

Sensation, Perception, Action – An Evolutionary Perspective

Chapter 4

Vision 2: Colour



‘White Line Square III’ Josef Albers, 1966, Tate Collection, London

Colouring surfaces as means of decoration and embellishment can arguably be seen as the root of visual arts – over centuries painters collected a large body of knowledge about how colours are perceived, depending on illumination, and relative to each other.

Overview

Why do humans have colour vision? In other words, what can we see in a colour but not in a black-and-white movie, and what are you missing from everyday experience if you are colour blind? Recognising the value added by colour information to everyday experience is the starting point to study the physical basis and the neural encoding of colour in the human visual system. Colour space, defined by hue and saturation, is a crucial concept to compare the number of different colours and saturation levels that can be seen, and to assess colour resolution of natural colouration and technical displays that surround us. A brief reflection of colour names highlights how difficult it is to describe colours in everyday language, and the cultural dependence of such descriptive terms. To put these observations into a conceptual perspective, the 'trichromatic' and 'opponent process' theories of colour vision are introduced, which account for properties like colour mixing and colour contrast, and for a long time have been discussed as alternative 'theories' that exclude each other. Science has now accumulated a wide body of evidence recognising the two perspectives as complementing each other, reflecting different stages of neural encoding. Some spatial and temporal aspects of the neural encoding of colour are compared to that of brightness, which prepares us to understand the phenomena of colour contrast and after-effects. Finally, a few higher-level mechanisms in colour vision, such as assimilation and colour constancy are considered, suggesting that context-dependent colour information is represented in rather different ways at different levels of the brain, providing vital cues to navigate the world under a wide range of operating conditions. The reconfiguration of information in the visual system brings us back to the initial questions about behavioural and evolutionary aspects of colour vision.

Physical properties of colour

The first and most immediate question we should ask ourselves is: why do we have colour vision? What can we see in colour, which we can't see in black and white, or in other words, what is the added value of a colour? Comparing old-fashioned black-and-white movies with contemporary Technicolor, we might say it is more realistic and it is more pleasant to the eye. Obviously, it is more convincing and pleasant to see artificial renditions of the world that resemble the real world, as we do in the contemporary movie – however this doesn't answer the question why we have colour vision, because it only reminds us that we need to find out what is the evolutionary advantage of seeing colours in the real world. So let us look at the example in figure of 4.1, which illustrates some interesting aspects of object identification. Imagine you want to point a friend towards your car which you left in a carpark in the midst of many of others. In order to identify your car, you either would need to describe exactly the location where you left it, or you would need to describe the peculiar make or the properties of your car such as the size or shape, or any fancy engineering work such as extra exhaust pipes. If, however, you have

access to colour vision you just could point your friend towards the bright blue car. Colour vision adds a lot of extra information to your retinal images! We make constant use of this extra information. Just think of red and green traffic lights or the use of the colour orange in advertising. Colour also helps us to recognise objects and to keep them in our memory (Gegenfurtner and Rieger 2000). In terms of our evolution, where traffic lights, and mobile phone ads didn't feature highly, it is argued that a key function of colour vision is related to tasks like the detection and recognition of predators, prey, or fruits which often are distinguished by a strong contrast to the green foliage in which they are embedded (Osorio and Vorobyev 1996).



Figure 4.1: When trying to identify one particular object within a group, such as an individual car in a carpark (a: see black and white picture in), you could describe the exact location, or use of a set of properties such as shape, size, or any engineering peculiarities. If you are able to perceive colour you just need to know how it is painted (b: see the blue car in the picture colour picture). (see Colour Plate III.1)

The second question we should ask, which is perhaps even more fundamental than the first one, is what is colour and how can it be described. For a physicist, who masters the 20th century knowledge of electromagnetic waves, this question is easy to answer: each pure or 'monochromatic' light source can be described by its wavelength within the visible range of electromagnetic waves, which is perceived as a particular colour, and its intensity, which is perceived as brightness (Hubel 1988). A natural light source, such as the sun, rarely is monochromatic (i.e. composed of a single wavelength) but usually is the combination of a range of wavelengths which contribute to the light with different intensities – this distribution wavelengths between 400 nm (violet) and 700 nm (red) is called the 'visible spectrum' of the light source (see figure 4.2 a). Although the light source is made up from several monochromatic components, an observer cannot separate these components of its spectrum and perceives it as one single colour: the spectrum of a (white) fluorescent light, for instance, has a number of bright peaks superimposed on a

broad wavelength distribution across the entire visible range –which you only can see on their own if you separate them by means of a prism (or by looking at the bands of colour in the reflections from a CD!). It is important to note that wavelength and relative intensity of each wavelength constitute two independent dimensions, which are both needed to describe the light, apart from its overall brightness.

