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colour vision, tetrachromatic 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 colour 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 colour 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 colours.

Established theory states that humans with normal colour vision 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-wavelength sensitive (SWS, MWS, LWS) cones. Three cone classes alone do not establish a trichromat colour code, however. A postreceptoral code for three categories of signal is also needed. A standard assumption in vision science is that the postreceptoral recoding of cone

outputs initiates the neural trivariant (or trichromatic) property of human colour perception, and the need for only three primary lights to match any test light.

1. Animal tetrachromacy
2. Potential human tetrachromacy
3. Empirical studies of human tetrachromacy
4. Tetrachromacy controversies

1. Animal tetrachromacy

Tetrachromacy is an early vertebrate characteristic, existing in fish and reptiles, and is evolutionarily more ancient than primate trichromacy. Essentially all diurnal birds have four retinal cone types (two SWS classes, plus a MWS and a LWS class) which neurally produce four-dimensional colour experience, or tetrachromatic colour vision. Such birds probably perceive a greater number of distinct colours than humans do, and many more colours than dichromat mammals. Generally, non-human Old World primates tend to be trichromatic and New World primates dichromatic. Recent studies have found that some New World monkeys—the squirrel monkey, spider monkey, marmoset, and dusky tit—are colour vision polymorphic species in which the base condition is dichromacy, although a considerable proportion of individuals are trichromats (Jacobs 1996, Jacobs and Deegan 2005). Many animal species (e.g. squirrels, rabbits, some fishes, cats, and dogs) are dichromatic (as are some colour-deficient humans); they possess only two functioning classes of cone photopigments and need only two primary lights to match the colour of any test light.

2. Potential human tetrachromacy

Physiological considerations of potential human tetrachromacy began in the 1940s with genetic studies of inherited colour vision deficiencies or *Daltonism*. Approximately 8% of Caucasian males exhibit some degree of colour vision deficiency caused by inheriting altered LWS and MWS photopigment genes on the X chromosome. Males, possessing a single X chromosome, are less likely to express both LWS and MWS retinal photopigments than are females, who have two X chromosomes. Furthermore, a female carrying altered photopigment genes may not experience colour vision deficiency, although her male offspring will likely inherit it. Photopigment gene deletions during expression (due to intergenic non-homologous recombination), and alterations (due to missense mutations, coding sequence deletions, or intragenic crossover 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 colour vision anomalies.

colour vision, tetrachromatic

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 colour 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 Caucasian females who are potential tetrachromats range between 15% and 47% depending on the heterozygote genotypes considered. Less is known 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 colour signal. Thus, four retinal cone classes are a necessary (but not a sufficient) condition for tetrachromatic colour perception, and for true tetrachromacy a tetravariant colour 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 and Mollon 1993), implying that cortically humans might process four colour 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 colour vision. Gene variants thereby allow some female monkeys to experience a dimension of colour experience that other females and males do not (Jordan and Mollon 1993).

3. Empirical studies of human tetrachromacy

Anomaloscope investigations. Typically, psychophysical anomaloscope 'colour-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 'colour match' with a fixed test light in the other half-field is obtained. Nagy et al. (1981) examined potential tetrachromacy using such a task with chromatic annulus-surround stimuli and a large-field Rayleigh match task variant. Jordan and 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 anomaloscope 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 post-receptor capacity to transmit four truly independent colour signals. Nagy et al. (1981) demonstrated this form in potential tetrachromats who accepted trichromatic colour 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 coloured 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 colour matches and require four variables to match all colours. Jordan and Mollon (1993:1501) showed 8 out of 14 candidate tetrachromats refused large-field Rayleigh matches providing 'preliminary evidence for [the strong form of] tetrachromacy'. 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' (1993:1503) although she 'remains in play as a candidate tetrachromat in the strong sense' (1993:1505). Jordan and Mollon (1993) nevertheless remain tentative concerning the existence of 'strong' human tetrachromacy.

Conservative interpretations of both Nagy et al. (1981) and Jordan and 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 colour 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 (e.g. Bimler and Kirland 2009).

Non-anomaloscope investigations. Some investigations have employed increased stimulus complexity, examined more natural processing conditions and behaviours, and obtained human observer genotype information (Jameson et al. 2001, 2006, Sayim et al. 2005). These investigations used molecular genetic methods to identify potential retinal tetrachromats, and found differences in perceptual behaviours when a genetic potential existed for more than three photopigment classes. Behaviours that differentiated these potential tetrachromats from trichromat controls included perceiving more colours in diffracted spectra (Jameson et al. 2001); performance variation on a standardized test for trichromacy that was correlated with indices of richer colour experience (Jameson et al. 2006); and colour similarity and colour naming patterns showing cognitive colour processing variation among potential tetrachromats (Sayim et al. 2005). Although such investigations were not designed to address colour 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 colour categorization, naming, and colour similarity judgements. These findings are among the first to suggest human tetrachromat differences for such colour processing behaviours.

