

Some Readings about Color Vision

COLOUR EFFECTS

When a person views an opaque coloured object, it is only the light deflected from the object that can activate the visual process in the eye and brain. Because different illuminants have different spectral energy distributions, as shown in Figure 4, a given object in these illuminations will reflect different energy distributions. Yet the eye and brain are such superb systems that they are able to compensate for such differences, and normal-appearing colours are perceived, a phenomenon called colour constancy.

Colour constancy does not apply, however, when there are subtle differences in colour. If, for example, two orange objects, one coloured by an orange pigment, the other by a combination of red and yellow pigments, match precisely in daylight, in the light of a tungsten lamp one may appear more reddish than the other. Because of this effect, called metamerism, it is always necessary to follow precisely the illumination and viewing conditions specified when comparing a sample colour to one in a colour atlas.

The intensity of illumination also affects colour perception. At very low light levels, blue and green objects appear brighter than red ones compared to their relative brightness in stronger illumination, an effect known as the Purkinje shift. At higher levels of illumination, there is a related shift in hues, called the Bezold-Brücke effect, such that most colours appear less red or green and more blue or yellow as the intensity of illumination increases.

If a bright spot of white light is projected onto a screen uniformly illuminated with a pale blue light, the effect known as simultaneous

colour contrast makes the white light appear pale yellow and the blue light seem grayer than if the two were viewed separately. The complementary hue is induced by the adjacent illumination. Successive colour contrast, which occurs when a person stares at one colour and then shifts to another, produces the same effect. A person who stares at a pattern of colours for some time and then looks at a white area sees a negative afterimage of the pattern in complementary hues. This effect, also called chromatic adaptation, is what causes browns to appear reddish to someone who has just viewed a green lawn. Thus, even when the colour of a given object is measured and its physical cause identified, visual effects can prevent the precise perception of that colour from being specified. Some of these effects can be explained fairly simply by changes in the sensitivity of the eye's receptors to different colours as intensity changes, by fatigue in specific receptors, or by receptor inhibition; others are not understood. In fact, scientists did not know the process by which the eye and brain perceive colour until the early 1960s and even now do not understand all the details.

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Color vision

One of the most successful theories of colour vision, the trichromatic theory, was first proposed around 1801 by Thomas Young, an English physician, and refined about 50 years later by the German scientist Hermann von Helmholtz. Based on experiments in colour matching, this theory postulates three types of colour receptors in the eye. The actual existence of such receptor cells, known as cones (from their shapes), was finally confirmed in the early 1960s. The three types of cones have maximum sensitivities in the blue, green, and red regions of the spectrum, with absorption peaks near 445 nm, 535 nm, and 565 nm, respectively. These three sets are often designated as S, M, and L for their sensitivity to short, medium, and long wavelengths. The trichromatic theory explains that colour vision results from the relative intensity of response of the S,

M, and L cones. (Equal stimulation of all three gives the perception of white.) There is obviously a close connection between this trichromatic theory and the tristimulus value system.

One of the trichromatic theory's strengths is that the existence of several kinds of colour blindness can be simply explained as the lack of function of one or more sets of the cones. If one set of cones does not function, dichromatism results. People with deuteranopia (M set missing) or protanopia (L set missing) perceive only blue and yellow. In the much rarer tritanopia the S cones are missing and only green and red are perceived. Persons who have no functioning cone system suffer from the extremely rare monochromatism and can perceive only grays.

Although the trichromatic theory seems to explain much about colour vision, other theories have also been supported and studied, especially the opponent process theory. First proposed by the German physiologist Ewald Hering in 1878, this approach presumes that colour vision involves three mechanisms, each responding to a pair of opposites, namely, light-dark, red-green, and blue-yellow. It is based on many psychophysical observations, including the fact that blue and yellow (and also red and green) cannot coexist in any perceived colour; there are no bluish yellows (or reddish greens). Several of the contrast and afterimage effects can be explained very simply by this approach.

It is now recognized that the trichromatic and opponent process theories are not incompatible. They have been combined in a number of zone theories, which postulate that the cones function in a trichromatic manner in one zone, while in another zone the signals from the cones are combined in neural cells so as to produce one achromatic (white-black) and two chromatic (blue-yellow and green-red) signals, which are then interpreted in the brain. Although it is clear that zone theories, encompassing both trichromatic and opponent colour theories, are fully successful in explaining the many aspects of colour perception, there are still details that remain to be worked out.