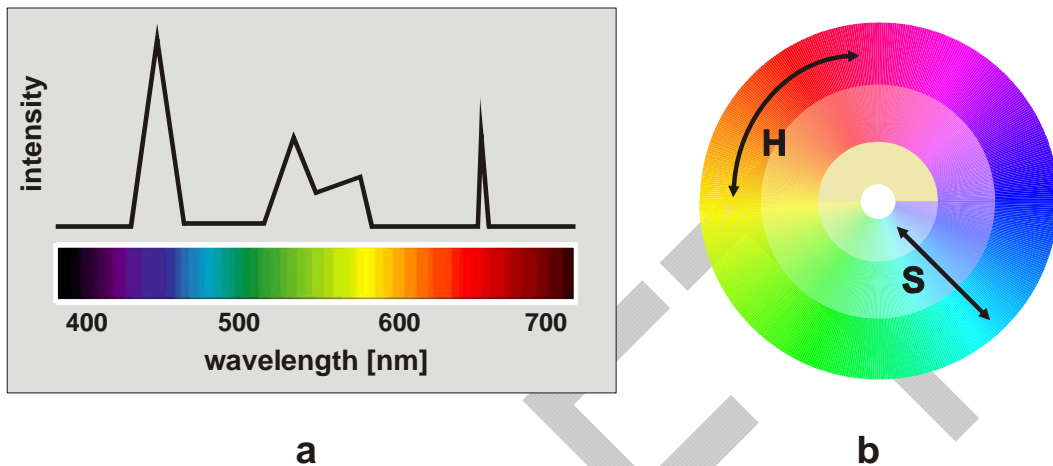


Figure 4.2: The physics of colour. (a) The physical description of the light source is defined by the combination of wavelength and relative intensity between 400 nm and 700 nm, its ‘visible spectrum’. (b) The perceptual description of colour reflects these two independent dimensions, because we need to identify a position along the colour wheel (e.g., blue, green, yellow, red, indicated by arrow H) – the **hue** of the patch of image we are looking at – and the **saturation** of the perceived colour in the patch (indicated by arrow S). These two dimensions are independent of overall amount of light captured by the eye, which corresponds to **brightness**. (see Colour Plate III.2)

Perceptual properties of colour

Whereas the physical description of colour is comparatively easy, albeit specific equipment is required to record the spectrum of particular light source, the perception of colour is immediate, but difficult to describe. The most important relationship between the physics and perception of light has been captured by Isaac Newton (Newton 1704) in his radical statement: “the rays, to speak properly, are not coloured. In them there is nothing else than a certain power and disposition to stir up a sensation of this or that colour.” In other words, there is no immediate relationship between the physical properties of the light beam which cannot be seen directly, and the perceived quality of the corresponding area of the visual field, which appears to the observer as one particular colour. However, the perceived colour of objects is what matters in everyday life – professionals like painters, drapers, and printers know very well that the choice and persistence of colours is key to their business. At the current day and age it would be

considered as almost impossible to sell a newspaper or magazine, which is printed purely in black and white rather than being illustrated with colour photographs. Despite of its great importance, the perceptual quality of colours is very difficult to describe. We will look now at various possibilities to identify particular colours and arrange them in a systematic way, and will return in the next section to the question of how the physical properties of light are encoded in the visual system to generate such perceptual properties.

In the first instance, we tend to identify colours by names such as ‘yellow’, ‘red’ or ‘green’. It is a commonplace that sometimes it can be rather difficult to convince different observers to agree about the name of a chosen colour, and indeed different individuals use the same names only for a small number of colours (Boynton and Olson 1990). However, it is crucial to define perceived colours precisely, for instance when one tries to reproduce colours veridically, or when a colour should be reserved for a particular use, such as particular colours ‘owned’ by a brand. Just think of a the impact of a special red that is used to advertise a certain fizzy drink, and later was affiliated to the coat of Father Christmas. Colour systems such as the CIE 1931 colour space (Broadbent 2004) were developed to reliably identify colours across inter-individual differences. Systematic experiments to investigate the use of colour names accurately with a general colour system built from colour chips that are easy to use (Munsell 1912; Munsell and Farnum 1941) started in the 1960s. Apart from confirming scientifically a considerable variation between individuals for the use of colour names, an interesting observation was made when comparing colour names in different cultures. The system and number of colour names can vary considerably in different cultures, and additional colour names seem to be introduced in languages in a peculiar order (shown in figure 4.3a) that resembles an evolutionary sequence (Berlin and Kay 1999). Even more intriguingly, the frequency of using colour names in English seems to reflect this hierarchy of colour names, and there is some discussion whether the order of acquisition of colour names follows a similar sequence (Pitchford and Mullen 2005). The biggest limitation of colour naming in describing percepts arises from the fact that there is only a small number of true colour names which requires inherently difficult categorisation (Davidoff 2001), whereas there is a huge number of different colours – as a work-around, we often tend to use mixed names or well-known objects to refer to a colour, like ‘blue-green’ or ‘plum’. Still, can you easily agree with your friends what exactly is a ‘tomato-red’ T-shirt?

Since the different colours seem to be located in a continuum of subtle changes between their appearance, a lot of effort by many thinkers and practitioners, went into designing systems of similarity that can be used to arrange colours in a systematic way, which sometimes is referred to it as a ‘colour atlas’ (Irtel 2000). The rationale behind various colour schemes led to sometimes heated debates, for instance between the scientist Newton and the poet Goethe, about the value, limitations, and flaws of each of these systems (Duck 1988). In the most simple version of a map, colours can be arranged according to similarity on a circle, as illustrated in figure 4.3b based on colour labels used for Munsell chips. Whereas it is clear that this basic ‘Munsell colour wheel’ covers some

very prominent colours, there are many mixed colours missing from the wheel, and it presents only a single level of saturation (how pale or strong a colour is, sometimes also known as ‘chroma’) and a single level of brightness.