4. 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 colour 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 colour 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 colour 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 colour processing differences; thus, even under an as-

sumed 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 and Deegan 2005).

Exactly how the human visual system processes retinal signals to produce colour 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 colour 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 analyse relations between individual perceptual colour experience and colour-processing behaviours. Trichromacy allows humans to distinguish an estimated 2 million different colours. 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 modelling perspective. Given findings suggesting the possibility of human tetrachromacy, future research should clarify the nature of this potential variation in human perceptual experience.

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coma

Sayim, B., Jameson, K. A., Alvarado, N., and Szeszel, M. K. (2005). 'Semantic and perceptual representations of color: evidence of a shared color-naming function'. *Journal of Cognition and Culture*, 5.

coma See BRAIN DAMAGE

commissurotomy and consciousness Fifty years ago a surgical procedure for research with cats and monkeys initiated new research on cortical connections and consciousness. This commissurotomy or 'split-brain' procedure combined division of the commissures linking left and right cerebral cortices, including the massive corpus callosum, with an operation to the optic chiasma to separate the inputs from the two eyes.

1. Investigating the organ of consciousness
2. How animals act and know with a divided cortex
3. Manual dominance and antecedents of human cerebral asymmetry
4. Consciousness in the human split brain
5. Cerebral asymmetry, speaking, and knowing
6. Allocation of consciousness between the hemispheres

1. Investigating the organ of consciousness

Brains of animals that swim, fly, or walk map directions for movements in a body-related behaviour space, and they have sensory fields that take up awareness of the world to guide them in the same space. They are bisymmetric, with left and right halves at every level. Larger, longer-lived, more agile, and more intelligent animals have bigger brains, the area of the cortex of the two cerebral hemispheres being in proportion to how long they live and learn. Humans have the largest cortex, and injury or malfunction in it disturbs both intentions of moving and the consciousness of perceiving.

Medical scientists using anatomical studies and clinical accounts of the effects of restricted *brain damage have long tried to fathom how the cortex mediates consciousness, and what the rest of the brain (the limbic system, thalamus, basal ganglia, brainstem, and cerebellum), with many more neurons, contributes. In the 17th century some proposed that the *corpus callosum*, the conspicuous bridge of fibres that connects the cortices of the two hemispheres, is the seat of the soul, conferring an essential unity to consciousness. The innate asymmetry of the human brain became an exciting topic in the 19th century with evidence that lesions confined to the left hemisphere could cause loss of speaking or comprehension of speech, as well as one-sided problems with intentions of the hands. It seemed to some that this indicates that only that the language-aware hemisphere is conscious. The work of neurologists Carl Wernicke, Hugo Liepmann, Jules Dejerine,

and Kurt Goldstein confirmed that left and right cortices are different, specifically in the cultivated functions of intelligence, and they concluded that the corpus callosum must contribute to normal integration of mental states, given that damage to it could render the left hand of a right-handed person incapable of obeying verbal instructions, though its manipulatory habits remained normal.

The commissurotomy procedure was further refined for medical use in development of an operation that, by sectioning parts of the commissures, helped children and adults with life-threatening epilepsy to live more normal lives. Roger Sperry received the Nobel Prize for Physiology and Medicine in 1981 for his contributions to this research clarifying cerebral functions of consciousness in animals and humans. Now there is a very large literature on the effects of commissurotomy on perception, learning, and motor coordination. The cerebral asymmetry of human consciousness, and its great variety, is better appreciated, as well as its relation to motivations and emotions that involve the whole brain asymmetrically. Great popular interest has been excited concerning how, and why, individuals come to use left and right brains differently.

2. How animals act and know with a divided cortex

In 1952 Sperry published an essay entitled 'Neurology and the mind-brain problem' in which he argued that speculations about the nature of consciousness are best inferred from patterns of *motor output*—from actions of the body generated by expectant 'motor images' or 'motor sets'—rather than from hypothetical 'processing' of *sensory input* by a disembodied intelligence. This theory guided Sperry's investigation of the mechanisms of consciousness over the next 40 years. He believed that axonal connections spanning long distances in cortical white matter mediate intentions and awareness, and he proposed this idea should be tested by surgical experiments.

Also in 1952, Ronald Myers, working with Sperry in Chicago, divided the optic chiasma so each eye of a cat was connected only to the cortex on the same side, and then trained the cat to choose between visual stimuli with one eye at a time. Myers proved, first, that learning transferred between the separated inputs of the eyes, then that transfer was abolished when the forebrain commissures were divided in a second operation. The chiasma-commissure sectioned 'split-brain' cats could even be trained to make opposite choices with the two eyes. Apparently their visual consciousness was divided. Nevertheless, when free they walked normally, showing no obvious clumsiness or confusion about how to see the world. Presumably the freely moving cat could distribute its brain activity to see with one cortex