# Seeing Colour

Colour is such an integral part of our visual experience that most people assume perceived colour comes directly from the physical properties of objects themselves – my shirt *looks* yellow because it *is* yellow. That this assumption is not continually proved wrong by everyday experience is a testament to the cleverness of our visual system. But the assumption is wrong because colour is invented within the brain, and the colours we perceive are determined by many factors that differ between species, between people, between different parts of the retina, between each environment an object may be seen in, and also between moments in time. Therefore there is no consistent one-to-one mapping of the light entering my eye into the colour I perceive.

Yet, whenever and wherever I look at my shirt, it (nearly) always looks yellow. This is no happy accident: achieving such consistency underpins the main advantages of having colour vision – detecting and recognising objects by their colour.[1] In fact, one could say that the aim of a clever visual system is to create the illusion of simple correspondence between an object and its perceived colour – to enable us to live by that wrong assumption.

## The physics

Electromagnetic radiation in the visible range (wavelengths between about 350 and 700nm) is not categorically different from other wavelengths of electromagnetic radiation, but it happens to be very useful for perceiving the world: lots of it reaches the Earth's surface from the sun and most objects reflect some portion of it. Crucially, differences in chemical and physical properties cause most objects to differ in the proportion of each wavelength they reflect, and this spectral signature, the object's 'reflectance spectrum', can potentially be used to identify the object.

Our visual system attempts to represent these useful differences in reflectance as differences in colour, such that objects reflecting mostly longer wavelengths are perceived as reddish, while those reflecting shorter wavelengths are perceived as bluish. However, the light reflected from each object is a product of both the reflectance spectrum and the incident light that hits the object in the first place, and the incident light will change between sun and shade, blue sky and cloud, indoors and out, and also due to different objects reflecting light towards each other. Thus every time we see an object, the actual pattern of wavelengths reaching the eye from it may be markedly different.[2]

## Sampling the received light

Humans sample daylight mainly using three types of cone photoreceptor, which have different spectral sensitivity: longwave (L), middlewave (M) and shortwave (S) cones with peak sensitivities at about 560 nm, 530 nm and 430 nm respectively.[3] The fundamental building blocks of colour perception are created from the ratio of responses in each cone class. Relatively high L cone activity leads to perceiving red, relatively more M cone activity produces perceived green, and more S cone activity produces a blue sensation.

The outputs of the cones are coded by other retinal cells into two channels: a comparison between L and M cone signals (often referred to as red-green) and a comparison of the S cone signal to the pooled signals of L and M cones (often referred to as blue-yellow, but more accurately, lilac-yellow).[1] 'Trichromatic" colour vision, based on three types of cone, is also present in some fish and probably many marsupials,[4] but it is not the norm amongst vertebrates, and even where it occurs it is not normally like human colour vision. For example, a maturing flower that changes from green to yellow in humans, due to increasing ratio of L to M cone response, changes colour in the opposite direction for honey possums: their L to M cone ratio decreases.[5] This happens because the spectral tuning of the honey possum's M cone, with peak sensitivity near 500 nm, is very different from ours.

Genetic mischief among the human L and M pigment genes causes around 2% of men to go without either L or M cones, and with such 'dichromatic' vision they cannot discriminate between spectra that to the rest of us appear highly distinct (eg. red vs green, or blue vs pink[6]). Similarly, most placental mammals have only two types of cone, but they certainly don't all perceive the world in the same way: the S cone in many rodents, for example, is maximally sensitive to wavelengths shorter than 400 nm, which humans cannot see and call 'ultra-violet'.[7] Some mammals have no colour vision at all (notably all whales and seals tested so far[8]), while most birds, on the other hand, have four types of cone pigment, and potentially have colour vision that can discriminate between many spectra that look the same to us.[9]

Thus the way we sample the received light is the first big influence on how we perceive colour, and the sampling is different for different animals. It differs even amongst human trichromats: around 6% of men have 'anomalous' sensitivity in their L or M cones, and even amongst 'normal' trichromats, only about 60% of L pigments have the longest known sensitivity.[10] Thus there is really no such thing as 'normal colour vision'.

## Adaptation

The myriad of ways animals may sample light need not concern the individual human, for whom incoming spectra might still be consistently mapped to perceived colour according to the ratio of responses in his particular L, M and S cones. But the ratio produced by any given spectral input changes from moment to moment and across the retina, because each cone cell is continuously changing sensitivity due to adaptation (see Figure 1). A general rule of sensory cells is that when they are active they become less sensitive, and it is chiefly by this method that we cope with the large changes in light

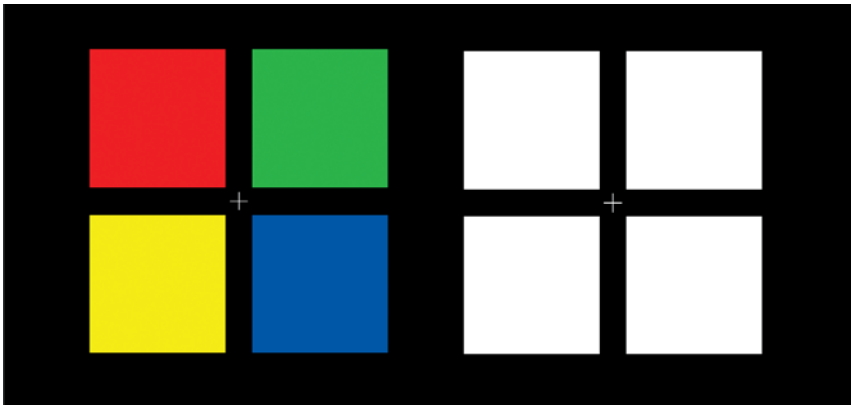

Figure 1. Adaptation to colour: Stare at the cross between the coloured squares on the left for 2 minutes. Then look at the cross between the white squares on the right. Where your L cones are most adapted from viewing red, the square now looks greenish. Similarly, adaptation to green, blue and yellow produce pink, yellow and lilac after-effects, respectively.

