypes to investigate behaviors associated with phenotype variation.

Interestingly, the X-linked inheritance of these photopigments implies that some women have different long-wavelength sensitive opsin genes on each X-chromosome and, consequently, the genetic potential to express more than the usual three photopigment classes (see online supplement at [www.](http://www.)

glimpsejournal.com/2.3-KAJ.html#1). These heterozygous females are among those considered *putative retinal tetrachromats*<sup>17</sup> and may express (in addition to rods) four retinal cone classes, each with a different spectral sensitivity distribution, thus having the potential to experience tetrachromatic vision.<sup>18</sup>

### Individual variation and color perception experience.

**M**uch human color perception research has explored the impact of individual differences in photopigments on color perception. Response curves of observer types in the top row of Figure 3 are well-understood. Figure 3 shows (a) a normal Trichromat; (b) a deficient Dichromat; and (c) an Anomalous Trichromat. Types (b) and (c) are measurable color perception deficiencies.

Figure 3 (d), (e) and (f) show less well-understood forms of normal individual variation that approximate phenotypes which in theory could arise due to expressed opsin gene variation. Demonstrating such types *in vivo* is difficult due to considerable response similarity among the photoreceptor classes. However, their existence has been described in several studies.<sup>17, 18, 20, 21, 22</sup> Existence of type (d) individuals with four distinct retinal cone classes is now generally acknowledged, even if types (e) and (f) are still debated.<sup>13</sup> Type (d) is key here, and is referred to as a retinal tetrachromat.<sup>22, 23</sup>

Figure 3's message is that flexibility in the structure of the X-linked opsin genes facilitates change in the genetic basis for human color vision. This same flexibility is widespread across species<sup>12</sup> perhaps suggesting that evolving opsin gene variety itself poses no inherent evolutionary disadvantages.

### What do individual differences imply for emergent tetrachromacy?

**T**he observer modeled in Figure 3(d) is a retinal tetrachromat, and possibly a *functional tetrachromat*<sup>23</sup> who might experience color perception differences compared to a normal trichromat, and could exhibit non-normative color processing behavior on certain color perception tasks<sup>18</sup> (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#2](http://www.glimpsejournal.com/2.3-KAJ.html#2)). Figure 4 simulates some color perception differences arising from variations shown in Figure 3(a-c) and illustrates that under such observer variations object color is clearly observer-dependent and cannot *belong* to the object.

Understanding these normal individual differences and color vision deficiencies<sup>24</sup> help us appreciate: (1) the extent of natural variation in color perception, (2) how little such differences have mattered historically with respect to color utility, and (3) the implications for emerging tetrachromacy at both observer- and species-level.



### THE AMERICAN FLAG AS SEEN

- I.- BY MOST PEOPLE.
- II.- BY RED-BLIND PERSONS.
- III.- BY GREEN-BLIND PERSONS.
- IV.- BY VIOLET-BLIND PERSONS.
- V.- BY TOTALLY COLOR-BLIND PERSONS.

**Figure 4.** Illustration approximating the appearance of a United States Flag for color vision normals and some color deficient observers. Courtesy of the National Archives (University of Wisconsin, Americana collection, 1437652)

Neitz et al. suggested that "extra pigment types in people with normal color vision are sufficiently different to support tetra- or even pentachromacy," but like most early researchers, downplayed the possible effects of retinal tetrachromacy, further stating, "The fact that they don't indicates that the trichromacy of normal vision has its origin at a level of the visual pathway beyond that of the cone pigments, likely beyond the receptors."<sup>25</sup>

Recent results demonstrating perceptual consequences of retinal tetrachromacy complicates this accepted model of trichromacy. A three-channel post-receptor processing constraint would eviscerate new information available through retinal tetrachromacy by reducing it to a trivariant signal. Observing that signals from additional photoreceptors get used, and yield variation in perceptual experience, therefore requires an update to accepted theory. This remains a topic of considerable debate.

