# TETRACHROMATIC COLOR VISION

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The term"tetrachromacy" describes the physiological possession of four different classes of simultaneously functioning retinal photopigments (also called "weak tetrachromacy"). From an empirical standpoint, tetrachromatic color vision (or "strong tetrachromacy") additionally requires demonstrating that mixtures of four independent appropriately chosen primary lights will simulate all distinctions in appearance possible in visible color space. Independence of the primary lights implies that no mixtures of any subset of these lights (or their intensity variants) will produce an identical match to any combination of mixtures of the remaining lights. By comparison, trichromacy empirically requires only three primaries to simulate all visible colors.

Established theory states that normal color vision humans are trichromats (as, primarily, are Old World monkeys and apes). The first element of trichromacy is the output from three simultaneously functioning retinal cone classes: Short-, Medium-, and Long- Wavelenth Sensitive (SWS, MWS, & LWS) cones. Three cone classes alone do not establish a trichromat color code, however. A postreceptoral code for three categories of signal is also needed. A standard vision science assumption is that the postreceptoral recoding of cone outputs initiates the neural trivariant (or trichromatic) property of human color perception, and the need for only three primary lights to match any test light.

## ANIMAL TETRACHROMACY:

Tetrachromacy is an early vertebrate characteristic, existing in fish and reptiles, and is evolutionarily more ancient than primate trichromacy. Essentially all diural birds have four retinal cone types (two SWS classes, plus a MWS and a LWS class) which neurally produce four dimensional color experience, or tetrachromatic color vision. Such birds likely perceive a greater number of distinct colors compared to humans, and many more colors compared to dichromat mammals.

Generally, non-human Old World primates tend to be trichromatic and New World primates dichromatic. Recent studies find some New World monkeys – the squirrel monkey, spider monkey, marmoset, and dusky titi – are color vision polymorphic species in which the base condition is dichromacy, although a considerable proportion of individuals are trichromats (Jacobs 1996, Jacobs & Deegan 2005). Many animal species (e.g., squirrels, rabbits, some fishes, cats and dogs) are dichromatic (as are some color deficient humans) and possess only two functioning classes of cone photopigments and need only two primary lights to match the color of any test light.

## POTENTIAL HUMAN TETRACHROMACY:

Physiological considerations of potential human tetrachromacy began in the 1940's with genetic studies of inherited color vision deficiencies or "Daltonism." Approximately 8% of Caucasian males exhibit some degree of color vision deficiency caused by inheriting altered LWS and MWS photopigment genes on the X-chromosome. By possessing a single X–chromosome males are less likely to express both LWS and MWS retinal photopigments compared to females with two X–chromosomes. Furthermore, a female carrying altered photopigment genes may not experience color vision deficiency, although her male off-spring will likely inherit color vision deficiency. Photopigment gene deletions during expression (due to intergenic nonhomologous recombination), and alterations (due to missense mutations, coding sequence deletions, or intragenic cross–over between different genes) underlie Daltonism. Failure to express either the LWS or MWS photopigment produces a Daltonian form of dichromacy, and expression of altered photopigment genes can lead to color vision anomalies.

For many years scientists have known that some fraction of human females inherit the genetic potential to produce four cone photopigment variants, and actually express these variants as distinct retinal cone classes with four different spectral sensitivity distributions. Certain females of "heterozygous" genotypes can express both altered and "normal" forms of photopigment genes thought to underlie color matching differences. Retinal expression of four distinct cone classes requires random X–inactivation during embryonic development so that genes from both altered and normal pigment genes are alternatively expressed as photopigments across the retina's cone cell mosaic. The resulting mosaic may include a patchwork of usual SWS, MWS and LWS cone types, plus, for example, a fourth long–wavelength class variant with peak sensitivity differing from the usual LWS class by 4–7 nm. Frequency estimates of female Caucasians who are potential tetrachromats range between 15% and 47% depending on the heterozygote genotypes considered. Less is know about the actual frequency of expressing four retinal cone classes.

While the potential for human tetrachromacy exists, the general theory suggests that humans process no better than a trivariant color signal. Thus, four retinal cone classes are a necessary (but not a sufficient) condition for tetrachromatic color perception, and for true tetrachromacy a tetra–variant color signal processing is also needed.