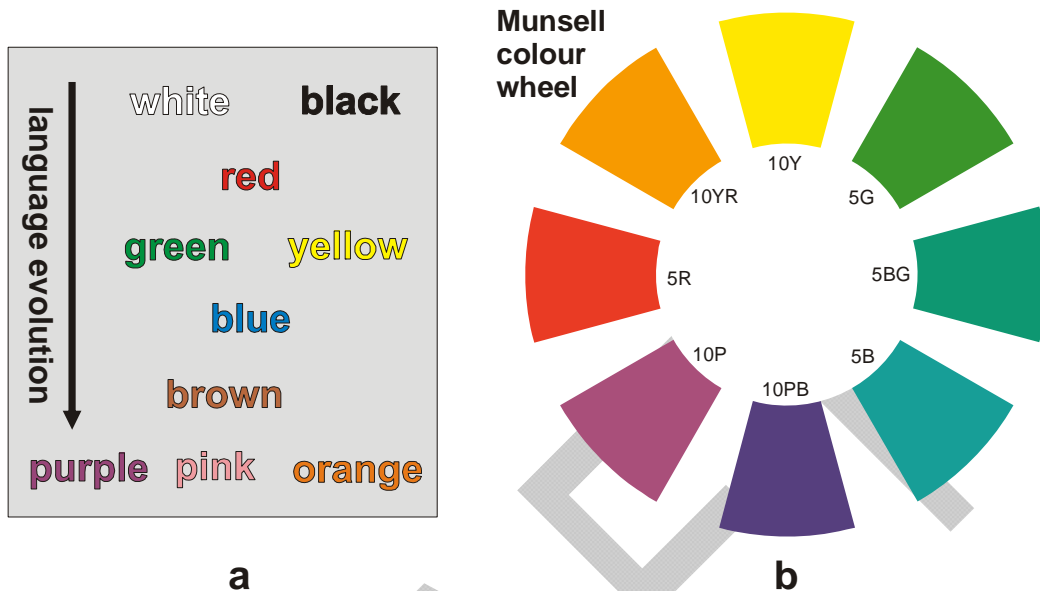


Figure 4.3: Identifying colours. (a) Colour names are notoriously variable in their use and appear in a particular order in different languages, suggesting some kind of evolution. (b) In this simple Munsell colour wheel the different hues (at fixed saturation and brightness) are arranged in a circular fashion such that neighbouring colours resemble each other. (see Colour Plate III.3)

There is now general agreement that the best way of arranging colours is according to their similarity to allow for smooth neighbourhood relationships and well-defined distances. This method leads to the colour circle (cf. figure 4.3b), which follows and sequence of colours in the rainbow: red, orange, yellow, green, blue, indigo, and finally violet, which is close again to red and closes the circle. The next step then as to add concentric circles of the same sequence of colours, which differ in the strength of the colours from pale white in the centre to very strong colouration in outer rings. This arrangement of colours creates a two-dimensional colour wheel, reflecting the two independent physical dimensions and corresponding to the two independent perceptual dimensions, which are usually referred to as *hue* and *saturation*. Hue refers to the perceptual quality that is related to discriminating categories of colour, like red, green, blue, and their intermediate stages. The saturation refers to the perceptual quality related to be intensity or richness of colour sensation – it tells us how strong or vivid a colour is as compared pale grey region. Two patches in a visual scene, which differ in their hue or saturation, or both, but are identical in their brightness, called *isoluminant* – they only can be discriminated on basis of their colour. It is worth to note that in the colour space

contrast can be created in two independent dimensions, through differences in hue or through differences in saturation, whilst keeping brightness contrast constant (cf. figure 4.2b). If we also consider the intensity (overall energy) of a light source, which will affect its brightness, we have to deal with a set of colour wheels that contain dark (low intensity) and light (high intensity) colours, and correspondingly vary from black to white in the centre of each wheel. A more comprehensive system that adds the brightness dimension (called 'HSB' with reference to the three independent components, hue, saturation, and brightness) therefore looks more like a cylinder, with the *brightness* axis running up and down through it. Each horizontal slice of the cylinder then looks like a solid colour wheel, in which the *hue* is given by the angular position and the *saturation* by the distance from the centre.

In summary, a two-dimensional system can be understood as a prototype for a reasonable perceptual description and neural representation of arbitrary colour stimuli. In other words, such a colour space could be used to measure perceived colour. The metric of such measurements is based on the fact that every spectral composition of a stimulus, at a given brightness, can be converted into a unique combination of hue and saturation. Such a colour space can then be used to investigate colour perception objectively and systematically, for instance using the standardised set of coloured chips developed by Munsell that covers the complete colour space (Munsell and Farnum 1941). Using these Munsell chips, discrimination thresholds can be measured for similar colours, which are perceptually just about separable, which allows us in turn to estimate the number of different colours we can see: about 5 millions! Note that this is about 1000 times more than the number of grey levels, which we are able to discriminate, but only a third of the colours which can be produced by means of a 24 bit computer display (16 million colours). This supports the general statement made at the beginning of this chapter that colour vision increases considerably the amount of information which can be collected by the human visual system.

Theories of Colour Vision

The relationship between the physical properties of light and the perceptual quality of colour needs to be addressed by developing a theory of colour vision, which in itself should be related to the physiological properties of the neural system that is responsible for the transformation of this visual stimulus into a percept. In the basic condition for an appropriate model is given by the properties of the colour space, with independent encoding of hue and saturation, but on top of this a valid model also needs to explain other perceptual phenomena in the colour domain. A good theory of colour vision needs to consider the physiological basis of colour processing in the visual system, which was briefly mentioned in chapter 2 in the overview of the visual stream. Additional detail will be filled in where needed, but the colour vision stream is not discussed comprehensively because our focus is on the fundamental design principles of colour vision, and not on the actual implementation in the nervous system. In the following sections, the two central

historical theories of colour vision will be reviewed, compared, and put into the context of more recent research.

The first theory, which usually is referred to as the *theory of trichromatic colour vision*, is attributed to its most prominent promoters, Thomas Young (Young 1802) and H. v. Helmholtz (von Helmholtz 1852). This theory is based on the fundamental observation of additive colour mixing: superposition of coloured spotlights produces new colours. Most importantly, each coloured spotlight can be generated by superimposing three basic colours, sometimes referred to as ‘primaries’ (see figure 4.4a). This phenomenon, for instance, provides the rationale for designing RGB computer and TV screens, which in each pixel mix red green and blue light to create any visible colour. It should be noted in passing that additive mixing of spotlight colours is quite different from subtractive colour mixing in paints – the pigments which define the perceived colour of a paint remove specific components from the spectrum of the illuminating light in the reflected light (i.e. blue paint removes green and red components from a white illuminant), which leads to radically different mixing properties that resemble tinted filters.