### **Is the idea of potential human tetrachromacy really so strange?**

Since the discovery of allelic variants of human long-wavelength and medium-wavelength photopigments, there's been a good deal of popular speculation about the implications for color perception. For example, the *Financial Times*, "Weird Science" section explored "Women Who Can See More Than Red" (March 10, 2001, p. 11).

The potential for human tetrachromatic color perception need not be spun into a Sci-Fi fantasy of beings with supranormal vision. In fact, opsin gene diversity within primate species, and the natural adaptive flexibility of opsin gene structure and function, both foreshadow a real potential for human tetrachromacy in the evolutionary pipeline.

Already, evidence of tetrachromacy exists in a number of animal species (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3](http://www.glimpsejournal.com/2.3-KAJ.html#3)). While most mammals are dichromats, three to five photopigments are otherwise common. At the upper extreme are mantis shrimp which seem to make use of eleven different photopigments.<sup>26</sup> Responding, in part, to environmental changes, formerly trichromatic fish species have evolved several extra photopigments in as short as 1-2 million years, and this is linked to species' opsin gene diversity driven by evolutionary selection pressures<sup>27</sup> (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3a](http://www.glimpsejournal.com/2.3-KAJ.html#3a)). Opsin gene diversity and flexibility is also seen in non-human primates. Some New World primates exhibit considerable opsin gene diversity within species<sup>28</sup> (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3b](http://www.glimpsejournal.com/2.3-KAJ.html#3b)). Old World primate studies comparing human and chimpanzee opsin genes suggest an ongoing processes of gene conversion for some human photopigment opsin genes<sup>29, 30</sup>

(see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3c](http://www.glimpsejournal.com/2.3-KAJ.html#3c)). And advances using transgenic therapy have transformed dichromat primate individuals into trichromats, permitting otherwise unexperientable color sensations, and demonstrating that rapid, dramatic changes are possible in the primate neural coding of color<sup>31, 32</sup> (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3d](http://www.glimpsejournal.com/2.3-KAJ.html#3d)).

### **But isn't human trichromacy already optimized for our environment?**

Shepard describes human trichromacy as the most effective way to visually process and encode terrestrial light.<sup>33</sup> However, considering that many other terrestrial animals need more than three functional photopigment classes, the optimality of the human system feels anthropocentric. Additional complications come from species with more than three photopigments operating in spectral ranges not hugely different from humans. The European Starling's color discrimination performance, for example, suggests that at least some of the bird's three photopigments couple with a fourth (that peaks in the near UV) within the range of 400-700 nm (see online supplement at [www.glimpsejournal.com/2.3-KAJ.html#3e](http://www.glimpsejournal.com/2.3-KAJ.html#3e)). Thus, in the human visible range, Starling tetrachromacy is a viable form of color processing.<sup>34</sup>

### **What are the selection pressures that might cause tetrachromacy to emerge?**

The possibility of human tetrachromacy raises two intriguing considerations: (1) what visual processing demands provide positive selection pressure for tetrachromacy? and (2) what would color vision be like for a tetrachromat?

We don't know the answers to either question, but recent investigations of putative female tetrachromats are places to start. Research has found color perception differences (albeit, subtle) in comparisons of possible tetrachromat women with trichromat controls.

Rigorous psychophysical studies of potential tetrachromat color perception exist<sup>20, 21, 35</sup> but are equivocal on the precise variation experienced under retinal tetrachromacy. Limitations in display technology and stimulus presentation formats may have historically hindered demonstration of such differences, if they exist, using traditional psychophysical methods.<sup>23</sup> Investigations attempting to avoid such obstacles employ increased stimulus complexity and more

naturalistic color processing conditions and behaviors.<sup>17, 22, 36</sup> These investigations used molecular genetic methods to identify potential retinal tetrachromats and found differences in perceptual behaviors when the genetic potential for more than three photopigment classes was present. Behaviors differentiating tetrachromat genotypes from trichromat controls included: (1) perceiving more colors in diffracted spectra;<sup>22</sup> (2) correlation between performance variation on a standardized test for trichromacy and indices of richer color experience;<sup>17</sup> and (3) color similarity and color naming pattern variation found in shared group consensus measures from potential tetrachromats compared to female trichromat controls.<sup>36</sup>

