

Comparative Color Categories

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Synonyms

[Cone fundamentals](#); [Dichromacy](#); [Primate color vision](#); [Trichromacy](#)

Definition

Comparative color categories are salient partitions in the perceived color spaces of primates that are known to vary when encoded by signaling systems that differ across species.

The Neurophysiology of Color Vision

The entire range of human color perception, in all its vibrancy, is due to the operation of just three types of photosensitive retinal cone cells and the neural mechanisms responsible for interpreting their signals. These cone cells contain photosensitive opsin pigments that preferentially absorb light at different wavelengths. The short-wavelength (S) pigment has peak absorption of light at about 430 nm, roughly corresponding to blue light; the medium-wavelength (M) pigment has peak absorption at about 530 nm, corresponding to green light; and the long-wavelength (L) pigment has peak absorption at about 560 nm, corresponding to red light (see Fig. 1).

Dysfunction in the cone cells or in the coding of their pigments leads to various types of color blindness. In humans, genes for S-type cones are located on chromosome 7, while those for the M- and L-type cones are located on the X chromosome. This largely explains why color blindness is a much more common phenomenon in men, as women possess independent copies of the M- and L-pigment genes on their two X chromosomes.

The M- and L-type pigments are nearly identical in their genetic specifications. The small difference in their light-absorption profiles is due to a difference in only 3 out of 364 amino acids that code for their respective proteins [8]. The S-type pigment, on the other hand, is more distinct on the molecular level.

Each type of cone cell responds over a range of wavelengths, and the intensity of a cone's response to a light signal depends not only on that signal's wavelength but also its intensity. This creates a situation in which the wavelength of a light signal cannot be uniquely identified based on the response of a single type of cone cell. Unique color information is only recoverable through the simultaneous and concerted action of different types of cone cells operating within a small neighborhood of each other.

In a sense, the response profile of each type of cone cell can be viewed as a “basis vector” that, along with the other cones that make up the basis, defines a multidimensional color space. This

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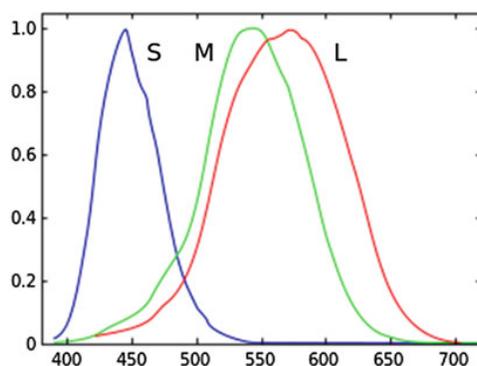


Fig. 1 Sensitivity curves for human photopigments (Attribution: ► [Vanessaezekowitz at en.wikipedia](#))

analogy is made more concrete when considering the *color-matching* experiment that is foundational to the field of color science. In this experiment, observers are presented with a test light with an arbitrary spectral power distribution on one side of a bipartite white screen. The observers' task is then to try to match the appearance of the test light by individually adjusting the intensities of a series of primary lights focused on the other side of the screen. The lights on each side of the screen, while physically different in their spectral distributions, are perceived to be the same. Appearance-matched lights produced in this way are called *metamers*.

For people with normal color vision, exactly three primary lights are required to perform the color-matching task. As a result, normal human color vision is said to be three-dimensional or *trichromatic*. Establishing the dimensionality of color vision in nonhuman animals is an often difficult task requiring extensive training and testing of the animals [7]. A frequent practice in the literature – arguably justified – is to equate an animal's color-vision dimensionality with the number of distinct color photopigments it expresses in its retina. However, the tarsier provides an example of a primate with a fairly uneven retinal distribution of its two cone types, challenging classical views about how color identification works through local networks of opponent cone cells [5]. The tarsier's labeling as a dichromat based on a photopigment-type count alone should therefore be done cautiously [7].

The Evolution of Primate Color Vision

It is believed that gene duplication and mutation of cone pigments, which ultimately made multidimensional perceptual color spaces possible, traces back to the time of the first vertebrates [1]. Almost all vertebrates have an S-type pigment very similar to that possessed by humans [8]. Most mammals have a single X-chromosome cone opsin gene, typically coding for a single long-wavelength visual pigment, and are *dichromats*. But even among primates, only the Old World monkeys, apes, and humans are *trichromats*, having a second – and highly homologous – cone opsin gene on the X chromosome, which codes for a medium-wavelength visual pigment [8, 12]. The generation of these red- and green-pigment genes is thought to have occurred following a duplication event after the split between the New World monkeys and the *catarrhines*, a group of higher primates made up of the Old World monkeys and apes (including humans), about 40 million years ago [12].