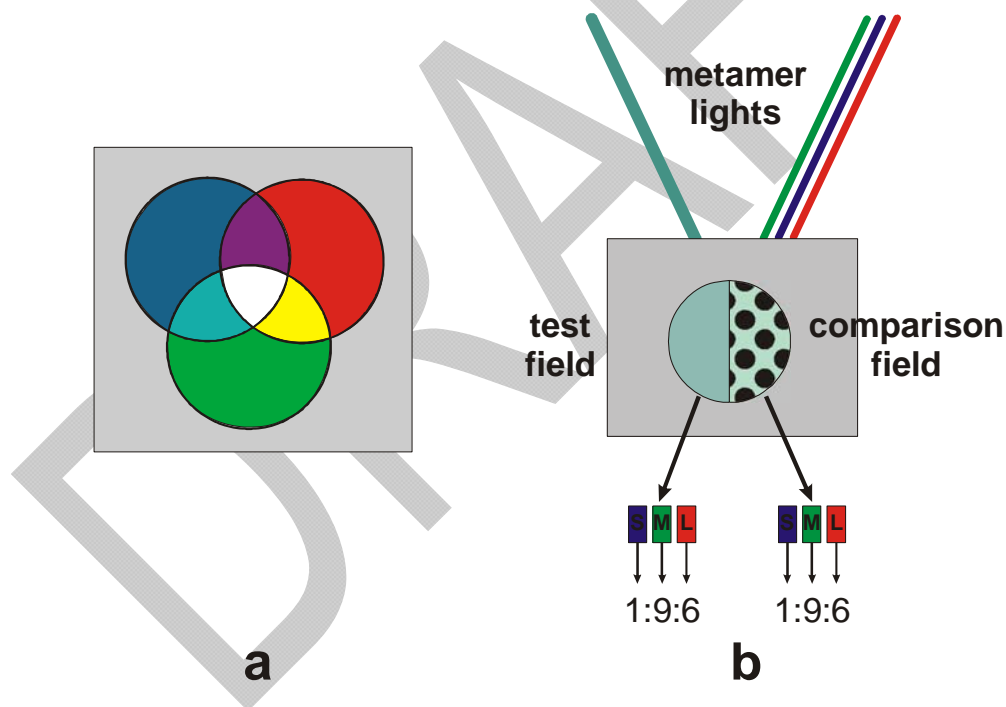


Figure 4.4. Trichromatic theory of colour vision. (a) Additive colour mixing in spotlights: red and green superimposes to yellow; green and blue superimposes to cyan; blue and red superimposes to magenta; and all three lights superimpose to white. (b) The key experiment to support the trichromatic theory demonstrates that any arbitrary colour projected into a test field can be matched by the superposition of three primary colours superimposed onto a comparison field, such that the two fields cannot be separated from each other by a human observer. (see Colour Plate IV.1)

The crucial observation supporting the trichromatic theory of colour vision is that in a controlled experiment any colour can be matched by the additive superposition of three differently coloured lights (.see figure 4.4b) that serve as ‘primary’ colours. Two such lights that are composed of different spectral components but appear identical to the human observer are called ‘metamers’. This could happen in the simple comparison of white sunlight that covers the full spectrum with the combination of red, green and blue monochromatic lights, as in the basic case shown in figure 4.4a, or by mixing carefully the same primaries to generate the light blue-green shown in figure 4.4b. Blue, green, and red are a popular choice for the primaries correspond to the wavelength sensitivity of the three types of photoreceptors that can be found in the retina (Hubel 1988), which by the use of different light-sensitive pigments are tuned to short (S), middle (M), and long (L) wavelengths, respectively. As shown in figure 4.5a, each receptor type absorbs light over a broad range of wavelengths and peak at different locations. The relative activation of these three receptors give rise to the phenomenon of metamers (see figure 4.4b): each light source will activate the three receptors in a particular proportion that can be matched exactly by another light, for instance an appropriate combination of the RGB primaries, which therefore must lead to the same perceived colour. This characterisation of perceived colour space, however, only holds for the ‘normal’ visual system. In humans, we can find a variety of genetic alterations that affect the structure and function of retinal photopigments and lead to substantial changes in the range of perceived colours, which commonly are known as ‘colour vision deficiencies’ or ‘colour blindness’ (Sharpe et al 2001).

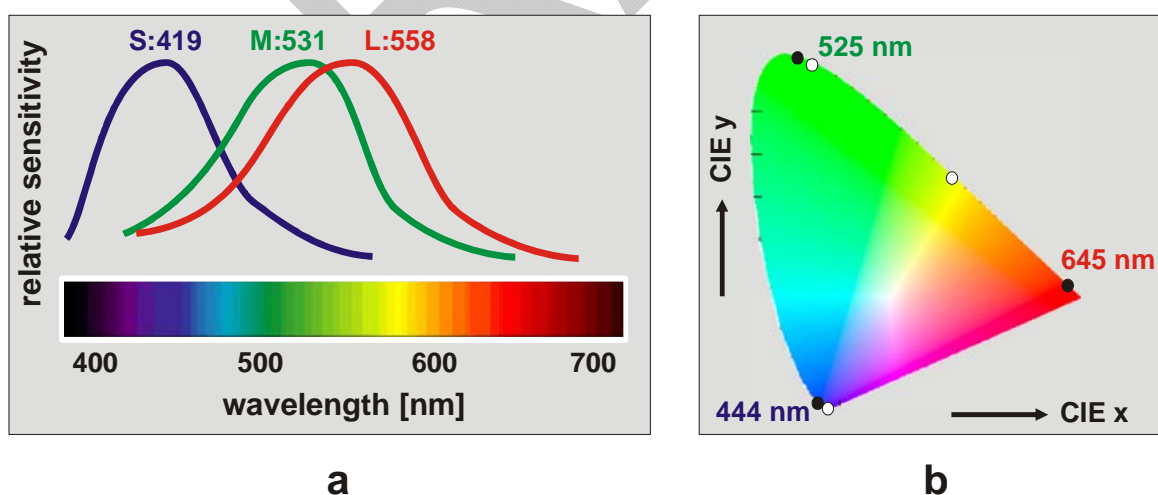


Figure 4.5: Physiological basis of the trichromatic processes of colour vision. (a) Absorption spectra for the three types of cones in the retina that preferentially respond to short (S: blue line), medium (M: green line), and long (L: red line) wavelengths of monochromatic stimuli. (b) This photoreceptor colour sensitivity are located in key locations in the CIE 1931 colour space