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The Psychology of Color

The most important aspect of colour in daily life is probably the one that is least defined and most variable. It involves aesthetic and psychological responses to colour and influences art, fashion, commerce, and even physical and emotional sensations. One example of the link between colour and emotion is the common perception that red, orange, yellow, and brown hues are "warm," while the blues, greens, and grays are "cold." The red, orange, and yellow hues are said to induce excitement, cheerfulness, stimulation, and aggression; the blues and greens security, calm, and peace; and the browns, grays, and blacks sadness, depression, and melancholy. It must be remembered, however, that the psychological perception of colour is subjective, and only general comments about its features and uses can be made.

Colours are not universal. Some languages do not contain separate words for green and blue or for yellow and orange, while Eskimos use 17 words for white as applied to different snow conditions. When colour terminology in different cultures is compared, certain patterns are observed consistently. All languages have designations for black and white. If a third hue is distinguished, it is red; next comes yellow or green, and then both yellow and green. Blue is the sixth colour named, and brown is the seventh. Finally, in no particular sequence, the colours gray, orange, pink, and purple are designated.

Like colour terminology, colour harmony, colour preferences, colour symbolism, and other psychological aspects of colour are culturally conditioned, and they vary considerably with both place and historical period. One cross-cultural study showed that American and Japanese concepts of warm and cold colours are essentially the same, but that in Japan blue and green hues are perceived to be "good" and the red-purple range as "bad," while in the United States the red-yellow-green range is considered "good" and oranges and red-purples "bad." The colour of mourning is black in the West, yet other cultures use white, purple, or gold for this purpose. Many languages contain expressions that use colour metaphorically (common examples in English include "green with envy," "feeling blue," "seeing red," "purple passion," "white lie," and "black rage") and therefore cannot always be translated literally into other languages because the colour may lose its associated symbolic meaning.

Colour symbolism serves important roles in art, religion, politics, and ceremonies, as well as in everyday life. Its strong emotional connotations can affect colour perception so that, for example, an apple- or heart-shaped figure cut from orange paper may seem to have a redder hue than a geometric figure cut from the same paper because of the specific psychological meaning that is associated with the shape.

In addition to emotional associations, factors that affect colour perception include the observer's age, mood, and mental health. People who share distinct personal traits often share colour perceptions and preferences. For example, schizophrenics have been reported to have abnormal colour perception, and very young children learning to distinguish colours usually show a preference for red or orange. Many psychologists believe that analyzing an individual's uses of and responses to colour can reveal information about the individual's physiological and psychological condition. It has even been suggested that specific colours can have a therapeutic effect on physical and mental disabilities.

Although these medical benefits are still in question, colour has been shown to cause definite physical and emotional reactions in humans and in some animals. Rooms and objects that are white or in light shades of "cool" colours may appear to be larger than those that are in intense dark or "warm" colours; black or very dark colours have a slimming, or shrinking, effect, as is well known to designers and decorators. A "cool" room decorated in a pale blue requires a higher thermostat setting than a "warm" room painted a pale orange in order to achieve the same sensation of warmth. People who view a display of unusual colours produced by special illumination may experience headaches and nervous disorders; tasty wholesome food served under such conditions appears repulsive and may even induce illness. Some colours induce a feeling of pleasure in the observer. When an affectively positive, or pleasurable perceived, colour is viewed after a less pleasant colour, it produces more pleasure than when viewed by itself, an effect known as affective contrast enhancement.

The effect of combinations of colours on an observer depends not only on the individual effects of the colours but also on the harmony of the

colours combined and the composition of the pattern. Artists and designers have been studying the effects of colours for centuries and have developed a multitude of theories on the uses of colour. The number and variety of these theories demonstrates that no universally accepted rules apply; the perception of colour depends on individual experience.

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Colour vision.

The spectrum, obtained by refracting light through a prism, shows a number of characteristic regions of colour--red, orange, yellow, green, blue, indigo, and violet. These regions represent large numbers of individual wavelengths; thus, the red extends roughly from 7600 angstrom units to 6500; the yellow from 6300 to 5600; green from 5400 to 5000; blue from 5000 to 4200; and violet from 4200 to 4000. Thus, the limits of the visual spectrum are commonly given as 7600 to 4000 angstroms. In fact, however, the retina is sensitive to ultraviolet light to 3500 angstroms, the failure of the short wavelengths to stimulate vision being due to absorption by the ocular media. Again, if the infrared radiation is strong enough, wavelengths as long as 10,000-10,500 angstroms evoke a sensation of light.