Some scientists conjecture that humans with four retinal photopigment classes might experience a dimension of perceptual experience denied to trichromat individuals (Jordan & Mollon 1993); implying that cortically humans might process four color channels, or otherwise learn to use the additional information. New World primate trichromacy suggests a parallel: Female spider monkeys possessing extra photopigment gene variants are trichromats, while both males and females without such variants experience only dichromat color vision. Gene variants thereby allow some female monkeys to experience a dimension of color experience that other females and males do not (Jordan & Mollon 1993).

## EMPIRICAL STUDIES OF HUMAN TETRACHROMACY:

### ***Anomaloscope Investigations:***

Typically, psychophysical anomaloscope "color-matching" investigations are used to study human tetrachromacy. In an anomaloscope task observers monocularly view a bipartite field of primary mixtures and adjust the primaries in one half-field until a "color match" with a fixed test light in the other half-field is obtained. Nagy, MacLeod, Heyneman & Eisner (1981) examined potential tetrachromacy using such a task with chromatic annulus-surround stimuli and a large-field Rayleigh Match task variant. Jordan & Mollon (1993) used both large-field Rayleigh matching and a ratio-matching task where ratios of pairs of primary lights are mixed to match a test light. For evaluating signal processing mechanisms most anomalscope investigations distinguish 'weak' and 'strong' forms of tetrachromacy to interpret mixture settings of potential tetrachromats.

Weak tetrachromacy occurs if an observer has four different cone classes but lacks the postreceptoral capacity to transmit four truly independent color signals. Nagy et al. (1981) demonstrated this form in potential tetrachromats who accepted trichromatic color matches made in a context-free (black annulus) background condition, but did not exhibit the stability of such matches under different chromatic background conditions (unlike trichromats). The observation that matched fields become distinguishable in a colored background clearly indicates weak tetrachromacy, suggesting that the kind of stimulus additivity found in trichromats fails for some potential tetrachromats, or that signals from the extra cone class produce perceptual differences when viewing is contextualized. Nagy et al. (1981) also imply that tetrachromat retinal mosaicism may be a contributing factor in their study.

Strong tetrachromacy arises from four different cone types plus the capacity to transmit four independent cone signals. Such observers would reject large-field trichromat color matches and require four variables to match all colors. Jordan & Mollon (1993) showed 8 out of 14 candidate tetrachromats refused large-field Rayleigh matches providing "preliminary evidence for [the strong form of] tetrachromacy" (p.1501). They also identified two subjects with precise matches in a ratio matching task (as would have been expected from a tetrachromat in their experiment), suggesting one subject's "tetrachromacy is not of the form we initially envisaged" (p. 1503) although she "remains in play as a candidate tetrachromat in the strong sense" (p. 1505). Jordan & Mollon (1993) nevertheless remain tentative concerning the existence of 'strong' human tetrachromacy.

Conservative interpretions of both Nagy et al. (1981) and Jordan & Mollon (1993) suggest weak tetrachromacy interferes with the ability of potential tetrachromats to repeat match mixture settings when producing mixtures with fewer than four variables. In this regard, at least, some potential tetrachromats differ from trichromats.

Additional factors are likely to influence the empirical identification of human tetrachromats: Complexity of color experience will increase with scene, stimulus, and viewing complexity. Monocularly viewed stimuli used in anomaloscope investigations impose empirical constraints on the dimensionality of perceptual experience, whereas naturalistic binocular viewing of contextualized scenes is more likely to uncover tetrachromacy. Thus, the empirical detection of human tetrachromacy is more likely to occur under complex stimuli and viewing conditions.