(white dots indicate optimum sensitivity for S, M, L), indicating that from the combined activation of these receptors the full gamut of all visible colours can be encoded. The diagram also shows the locations of the RGB primaries (black dots, plus characteristic wavelengths) – all visible colours can be generated by a combination of these three primaries. (see Colour Plate IV.2)

Note that the design of the sensory system, i.e. the spectral sensitivity of the photoreceptors, is limiting the information that can be collected, and thus determines the perceptual properties incorporated in the trichromatic theory of colour vision. The physiological colour space directly related to the photoreceptor sensitivity (LMS space) is used to determine specific colours that allow experimenters to separate photoreceptors in psychophysical experiments. The LMS colour space can be converted into other systems of colour definitions (for instance RGB, CMYK, or CIE colour norms) that are used in technical contexts such as monitors, or computer graphics software like Photoshop. Figure 4.5b shows the locations of the photoreceptor optima and of the RGB primaries in the CIE 1931 colour space, indicating schematically how the gamut of all visible colours (i.e., all different values of chromaticity in this diagram) can be generated from a combination of the primaries, and can be picked up through the different activation levels of the three receptor types.

Although the trichromatic theory of colour vision provides a good explanation for additive colour mixing and the existence of perceived colour metamers, there are other aspects of colour perception that are not accounted for by this theory. The fundamental observation that there is no colour that is perceived as ‘greenish’ red or ‘blueish’ yellow, and no ‘redish’ green or ‘yellowish’ blue, suggests that red and green, as well as blue and yellow, seem to exclude each other in perception. This mutual exclusion of two pairs of basic colours is the starting point for the *opponent process theory of colour vision* which was developed by E. Hering in the late 19th century (Hurvich and Jameson 1960). The central suggestion is that the perceptual space of colour vision determined by two pairs of opponent colours that exclude each other, constituting a red-green and a blue-yellow axis of colour perception, respectively. Arguably, the opponent process is most visible in the phenomenon of contrast enhancement in the colour domain where, for instance, a light grey line appears pale green in front of a red background and pale red in front of a green background (see figure 4.6a). Similarly, a homogeneous colour field tends to look more yellow in front of a blue background, and more blue in front of a yellow background (see coloured Koffka ring in figure 4.6b). Simultaneous colour contrast is masterly employed by many painters, and features strongly in the aesthetic theory of some artists such as Josef Albers (Albers 1975).

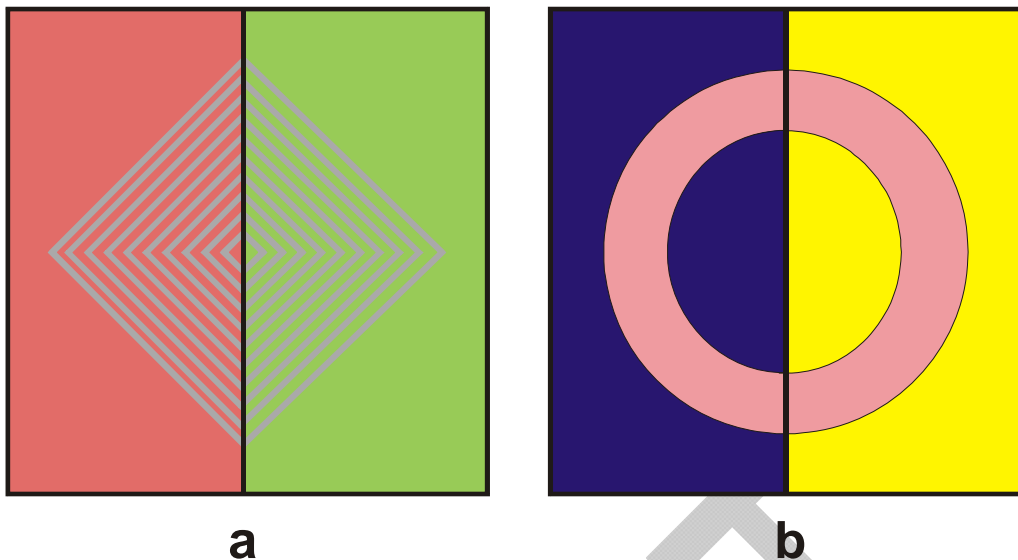


Figure 4.6: Simultaneous colour contrast illusions. (a) The diagonal lines generating the diamond shape pattern appear slightly tinted greenish in front of the red background, and pink in front of the green background, although they are printed in identical grey. (b) Partitioned 'Koffka Ring' in the colour domain – the left half of the ring (blue background) appears more yellow and the right (yellow background) half appears more blue. (see Colour Plate IV.3)