Within the bands of the spectrum, subtle distinctions in hue may be appreciated. The power of the eye to discriminate light on the basis of its wavelength can be measured by projecting onto the two halves of a screen lights of different wavelengths. When the difference is very small--e.g., five angstroms--no difference can be appreciated. As the difference is increased, a point is reached when the two halves of the screen appear differently coloured. The hue discrimination (hue is the quality of colour that is determined by wavelength) measured in this way varies with the region of the spectrum examined; thus, in the blue-green and yellow it is as low as 10 angstroms, but in the deep red and violet it may be 100 angstroms or more. Thus, the eye can discriminate several hundreds of different spectral bands, but the capacity is limited. If it is appreciated that there are a large number of nonspectral colours that may be made up by mixing the spectral wavelengths, and by diluting these with white light, the number of different colours that may be distinguished

is high indeed.

"Sensory Reception: HUMAN VISION: STRUCTURE AND FUNCTION OF THE EYE: The visual process: THE WORK OF THE RETINA: Colour vision."

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Spectral sensitivity curve.

At extremely low intensities of stimuli, when only rods are stimulated, the retina shows a variable sensitivity to light according to its wavelength, being most sensitive at about 5000 angstroms, the absorption maximum of the rod visual pigment, rhodopsin. In the light-adapted retina one may plot a similar type of curve, obtained by measuring the relative amounts of light energy of different wavelengths required to produce the same sensation of brightness; now the different stimuli appear coloured, but the subject is asked to ignore the colours and match them on the basis of their luminosity (brightness). This is carried out with a special instrument called the flicker-photometer. There is a characteristic shift in the maximum sensitivity from 5000 angstroms for scotopic (night) vision to 5550 angstroms for photopic (day) vision, the so-called Purkinje shift. It has been suggested that the cones have a pigment that shows a maximum of absorption at 5550 angstroms, but the phenomena of colour vision demand that there be three types of cone, with three separate pigments having maximum absorption in the red, green, and blue, so that it is more probable that the photopic luminosity curve is a reflection of the summated behaviour of the three types of cone rather than of one.

The Purkinje shift has an interesting psychophysical correlate; it may be observed, as evening draws on, that the luminosities of different colours of flowers in a garden change; the reds become much darker or black, while the blues become much brighter. What is happening is that, in this range of luminosities, called mesopic, both rods and cones are responding, and, as the rod responses become more pronounced--i.e., as darkness increases--the rod luminosity scale prevails over that of the cones.

It may be assumed that the sensation of luminosity under any given condition is determined by certain ganglion cells that make connections to

all three types of cone and also to rods; at extremely low levels of illumination their responses are determined by the activity aroused in the rods. As the luminance is increased, the ganglion cell is activated by both rods and cones, and so its luminosity curve is governed by both rod and cone activity. Finally, at extremely high luminances, when the rods are "saturated" and ceasing to respond, the luminosity curve is, in effect, compounded of the responses of all three types of cone.

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Colour mixing.

The fundamental principle of colour mixing was discovered by Isaac Newton when he found that white light separates spatially into its different component colours on passing through a prism. When the same light is passed through another prism, so that the individual bands of the spectrum are superimposed on each other, the sensation becomes one of white light. Thus, the retina, when white light falls on it, is really being exposed to all the wavelengths that make up the spectrum. Because these wavelengths fall simultaneously on the same receptors, the evoked sensation is one of white. If the wavelengths are spread out spatially, they evoke separate sensations, such as red or yellow, according to which receptors receive which bands of wavelengths. In fact, the sensation of white may be evoked by employing much fewer wavelengths than those in the spectrum: namely, by mixing three primary hues--red, green, and blue.

Furthermore, any colour, be it a spectral hue or not, may be matched by a mixture of these three primaries, red, green, and blue, if their relative intensities are varied. Many of the colours of the spectrum can be matched by mixtures of only two of the primary colours, red and green; thus the sensations of red, orange, yellow, and green may be obtained by adding more and more green light to a red one.

To one accustomed to mixing pigments, and to mixing a blue pigment, for example, with yellow to obtain green, the statement that red plus green can give yellow or orange, or that blue plus yellow can give white, may

sound strange. The mixing of pigments is essentially a subtractive process, however, as opposed to the additive process of throwing differently coloured lights on a white screen. Thus, a blue pigment is blue because it reflects mainly blue (and some green) light and absorbs red and yellow; and a yellow pigment reflects mainly yellow and some green and absorbs blue and red. When blue and yellow pigments are mixed, and white light falls on the mixture, all bands of colour are absorbed except for the green colour band.

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Colour defectiveness.