These results show that when color judgments were made in empirical conditions that approximated more naturalistic viewing circumstances (e.g. binocular viewing of contextualized large-field stimuli), processing variation correlated with human tetrachromacy was easier to demonstrate. But more specifically, the results show that the genetic potential to express more than three cone classes correlated with differences in color categorization, naming and color similarity judgments.

Such results imply real world consequences for individuals with extra opsin genes. For example, Jameson et al.<sup>17</sup> suggests that one color vision test widely used in industry and the military can inadvertently classify putative tetrachromats as deficient when they may actually have richer color perception experience.

Moreover, Sayim et al.<sup>36</sup> found that in some portions of color space individuals with tetrachromat genotypes shared, as a group, cognitive color-similarity representations and a color linguistic code with higher consensus (compared to trichromat controls), perhaps reflecting color expertise among such individuals. Such findings may suggest why individuals vary greatly regarding color judgments in art, publishing, architecture and design.

Finally, concerning color categorization research, one might think the existence of specialized groups of color observers in a population would create problems for a population's evolution of a shared color naming and categorization system. That is, if subsets of a society's individuals use different perceptual categories for identifying objects, how can successful communication occur among all members, and how could a shared color communication system evolve?

We used computer simulation approaches from evolutionary game theory to investigate such questions using simulated color category learning scenarios.<sup>37, 38, 39, 40</sup> Our results showed no obstacles to evolving stable categorization solutions in populations that include agents modeled with normal, deficient and putative tetrachromat discrimination data. Indeed, some aspects of population observer

diversity actually help color categorization systems form and stabilize in simulation scenarios.<sup>37, 38</sup> If analogous to color category evolution in real world linguistic societies, these results suggest that no significant communication obstacles would be expected from societies comprised of realistic proportions of normal, dichromat and tetrachromat individuals, each with varying forms of color perception and potentially different salient color categories for object identification and communication.

### **Speculations on a future for tetrachromacy...**

**T**he foregoing gives clues concerning how human tetrachromacy might prove advantageous today, but we can't predict which kinds of present-day color judgments herald behavioral advantage for the long-term. It's possible that early non-human primate mutations in the gene structure may have been largely due to selection pressure from the environment, whereas more recent mutations may be additionally driven by social and sexual forms of evolutionary pressure. Under changing circumstances, several future evolutionary scenarios are plausible:

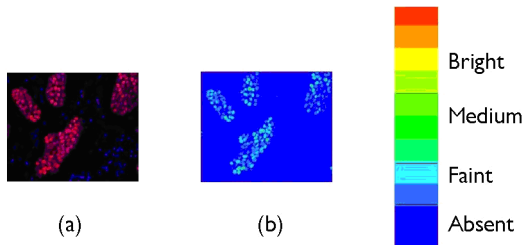
#### ***Interpretation of human emotion states.***

Changizi et al.<sup>41</sup> suggested trichromacy evolved to detect important physiological states using color correlates of blood-oxygenation levels among non-human primates. So too, color correlates of emotion states might be important cues for successful social interaction and appropriate interpretation of emotion expressions among human conspecifics.<sup>42</sup>