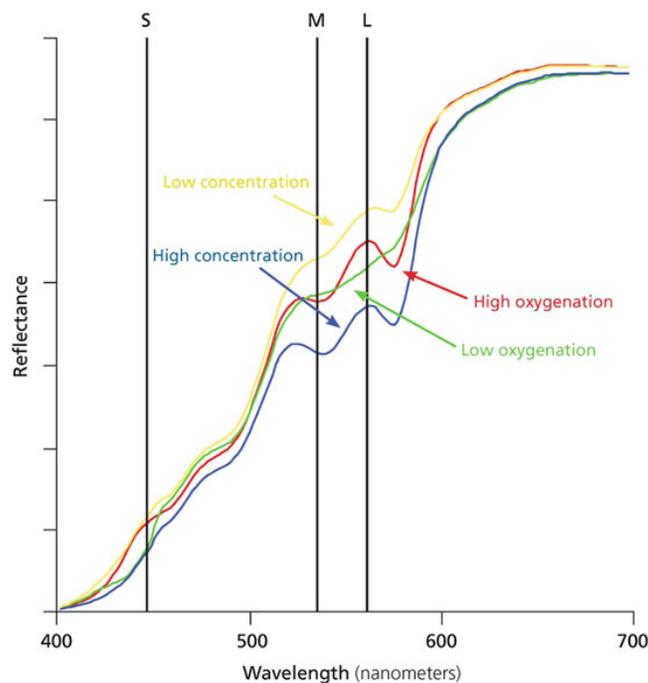


Fig. 2 Skin reflectance changes due to varying blood oxygenation and concentration

Opsin-gene and cone-pigment complements appear to be largely the same among the catarrhines [8, 12]. Psychophysical studies of macaques provided much early information on the color-discrimination abilities of the Old World monkeys [7], and much of this research showed performance very similar to that of humans, suggesting a concordant perceptual color space [15]. Studies of chimpanzees also showed wavelength discrimination similar to human performance [4]. For a review, see [6, 7].

Among the placental mammals, trichromacy appears to be found only in certain primates [7]. However, it is possible to enhance color-discrimination behavior in dichromatic mammals through genetic engineering. Behavioral tests have shown strong evidence for novel color vision in knock-in mice expressing the human L-opsin gene [9]. This suggests that the visual systems of traditionally dichromatic mammals can readily make use of higher-dimensional color signals.

Why, then, when traditionally dichromatic animals can be easily made to demonstrate three-dimensional color vision, is trichromacy seemingly restricted to certain primates? Further, why does trichromacy in primates manifest the way that it does, namely, with such a large spectral overlap between the M- and L-pigment sensitivities? Several hypotheses have been advanced to answer these questions. They are of two basic types: one focusing on the potential advantage of three-dimensional color vision in finding food and the other suggesting that trichromatic color vision was selected for perceiving subtle, behaviorally relevant cues on exposed skin.

The experience of humans with various forms of reduced color vision suggested the hypothesis that color vision was selected for its benefit to detecting targets in visual scenes. Specifically, it has been conjectured that color vision is especially useful for detecting ripe fruit and edible leaves [11]. Consistent with this hypothesis is the observation that ripe fruit is more easily detected against a background of leaves in a trichromatic perceptual space [13]. Also, in one study, several species of frugivorous (fruit-eating) primates tended to eat and disperse seeds from fruit whose reflectance

spectra are tightly clustered in the color space described by trichromatic catarrhine photopigments, while non-preferred fruit is more diffusely distributed in this color space [14]. In another study, folivorous (leaf-eating) trichromatic primates that were surveyed tended to eat leaves shifted more toward the red end of the spectrum relative to leaves eaten by non-trichromatic primates [10].

The food-based hypothesis suggests an obvious evolutionary advantage for primates. However, a question remains as to why catarrhine trichromacy is so uniform in its cone sensitivities given the wide diets – not all of them strictly frugivorous or folivorous – of these primates. An alternative hypothesis suggests that the specific tuning of primate color vision is selected for its advantage in detecting changes in the concentration and oxygenation of blood in conspecifics as indicated by subtle color shifts displayed on exposed skin [3].

Skin reflectance can be modulated over two dimensions according to hemoglobin oxygen saturation and the concentration of hemoglobin in the skin [2, 3]. The effect of changes over the oxygenation-concentration dimensions result in shifts in skin reflectance that are predictable (see Fig. 2).

Particularly notable in this pattern of reflectance changes is that they occur exclusively in the region of color space at which the M and L pigments are maximally sensitive. That is, the characteristic “W” shape nestled within skin’s reflectance profile shifts its position in the region of peak sensitivity of the most recently evolved photopigments, which are nearly optimal for detecting this shift [3]. These shifts are also consistent across all skin types.

It has been observed that trichromatic primates tend to have either bare faces or large areas of exposed skin, such as a bare rump, a finding supportive of the skin-based hypothesis [3]. Further, dichromats are demonstrably poor at detecting changes in skin coloration [2]. Also, whereas the reflectance spectra of the collective primate diet vary widely, the shifts in skin reflectance across the oxygenation-concentration dimensions are stable across all primates [3].

While the typical human experience is that skin tone is itself barely noticeable as a color, subtle deviations from baseline coloration are obvious to people with normal trichromatic vision [3]. Consider, for instance, the “blueness” of an arm vein below the surface of the skin within the context of the surrounding skin. Outside of that context – namely, without reference to the surrounding skin, as though cropped from an image – the “blue” patch simply appears to be of normal skin tone.

More general shifts of skin color are often linked with various conditions of health and emotional status [3]. The skin-based hypothesis for trichromatic-vision selection is unique in that it suggests a *social* advantage for catarrhine color vision. This advantage applies not only to maintaining the integrity of the social group through a sensitivity to health-related cues but also to perceiving threats from conspecifics, such as signs of aggression in the form of increased oxygenation of blood.

Cross-References

- ▶ [Color Categorical Perception](#)
- ▶ [Cone Fundamentals](#)
- ▶ [Environmental Influences on Color Vision](#)
- ▶ [Metamerism](#)
- ▶ [Trichromats, Trichromacy, and Trichromatic Theory](#)

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