The colour-defective subject is one whose wavelength discrimination apparatus is not as good as that of the majority of people, so that he sees many colours as identical that normal people would see as different. About one percent of males are dichromats; they can mix all the colours of the spectrum, as they see them, with only two primaries instead of three. Thus, the protanope (red blind) requires only blue and green to make his matches; since, for the normal (trichromatic) subject the various reds, oranges, yellows, and many greens are the result of mixing red and green, the protanope matches all these with a green. In other words, he is unable to distinguish all these hues from each other on the basis of their colour; if he distinguishes them, it is because of their different luminosity (brightness). The protanope matches white with a mixture of blue and green and is, in fact, unable to distinguish between white and bluish-green. The deuteranope (green blind) matches all colours with a mixture of red and blue; thus, his white is a mixture of red and blue that appears purple to a person with normal vision. The deuteranope also is unable to discriminate reds, oranges, yellows, and many greens, so that both types of dichromat are classed as red-green-blind. For the protanope, however, the spectrum is more limited because he is unable to appreciate red. The tritanope (blue blind) is rare, constituting only one in 13,000 to 65,000 of the population; because he is blue blind, his colour discrimination is best in the region of red to green, where that of the protanope and deuteranope is worse. (see also Index: colour blindness)

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Responses of uniform population of receptors.

The scotopic (night) visual system, mediated by rods, is unable to discriminate between different wavelengths; thus, a threshold stimulus of light with a wavelength of 4800 angstroms gives a sensation of light that is indistinguishable from that evoked by a wavelength of 5300 angstroms. If the intensities are increased, however, the lights evoke sensations of blue and green, respectively. Rods are unable to mediate wavelength, or colour, discrimination while the cones can because the rods form a homogeneous population, all containing the same photopigment, rhodopsin. Thus, the response of a nerve cell connected with a rod or group of rods will vary with the wavelength of light. When the response, measured in frequency of discharge in the bipolar or ganglion cell, is plotted against the wavelength of the stimulating light, the curve is essentially similar to the absorption spectrum of rhodopsin when the same amount of energy is in each stimulus; thus, blue-green of 5000 angstroms has the most powerful effect because it is absorbed most efficiently, while violet and red have the smallest effects. In this sense, the rods behave as wavelength discriminators, but it is to be noted that there are pairs of wavelengths on each side of the peak to which the same response is obtained; thus, a blue of 4800 angstroms and a yellow of 6000 angstroms give the same discharge. Moreover, if the intensity of the stimulus is varied, a new curve is obtained, and now the same response is obtained with a high intensity of violet at 4000 angstroms as with blue at the lower intensity. In general, it is easy to show that, by varying the intensity of the stimulus of a single wavelength, all types of response may be obtained, so that the brain would never receive a message indicating, in a unique fashion, that the retina was stimulated with, say, green light of 5300 angstroms; the same message could be given by blue light of 4800 angstroms, red light of 6500 angstroms, and so on.

Ideally, colour discrimination would require a large number of receptors specifically sensitive to small bands of the spectrum, but the number would have to be extremely large because the capacity for hue

discrimination is extremely great, as has been indicated. In fact, however, the phenomena of colour mixing suggest that the number of receptors may be limited.

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Young-Helmholtz theory.

It was the phenomena of colour mixing that led Thomas Young in 1802 to postulate that there are three receptors, each one especially sensitive to one part of the spectrum; these receptors were thought to convey messages to the brain, and, depending on how strongly they were stimulated by the coloured light, the combined message would be interpreted as that due to the actual colour. The theory was developed by Hermann Ludwig Ferdinand von Helmholtz, and is called the Young-Helmholtz trichromatic theory. As expressed in modern terms, it is postulated that there are three types of cone in the retina, characterized by the presence of one of three different pigments, one absorbing preferentially in the red part of the spectrum, another in the green, and another in the blue. A coloured stimulus--e.g., a yellow light--would stimulate the red and green receptors, but would have little effect on the blue; the combined sensation would be that of yellow, which would be matched by stimulating the eye with red and green lights in correct proportions of relative intensity. A given coloured stimulus would, in general, evoke responses in all three receptors, and it would be the pattern of these responses--e.g., blue strongly, green less strongly, and red weakest--that would determine the quality of the sensation. The intensity of the sensation would be determined by the average frequencies of discharge in the receptors. Thus, increasing the intensity of the stimulus would clearly change the responses in all the receptors, but if they maintained the same pattern, the sensation of hue might remain unaltered and only that of intensity would change; the observer would say that the light was brighter but still bluish green. Thus, with several receptors, the possibility is reduced of confusion between stimuli of different intensity but the same wavelength composition; the system is not perfect because the laws of colour mixing show that the eye is incapable of certain types of discrimination, as, for example, between yellow and a mixture of red

and green, but as a means of discriminating subtle changes in the environment the eye is a very satisfactory instrument.