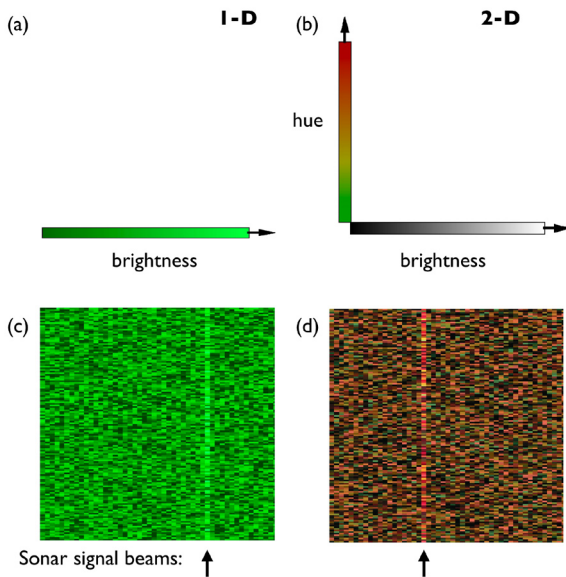
#### ***Disease detection.***

Historically, color perception has been important in medicine. Medical practitioners note red in a rash, yellowness of jaundice and the colors of a healthy body.<sup>43</sup> Modern day doctors use color stains in cell histology and color codes on medical instruments.<sup>24</sup> Color deficient doctors may miss symptoms because of an inability to perceive the color of disease.

Informally we observed results that, although unpublished, are consistent with the idea that tetrachromacy may inform us about the uses of color in evolving technologies, for example, in medical diag-



**Figure 5.** Digitized image (b) at right translates the fluorescent intensity of each cell in image (a) at left using the chromatographic scale shown at right. The scale shows that the brighter the cell, the more protein expressed. Raters count the number of bright, medium and faintly stained cells. The potential problem is that detection of the medium cells is likely to be different for raters possessing opsin gene polymorphisms (i.e., putative tetrachromats) compared to those who do not.



**Figure 6.** Multidimensional information coding: panel (a) shows the one dimensional gradient code used in monochrome (green) brightness code. Panel (b) shows two dimensions of a combined brightness and color code. Panel (c)--showing a sonar signal beam in monochrome code--and Panel (d)--showing a signal in a brightness-color code--show the two forms of the displays tested in visual processing circumstances experienced by sonar scope operators in U.S. military applications and college undergraduates.<sup>44</sup>

nosis. We found that laboratory assistants with tetrachromat genotypes gave different pathology diagnoses when certain cell stain scales were used in histology studies. Figure 5 (b) shows an example of the type of fluorescent cell marker (with adjacent color scale), that when used to color code panel (a) produced different estimates of cancer cell detection by potential tetrachromats compared to observers without such potential.

Co-evolutionary social pressures along these lines may have served in the past, and could serve in the future, as factors encouraging human tetrachromacy.

### **Processing color in contextually rich information displays.**

Using color to identify objects involves combining different types of information, or perceptual dimensions, during information processing. While trichromacy gives greater color discrimination, studies show that color deficient dichromats may be better at detecting targets in color camouflage.<sup>44</sup> Dichromats do this by picking out targets using luminance differences that get drowned out for trichromats by the chromatic content they appreciate. Such signal processing is a consideration for modern information displays, because while display designers want to simultaneously present all sorts of information, not all observers can easily interpret multidimensional display codes. Jameson and colleagues examined whether a one-dimensional brightness code typically used in sonar applications (Figure 6(a)) could be combined with a second dimension of color code (Figure 6(b)) to add an extra layer of information to the standard data display.<sup>45</sup> They found that normal trichromat observers could extract two forms of information from the 2-dimensional display codes on par with the 1-dimensional code performance. Thus, observers (i) reliably detected slightly brighter signal beams in the multicolored panels (Figure 6(d)), while (ii) correctly identifying information conveyed by color in the same display (e.g., whether a signal was primarily reddish, greenish, or yellowish). Dichromats would find task (i) easy, whereas task (ii) would be difficult for a dichromat with red-green confusion.

This ability to extract two forms of information from a combined code exemplifies how color dimensions could be easily separated under human tetrachromacy.

It's unclear whether in contextually-rich scenes tetrachromacy might permit identification of signal dimensions overlooked by trichromats when displayed information encodes two, three or

four dimensions of data. Obviously any such tetrachromat performance difference may be both subtle and might apply for some portions of the color space but not others.