The enhancement of colour differences across space resembles simultaneous brightness contrast as discussed in the previous chapter, apart from the fact that it always operates in the blue-yellow or green-red colour direction (see Jameson & Hurvich 1964). This similarity of contrast enhancement in the brightness and colour domain, respectively, suggests that similar component processing mechanisms are underlying the perceptual phenomenon. Indeed, neurons have been found in the LGN and primary visual cortex (DeValois and Jacobs 1968; Hubel 1988), which have distinct receptive field regions that are preferentially sensitive to opponent colours. Yet some other neurons, called 'double opponent cells', have concentric receptive fields (similar to those which we encountered the previous chapter in the brightness domain), which increase their activity when the centre is stimulated by one colour and decrease their activity when the centre is stimulated by the opponent colour, and respond inversely during stimulation of the surround (Livingstone and Hubel 1988; Ts'o and Gilbert 1988). Colour opponency in these neurons needs to be generated through reorganisation of the spectral information captured by the S, M, and L photoreceptors for each stimulus location (Chatterjee and Callaway 2003), as has been predicted on the basis of psychophysical results (Hurvich and Jameson 1960). Most importantly, this reorganisation of the encoding of colour in the nervous system between the retinal input count of representation at higher cortical levels, allows us to regard the trichromatic theory and the opponent process theory no longer as competitors for a single explanation of colour vision, but instead, there is complementary explanations which describe different aspects of the visual system at by different coding strategies at

different levels of neural processing (see figure 4.7). Their heated scientific debate about which of the two main theories of colour vision is right and which is wrong was dissolved into peaceful coexistence by assuming two processing stages!

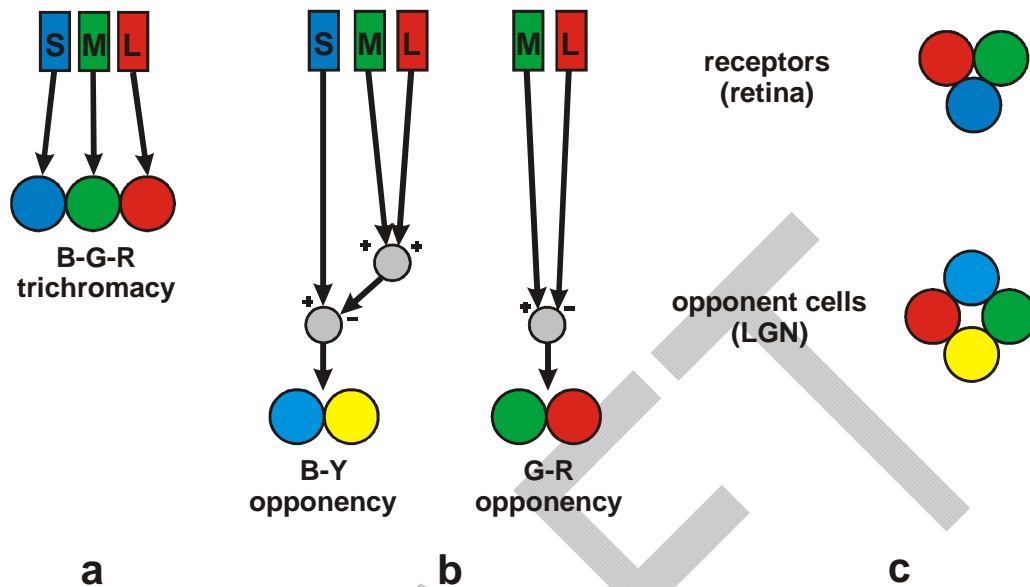


Figure 4.7: Connectivity of retinal photoreceptors in colour vision. (a) In the retina the three types photoreceptors tuned to different light wavelengths (S, L, M) separate three colour channels that are the basis for trichromatic encoding with primaries such as red, green, and blue. (b) In the LGN and cortical areas the S, L, and M inputs are reorganised to generate colour-opponent properties along the Blue-Yellow and Red-Green colour axes. (c) The coexistence of these two processing stages means that at different levels of the visual system different properties of colour vision can be found: trichromatic colour mixing at retinal level, and colour opponency at LGN and cortical levels. (see Colour Plate V.1)

Simultaneous and Successive Colour Contrast

Colour contrast may not only be experienced simultaneously across space, but can also be perceived in time, as after-effect: after staring at images of high contrast for some time, and opposite polarity after image is perceived when you look at a white or grey surface. For instance, after fixating the black dot in the centre of the left panel of figure 4.8 for a minute and then turning to the black dot in the right panel, you see a pink ring embedded in a pale green region. More generally, prolonged exposure to highly saturated versions of simple coloured patterns to leads to the perception of soft patterns of the opponent colour when the stimulus is removed and a uniform surface is shown. Such colour after-effects – opponent processing in time – is another dramatic demonstration of the perceptual organisation of colour space along the two independent dimensions red-green and blue-

yellow. How can we explain after-effect, what happens in the neurons encoding colour when such after-images are perceived?

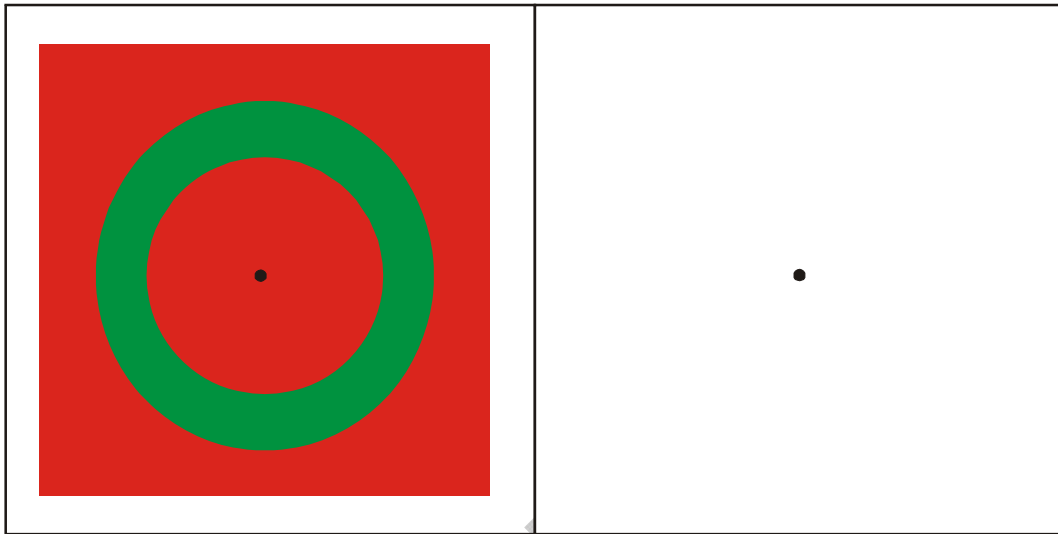


Figure 4.8: Fixate the black dot in the centre of the panel for about 60 seconds ... and then look at the black dot on the right! What you will see, is a pink ring embedded within a light green region – an opponent colour after-effect. (see Colour Plate V.2)