***Non-anomaloscope Investigations:***
Some investigations have employed increased stimulus complexity, examined more natural processing conditions and behaviors, and obtained human observer genotype information (Jameson, Highnote & Wasserman 2001, Jameson, Bimler & Wasserman 2006, Sayim, Jameson, Alvarado & Szeszel 2005). These investigations used molecular genetic methods to identify potential retinal tetrachromats, and found differences in perceptual behaviors when a genetic potential existed for more than three photopigment classes. Behaviors that differentiated these potential tetrachromats from trichromat controls included perceiving more colors in diffracted spectra (Jameson et al. 2001); performance variation on a standardized test for trichromacy that was correlated with indices of richer color experience (Jameson et al. 2006); and color similarity and color naming patterns showing cognitive color processing variation among potential tetrachromats (Sayim et al. 2005). Although such investigations were not designed to address color vision neural mechanisms or specify forms of 'weak' or 'strong' tetrachromacy, the results show that using empirical conditions that approximate more naturalistic viewing circumstances (e.g., binocular viewing and contextualized stimuli) makes tetrachromacy more apparent, and that the genetic potential to express more than three cone classes correlates with differences in color categorization, naming, and color similarity judgments. These findings are among the first to suggest human tetrachromat differences for such color processing behaviors.

## TETRACHROMACY CONTROVERSIES:

Despite the norm of human trichromacy, empirical support for human tetrachromacy exists, and other terrestrial species have evolved the neural hardware for tetrachromacy. Because the evolution of human color vision capacities is not static, cortical rewiring for tetrachromacy could occur similar to the remapping seen in other visual processing types (e.g., achromatopsia); suggesting that the assumed trivariant recoding of four retinal color signals may be more a conservative theoretical constraint than an actual neural limitation. Other human sensory domains show specialization: Gustatory "supertasters" exhibit taste threshold differences linked to variation in taste sensor densities. Human color vision abilities vary enormously across normal individuals and most of these differences have a genetic base, like the basis underlying tetrachromacy.

Anomaloscope results find a few 'strong' and 'weak' tetrachromat humans demonstrate subtle but reliable color processing differences, thus, even under an assumed neural trivariance constraint it is reasonable to expect some tetrachromat perceptual difference. Also, no radical hypotheses are needed for plausible human tetrachromacy given the prevalence of tetrachromacy in non-primate species, the precedents from New World primate trichromacy (Jacobs 1996), and primate diversity (Jacobs & Deegan 2005).

Exactly how the human visual system processes retinal signals to produce color experience remains unknown. However, the visual system can inductively reconstruct information from the environment (often inferring more than that which is present in the signal alone), and processing extra dimensions of color experience could be within the computational power of visual system neural circuitry.

Clearly, human tetrachromacy requires further empirical demonstration and discussion. Regardless of the frequency of occurrence of strong or weak tetrachromacy, the potential presence of retinal tetrachromats within a normal trichromat population provides additional opportunities to analyze relations between individual perceptual color experience and color processing behaviors. Trichromacy allows humans to distinguish an estimated 2 million different colors. Even if retinal tetrachromacy produces only minor discriminable differences in a small proportion of human observers, these phenomena remain important from both a perceptual and an evolutionary modeling perspective. Given findings suggesting the possibility of human tetrachromacy, future research should clarify the nature of this potential variation in human perceptual experience.

## REFERENCES:

Jacobs, G. H. (1996). Primate photopigments and primate color vision. *Proceedings of the National Academy of Science, 93*, 577–581.

Jacobs, G. H. & Deegan, J. F., II. (2005). Polymorphic new world monkeys with more than three M/L cone types. *Journal of Optical Society of America, A, 22*, 2072–2080.

Jameson, K. A., Highnote, S. M., & Wasserman, L. M. (2001) Richer color experience in observers with multiple photopigment opsin genes. Psychonomic Bulletin & Review, 8, 244–261.

Jameson, K. A., Bimler, D. & Wasserman, L. M. (2006). Re-assessing perceptual diagnostics for observers with diverse retinal photopigment genotypes. In *Progress in Colour Studies 2: Cognition*. Pitchford, N.J. & Biggam, C.P. (Eds). Amsterdam: John Benjamins Publishing Co.

Jordan, G. & Mollon, J. D. (1993) A study of women hererozygous for colour deficiencies. *Vision Research, 33*, 1495–1508.

Nagy, A. L., MacLeod, D. I. A., Heynemann, N. E., & Eisner, A. (1981). Four cone pigments in women heterozygous for color deficiency. *Journal of the Optical Society of America, A, 71,* 719–722.

Sayim, B., Jameson, K. A., Alvarado, N. & Szeszel, M. K. (2005). Semantic and perceptual representations of color: Evidence of a shared color-naming function. *Journal of Cognition & Culture, 5, (3-4),* 427–486.