## Summary

The story of photopigment evolution suggests human tetrachromacy may be in the pipeline. Visual pigments of vertebrates evolved about 500 million years ago (mya). Precursors of modern day human visual pigments were likely an adaptation that began in the Cretaceous period, around 150 to 80 mya. The flexibility of the opsin gene structure has permitted adaptive changes in the past, and is almost certainly ready to adapt if needed in the future. There's no need to assume that an evolutionary zenith is realized in modern human photopigment opsin genes. If the human species survives long enough, some selective advantage, or form of co-evolution, may provide strong a justification human color vision tetrachromacy. There seem to be distinctly different ways to think about emergent human tetra-chromacy:

On the one hand, one can entertain the possibility that human tetrachromacy reflects an on-going, natural, evolutionary potential for human visual processing. If a need arose in our environment (like dramatic environmental changes seen during the Cretaceous period, or a highly valued social trend that established a uniform color bias) human photopigment genes would be ready to meet the challenge.

On the other hand, a narrower approach focuses on sensationalizing deviations in perceptual experience brought about by tetrachromacy compared to trichromacy (cf. the *Financial Times* "super-perceiver" perspective noted earlier).

Of these, the view of human tetrachromacy as a natural evolutionary potential seems more useful. Considerable color perception variations already exist among and within dichromat, anomalous trichromat and normal trichromat observer groups without major behavioral consequences or evolutionary meltdowns. Further research should show human tetrachromacy to

be correlated with subtle individual color perception variations that are no more problematic than those that already exist. While the impact of potential human tetrachromacy may turn out to be important for some applications, in general, its impact is likely to be nonproblematic at the practical levels of modern life. Even so, tetrachromacy is highly significant for theories of perception and theories of human evolution. 

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## References

1. Mollon, J.D., "Tho she kneel'd in that place where they grew," *The Journal of Experimental Biology* 146, 21-38 (1989).
2. Osorio, D. and Vorobyev, M., "Colour vision as an adaptation to frugivory in primates," *Proceedings of the Royal Society B* 263, 593-599 (1996).
3. Regan, B.C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P. and Mollon, J.D., "Fruits, foliage and the evolution of primate colour vision," *Philosophical Transactions of the Royal Society B* 356, 229-283 (2001).
4. Dominy, N.J. and P.W. Lucas, "Ecological importance of trichromatic vision to primates," *Nature* 410, 363-366 (2001).
5. Lucas, P.W., Dominy, N.J., Riba-Hernandez, P., Stoner, K.E., Yamashita, N., Loría-Calderón, E., Petersen-Pereira, W., Rojas-Durán, Y., Salas-Pena, R., Solis-Madrigal, S., Osorio, D. and Darvell, B.W., "Evolution and function of routine trichromatic vision in primates," *Evolutionary Anthropology* 57, 2636-2643 (2003).