Three aspects of visual encoding are important to understand after-effects (Anstis et al 1978; Jameson and Hurvich 1964). (1) *Adaptation* is a natural property of sensory neurons, which reduces the response of individual cells during prolonged stimulation. Immediately after the onset of the red-green stimulus, when looking at the central fixation dot, the response of individual neurons sensitive to red or green jumps to a maximum value, depending on their location in the visual field, and then gradually returns to small levels by reduction of their sensitivity. Note that this ‘adaptation’ means that only temporal changes are encoded, the response is reduced when the stimulus is constant. This mechanism removes redundancy in the time domain, similar to the removal of redundancy in space by means of opponent receptive fields which you read about in the last chapter. Note that it also means that there is some kind of temporal ‘filling in’ because colours are not perceived as fading with time. (2) *Opponency* in the colour domain, according to the opponent theory of colour vision, means that stimulus components of opposite quality (red-green, or blue-yellow) are subtracted from each other at each given location in the receptive field. Therefore the perceived colour at any given location is determined by the difference between green and red activation. In the red areas of figure 4.8 the green input is zero, and the subtracted result of the opponent mechanism corresponds to the green input, adapting from a strong initial activity to much reduced levels after continuing stimulation; the inverse will happen for the green areas, where the red input is zero, and the green input reduces sensitivity through adaptation. (3) The *after-effect* is perceived by

looking at the neutral stimulus, the white field which provides the same stimulus energy to the red, green, blue, and yellow colour channels (remember that white light contains all colours and equally stimulates all photoreceptors). At the end of the adaptation period locations previously stimulated by green light are less sensitive to green than to red, and vice versa. After stimulus offset, when looking at the fixation spot in the white field, the white light appears red where the green light was shown before, because a larger neural signal is generated in the non-adapted red channel than in the adapted green channel, producing a red response after subtraction in opponent cells, and vice versa for regions that previously were exposed to red. This local imbalance between the red and green input to the opponent mechanism means that after stimulus offset weak colours are perceived with opponent hue to that presented before. What we observe, is colour contrast enhancement in the time domain. Colour afterimages can also be used to make greylevel photographs appear coloured, after the adaptation: to a coloured version of the same photograph in which the natural colours are inverted (see http://www.johnsadowski.com/big_spanish_castle.php).

The adaptation and after-effect phenomena discussed so far are reflecting mechanisms that change the properties of neurones, and thus of sensory systems, at rather short timescales of seconds to minutes. Such plasticity is very important for living beings to respond in the best possible way to a changing environment, and technically speaking move a system into a state where its operating range captures and processes the information available most efficiently. On a much longer timescale, we can interpret learning as plasticity with a similar function: as a child you have to learn that you pick and eat strawberries when they are red, but let them grow when they are still green, and have to learn how to use a knife to cut the strawberry into pieces. Apart from such elements of cognitive or motor learning, our sensory systems can be change on a long time scale of days or weeks, by repetitive exposure to the same stimuli, performance for perceptual tasks can improve substantially in what is called 'perceptual learning' (Fahle 2002). In colour vision a very peculiar case of plasticity was described on an intermediate timescale, the so-called McCullough effect: After a long exposure to patterns composed, for instance, from regions with red-black vertical gratings and others with green-black horizontal gratings, black and white gratings will appear pale green if oriented vertically and pale red if oriented horizontally (McCullough 1965). This contingent after-effect (it is called contingent because it relies on a combination of colour and orientation, and not on retinal location) works on an extended time scale – you not only need to look at the coloured induction pattern in the order of several minutes, but the after-effect most weirdly can stay with you for days! Recent work (Vladusich and Broerse 2002) suggests that this effect can be interpreted as result of a correction mechanism for colour-related imperfections of the eye (chromatic aberration). All this evidence seems to suggest that slow and longlasting adaptation processes in the visual system enable humans to adjust to changes of their typical environmental conditions.

In summary, simultaneous and successive contrast illusions demonstrate that image properties are not perceived in absolute terms, but relative to their immediate environment in space and time. We therefore can conclude that opponency, leading to contrast enhancement and redundancy reduction, is a fundamental process in the visual system, which is operating in the spatial the temporal, and temporal domain. What does this mean in terms of understanding the function of sensory systems? We have a starting point to develop a *theory of vision*, such as the general role of opponent filter mechanisms, which can be implemented as adaptation mechanisms and centre-surround receptive fields, and is perceived as the increase/decrease the apparent brightness of a line in front of a darker/brighter background (see previous chapter), the same perceptual changes for colour, or for other features such as orientation (Harris and Calvert 1989) or even faces (Hurlbert 2001; Zhao and Chubb 2001).

Can we see true colours?



Figure 4.9: Strawberries look most tempting when embedded in green leaves, independent of illumination – when you see red fruits or vegetables (like tomatoes) in supermarkets, they often presented in front of a green background to make them appear more attractive.