The direct proof that the eye does contain three types of cone has been secured, but only relatively recently. This was done by examining the light emerging from the eye after reflection off the retina; in the dark-adapted eye the light emerging was deficient in blue light because this had been preferentially absorbed by the rhodopsin. In the light-adapted eye, when only cone pigments are absorbing light, the emerging light can be shown to be deficient in red and green light because of the absorption by pigments called erythrolabe and chlorolabe. Again, the light passing through individual cones of the excised human retina can be examined by a microscope device, and it was shown by such examination that cones were of three different kinds according to their preference for red, green, and blue lights.

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The nervous messages.

If the three types of cones respond differently to light stimuli, one may expect to find evidence for this difference in type of response by examining the electrophysiological changes taking place in the retina; ideally, one should like to place a microelectrode in or on a cone, then in or on its associated bipolar cell, and so on up the visual pathway. In the earliest studies, the optic nerve fibres of the frog were examined--i.e., the axons of ganglion cells. The light-adapted retina was stimulated with wavelengths of light stretching across the spectrum, and the responses in arbitrarily selected single fibres were examined. The responses to stimuli of the same energy but different wavelengths were plotted as frequency of discharge against wavelength, and the fibres fell into several categories, some giving what the investigator called a dominator response, the fibre responding to all wavelengths and giving a maximum response in the yellow-green at 5600 angstroms. Other fibres gave responses only over limited ranges of wavelengths, and their wavelengths of maximum response tended to be clustered in the red, green, and blue regions. The investigator called these modulators, and considered that the message in

the dominator indicated to the brain the intensity of the stimulus--i.e., it determined the sensation of brightness--while the modulators indicated the spectral composition of the stimulus, the combined messages in all the modulators resulting in a specific colour sensation. In the dark-adapted retina, when only rods were being stimulated, the response was of the dominator type, but this time the maximum response occurred with a wavelength of 5000 angstroms, the absorption maximum of rhodopsin.

A more careful examination of the responses in single fibres, especially in the fish, which has good colour vision, showed that things were not quite as simple as the original investigator had thought because, as has been seen, the response of a ganglion cell, when light falls on its receptive field in the retina, is not just a discharge of action potentials that ceases when the light is switched off. This type of response is rare; the most usual ganglion cell or optic nerve fibre has a receptive field organized in a concentric manner, so that a spot of light falling in the central part of the field produces a discharge, while a ring of light falling on the surrounding area has the opposite effect, giving an off-response--i.e., giving a discharge only when the light is switched off. Such a ganglion cell would be called an on-centre-off-periphery unit; others behaved in the opposite way, being off-centre-on-periphery.

When these units are examined with coloured lights, and when care is taken to stimulate the centres and surrounding areas separately, an interesting feature emerges; the centre and surrounding areas usually have opposite or opponent responses. Thus, some may be found giving an on-response to red in the centre of the field and an off-response to green in the surrounding area, so that simultaneous stimulation of centre with red and surrounding area with green gives no response, the inhibitory effect of the off-type of response cancelling the excitatory effect of the on-type. With many other units the effects were more complex, the centre giving an on-response to red and an off-response to green, while the surrounding area gave an off-response to red and an on-response to green, and vice versa. This opponent organization probably subserves several functions. First, it enables the retina to emphasize differences of colour in adjacent parts of the field, especially when the boundary between them moves, as indeed it is continually doing in normal vision because of the small involuntary movements of the eyes. Second, it is

useful in "keeping the retina quiet"; there are about one million optic nerve fibres, and if all these were discharging at once the problem of sorting out their messages, and making meaning of them, would be enormous; by this "opponence," diffuse white light falling on many of these chromatic units would have no effect because the inhibitory surrounding area cancelled the excitatory centre, or vice versa. When the light became coloured, however, the previously inactive units could come into activity.

These responses show that by the time the effect of light has passed out of the eye in the optic nerve the message is well colour-coded. Thus all the evidence points to the correctness of the Young-Helmholtz hypothesis with respect to the three-colour basis. The three types of receptor, responding to different regions of the spectrum in specific manners, transmit their effects to bipolar and horizontal cells. The latter neurons have been studied from the point of view of their colour-coding. The potentials recorded from them were called S-potentials; these were of two types, which classified them as responding to colour (C-units) and luminosity (L-units).

The C-type of cell gave an opponent type of response, in the sense that the electrical sign varied with the wavelength band, red and green having opponent effects on some cells, and blue and yellow on others. These responses reflect the connections of the horizontal cells to groups of different cones, the blue-yellow type, for example, having connections with blue and red and green cones, while the red-green would have connections only with red and green cones.

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