6. Sumner, P. and Mollon, J.D., "Colors of Primate Pelage and Skin: Objective Assessment of Conspicuousness," *American Journal of Primatology* 59, 67-91 (2003).
7. Changizi, M.A., Zhang, Q. and Shimojo, S., "Bare skin, blood and the evolution of primate colour vision," *Biology Letters*, 2(2), 217-221 (2006).
8. Fernandez A.A. and Morris M.R., "Sexual selection and trichromatic color vision in primates: statistical support for the preexisting-bias hypothesis," *American Naturalist* 170, 10-20 (2007).
9. Sparkes, R.S., Mohandas, T., Newman, S.L., Heinzmann, C., Kaufman, D., Zollman, S., Leveille, P.J., Tobin, A.J. and McGinnis, J.F., "Assignment of the Rhodopsin Gene to Human Chromosome 3," *Investigative Ophthalmology & Visual Science* 27, 1170-1172 (1986).
10. Nathans, J., Thomas, D. and Hogness, D.S., "Molecular genetics of human color vision: The genes encoding blue, green, and red pigments," *Science* 232, 193-202 (1986).
11. Jacobs, G.H. and Nathans, J., "The Evolution of Primate Color Vision," *Scientific American*, 32-39 (April 2009).
12. Jacobs, G.H., "Primate color vision: A comparative perspective," *Visual Neuroscience* 25, 619-633 (2008).
13. Gegenfurtner, K.R. and L.T. Sharpe, "Color Vision: From Genes to Perception," (Cambridge University Press, 1999).
14. Winderickx, J., Lindsey, D.T., Sanocki, E., Teller, D.Y., Motulsky, A.G. and Deeb, S.S., "Polymorphism in red photopigment underlies variation in colour matching," *Nature* 356, 431-433 (1992).
15. Sanocki, E., Lindsey, D.T., Winderickx, J., Teller, D.Y., Deeb, S.S. and Motulsky, A.G., "Serine/alanine amino acid polymorphism in the L and M cone pigments: Effects on Rayleigh matches among deuteranopes, protanopes and color normal observers," *Vision Research* 33, 2139-2152 (1993).
16. Nathans, J., Piantanida, T.P., Eddy, R.L., Shows, T.B. and Hogness, D.S., "Molecular genetics of inherited variation in human color vision," *Science* 232, 203-210 (1986).
17. Jameson, K.A., Bimler, D. and Wasserman, L.M., "Re-assessing Perceptual Diagnostics for Observers with Diverse Retinal Photopigment Genotypes," In *Progress in Colour Studies 2: Cognition*, Pitchford, N.J. and Biggam, C.P., eds., (Amsterdam: John Benjamins Publishing Co., 2006)13-33.
18. Mollon, J.D., "Worlds of Difference," *Nature* 356, 378-379 (1992).
19. Dalton, J., "Extraordinary facts relating to the vision of colours: with observations," *Memoirs of the Literary and Philosophical Society of Manchester* 5, 28-45 (1798).
20. Nagy, A.L., MacLeod, D.I.A., Heyneman, N.E. and Eiser, A., "Four Cone Pigments in Women Heterozygous for Color Deficiency," *Journal of the Optical Society of America* 71, 719-722 (1981).
21. Jordan, G. and Mollon, J.D., "A Study of Women Heterozygous for Color Deficiencies," *Vision Research* 33, 1495-1508 (1993).
22. Jameson, K.A., Highnote, S.M. and Wasserman, L.M., "Richer Color Experience in Observers with Multiple Photopigment Opsin Genes," *Psychonomic Bulletin and Review* 8(2), 244-261 (2001).
23. Jameson, K.A., "Tetrachromatic Color Vision," Invited contribution to *The Oxford Companion to Consciousness*, Wilken, P., Bayne, T. and Cleeremans, A., eds. (New York: Oxford University Press, 2009), 155-158.
24. Birch, J., *Diagnosis of Defective Colour Vision*, (London: Butterworth-Heinemann, 2001).
25. Neitz, M., Neitz, J., and Jacobs, G.H., "More than three different cone pigments among people with normal color vision," *Vision Research* 33, 117-122 (1993).
26. Kelber, A., Vorobyev, M. and Osorio, D., "Animal colour vision - behavioural tests and physiological concepts." *Biological Reviews* 78, 81-118 (2003).
27. Carleton, K., "Cichlid fish visual systems: mechanisms of spectral tuning," *Integrative Zoology* 4, 75-86 (2009).
28. Jacobs, G.H. and Deegan, J.F., II, "Polymorphic New World monkeys with more than three M/L cone types," *Journal of the Optical Society of America A*, 22, 2072-2080 (2005).
29. Verrelli, B.C., Lewis, C.M. Jr., Stone, A.C. and Perry, G. H., "Different Selective Pressures Shape the Molecular Evolution of Color Vision in Chimpanzee and Human Populations," *Molecular Biology and Evolution* 25, 2735-2743 (2008).