The phenomena described so far, such as trichromatic metamers, spatial colour contrast, colour aftereffects, demonstrate very clearly that there is no one-to-one relationship between the physical nature of the world surrounding us and its neural representation as available to perception – we are far away from perceiving ‘true colour’. Furthermore, there are substantial individual differences in describing colours, which may have perceptual or cognitive origins (Davidoff et al 1999), and there are some indications that there are cultural and possibly even gender differences in perceiving colour (Hurlbert and Ling 2007). It might be necessary to dig deeper and ask what we mean by true colours, and what are we really interested in when collecting information about our environment. At closer inspection, the spectral composition of a light source in itself might be fairly irrelevant, and it is object properties that are important for an animal or a person operating

in a complex environment. The surface colour of a fruit (see figure 4.9), for instance, is an indicator of its state – we like it ripe and sweet – so we can ignore the actual spectral composition of the light reflected from such a surface, which can vary considerably depending on illumination (Osorio and Vorobyev 1996). The spectral composition of daylight changes dramatically over during the day (Wyszecki and Stiles 1982), and the light reflected from a white sheet of paper contains more short wavelengths at noon (in particular when looking at the north sky) and are dominated by long wavelengths at sunset. Nevertheless, the white paper does not appear to the human eye as tinted blue or red, but is always perceived as white. The veridical representation of surface properties, independent of illumination, is known as ‘colour constancy’ which is attributed to adaptation and contrast normalisation mechanisms (Land 1977; Webster and Mollon 1995). The same mechanisms are responsible for perceiving surface colours correctly in bright sunlight, in the shade, or when looking through coloured filters, such as tinted sunglasses.

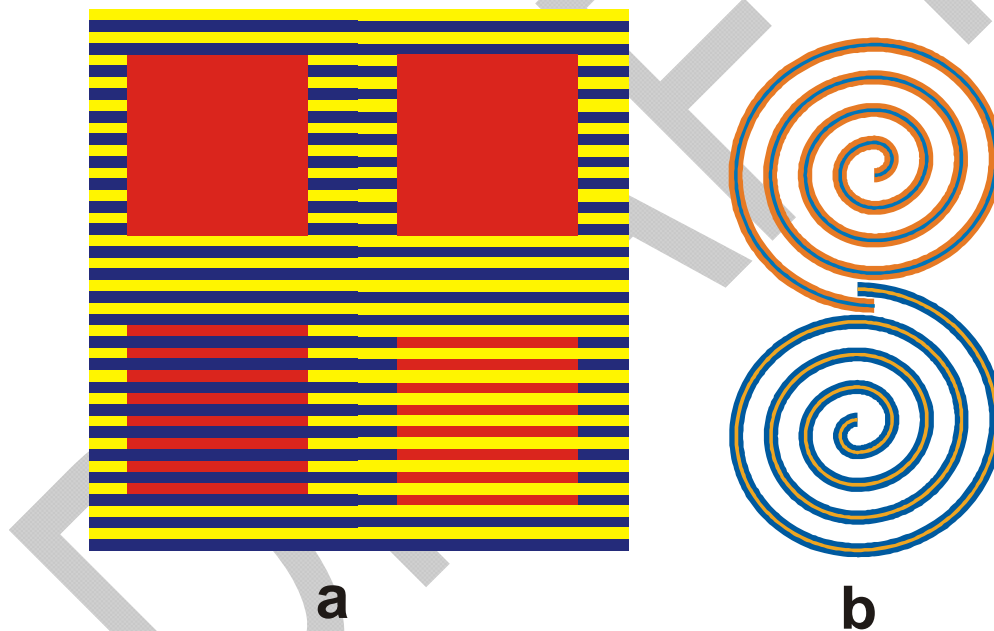


Figure 4.10: Colour assimilation. (a) Superposition of yellow or blue strips (bottom) on red squares (top) makes the red change its appearance dramatically – this Munker-White Illusion is a case of colour assimilation, where object boundaries override simple colour contrast effects. (b) In the Watercolour Illusion the coloured lines enclosing white image regions are spreading their chromatic properties into these regions as ‘neon colours’.

The importance of objects for visual perception may be key to understanding a variety of other illusions which are related to biasing perception towards uniform colours within enclosed regions, which is related to the transparency perceived for completed shapes

(Anderson 1997). The Munker-White effect (White 1979) shown in figure 4.10a in a colour version (Schober and Munker 1967) demonstrates the assimilation of surface properties, which induces a change of perceived colour in some areas to make them appear more similar to their immediate neighbourhood. Note that this effect shifts perception in the opposite direction of simultaneous contrast. In the example of figure 4.10a the coloured strips are perceived as more yellow when crossed by yellow gratings, and more blue when crossed by blue gratings, whereas the two red squares behind the gratings have exactly the same colour (see top panels). Such assimilation, being the opposite effect of simultaneous contrast, typically is related to the use of periodic occluders (gratings) and clearly outlined simple objects. In figure 4.10b another assimilation effect is shown, the 'watercolour illusion' (Pinna et al 2003). The coloured boundaries of the spirals spread as 'neon colours' into the physically white regions between the spiral lines. The images shown in figure 4.10 should remind us how much perceived colour can differ from the actual physical stimulus, and that in order to understand such perceptual distortions we need to know which perceptual tasks had been driving the evolution of neural encoding.

Take home messages

- colour vision adds value to visual processing by making chromatic information available that can be used for object recognition
- the basic properties of coloured light – spectra of light with different wavelengths – is the basis of designing systems to describe colour space (colour atlas)
- the trichromatic theory and the opponent process theory are the two major attempts to understand colour vision, which explain different aspects of perception, and can be related to different neural mechanisms
- the encoding of contrast in space and time reflects general principles of neural information processing and explain simultaneous and successive contrast illusions (aftereffects)
- higher level colour mechanisms, such as colour assimilation and colour constancy emphasize the importance of recover the properties of surface properties, and highlight the ecological function of colour vision

Discussion Questions

- Discuss the importance of colour vision in everyday life.
- What is meant by 'colour wheel'?
- Compare and evaluate the two most important theories of colour vision.
- How can we explain colour after-effects?

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