30. Verrelli, B.C., Tishkoff, S.A., "Signatures of selection and gene conversion associated with human color vision variation," *The American Journal of Human Genetics* 75, 363-375 (2004).
31. Mancuso, K., Neitz, J., Hauswirth, W.W., Connor, T.B. and Neitz, M., "Gene therapy treatment of color blindness in adult primates," *Journal of Vision* 7, 15a [Abstract 15, I doi:10.1167/7] (2007).
32. Mancuso, K., Hauswirth, W.W., Li, Q., Connor, T. B., Kuchenbecker, J.A., Mauck, M.C., Neitz, J. and Neitz, M., "Gene therapy for red-green colour blindness in adult primates," *Nature* [Advance online publication I doi:10.1038/nature08401] (2009).
33. Shepard, R.N., "The perceptual organization of colors: An adaptation to regularities of the terrestrial world?" In *The Adapted Mind; Evolutionary Psychology and the Generation of Culture*, Barkow, J.H., Cosmides, L., and Tooby, J., eds. (New York: Oxford University Press, 1992) 495-531.
34. Smith, E.L., Greenwood, V.J. and Bennett, A.T.D., "Ultraviolet colour perception in European starlings and Japanese quail," *The Journal of Experimental Biology* 205, 3299-3306 (2002).
35. Hood, S.M., Mollon, J.D., Purves, L. and Jordan, G., "Color discrimination in carriers of color deficiency," *Vision Research* 46, 2894-2900 (2006).
36. Sayim, B., Jameson, K.A., Alvarado, N. and Szeszel, M.K., "Semantic and Perceptual Representations of Color: Evidence of a Shared Color-Naming Function," *The Journal of Cognition & Culture* 5, 427-486 (2005).
37. Jameson, K.A. and Komarova, N.L., "Evolutionary models of color categorization. I. Population categorization systems based on normal and dichromat Observers," *Journal of the Optical Society of America A*, 26(6), 1414-1423 (2009).
38. Jameson, K.A. and Komarova, N.L., "Evolutionary models of color categorization. II. Realistic observer models and population heterogeneity," *Journal of the Optical Society of America A*, 26(6), 1424-1436 (2009).
39. Komarova, N.L. and Jameson, K.A., "Population Heterogeneity and Color Stimulus Heterogeneity in Agent-based Color Categorization," *Journal of Theoretical Biology* 253, 680-700 (2008).
40. Komarova, N.L., Jameson, K.A. and Narens, L., "Evolutionary Models of Color Categorization based on Discrimination," *Journal of Mathematical Psychology* 51, 359-382 (2007).
41. Changizi, M.A., Zhang, Q. and Shimojo, S., "Bare skin, blood and the evolution of primate colour vision," *Biology Letters* 2(2), 217-221 (2006).
42. Yasuda, M., Webster, S., and Webster, M., "Color and facial expressions," *Journal of Vision* 7(9), 946, 946a. [Abstract I doi:10.1167/7.9.946] (2007).
43. Spalding, J.A.B., "Medical students and congenital colour vision deficiency: Unnoticed problems and the case for screening," *Occupational Medicine* 49, 247-252 (1999).
44. Morgan, M.J., Adam, A. and Mollon, J.D., "Dichromats detect colour-camouflaged objects that are not detected by trichromats," *Proceedings of the Royal Society: Biological Sciences* 248, 291-295 (1992).
45. Jameson, K.A., Kaiwi, J. and Bamber, D.E., "Color-Coding Information with Psychological-Constant Hue Loci: Assessing Alternative Coding Schemes using Independent Brightness and Hue Dimensions," *Journal of Experimental Psychology: Applied* 7(2), 112-128 (2001).
46. DeMarco P., Pokorny J. and Smith, V.C., "Full-spectrum cone sensitivity functions for X-chromosome-linked anomalous trichromats," *Journal of the Optical Society of America A: Optics Image Science and Vision* 9, 1465-1476 (1992).