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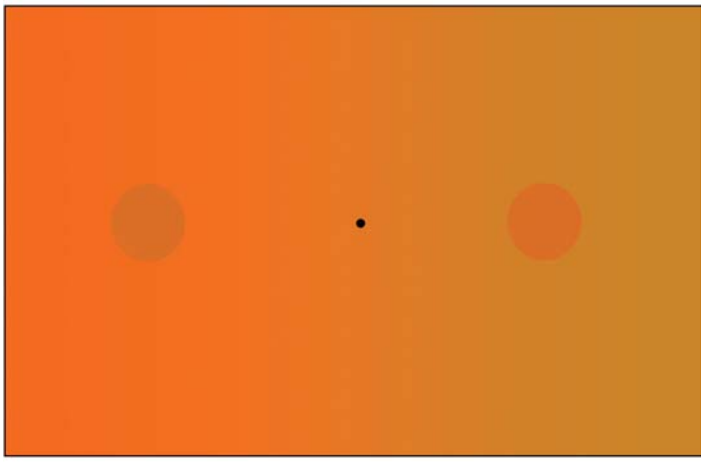

Figure 2: Simultaneous colour contrast: Look at the central dot and judge whether the two circles appear the same colour. They are identical, but the colour we perceive depends on the objects' environments.

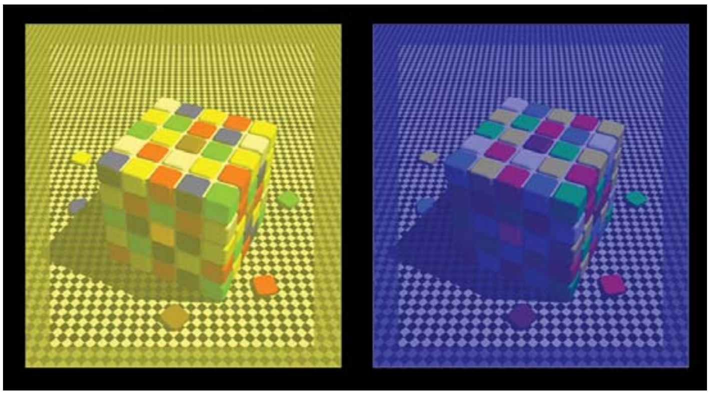

Figure 3: Colour constancy. The tiles that appear blue in the left image are physically very different from the tiles that appear blue in the right image. Likewise for all the other colours. In fact, the blue tiles on top of the left cube are identical to the yellow tiles on top of the right cube, which becomes apparent if you cover the rest of the images (with a paper cut-out for example, or see www.lottolab.org). This powerful 'illusion' is achieved because the brain interprets the images as two nearly identical cubes seen under very different illumination (yellow or blue), and the colours in each image were calculated to be consistent with this interpretation. In other words, our brain tries to 'see' objects rather than simply representing the actual light that reaches the eye. The images were created by Dr R Beau Lotto (www.lottolab.org).

intensity that occur when we step outdoors, for example, or when the sun appears from behind cloud. Adaptation means that from the earliest stage of processing, the ratio of cone responses represents changes in spectral input, rather than the absolute spectral input.[11] This serves three useful purposes for object identification:

1. Differences between objects are exaggerated.
2. The influence of the illumination colour (eg. yellow artificial light vs bluer natural light), is reduced.
3. Variations in spectral input across the retina, due to filtering by macular pigment for example, are largely not translated into differences in cone response ratio.

## Contrast

The same three purposes are also served by mechanisms that compare inputs across space. Colour is perceived relative to neighbouring colours (see Figure 2), and this contrast process also begins at the earliest possible processing stage. Horizontal cells in the retina attenuate the output of cone cells if other cones nearby are active. Such 'lateral inhibition', like adaptation, is a general principle of our visual system and probably operates at every level, meaning that everything is processed relative to the environment in which it is viewed.

## Colour constancy and visual knowledge

As discussed above, the spectrum of light we receive from any given object can vary greatly depending on the colour of the light source, shadows, and light reflected onto it from other objects. Despite this, we perceive a white shirt as white and a yellow shirt as yellow regardless of the environment it finds itself in.[2] This 'colour constancy' is achieved to a large degree by adaptation and contrast.[12] But on their own, these simple mechanisms are not enough, especially in the cases of shadows and local differences in light reflected from other objects.

To deal with this, our colour system has to take into account the shapes of objects, the layout of a scene and likely lighting source, before creating the colours we finally perceive (see Figure 3). It is not known exactly how this is achieved, but it must involve extensive communication between cells in different brain regions, especially those in cortical area V4 (if this region is damaged, colour perception is severely disrupted – a condition known as achromatopsia[13]). Importantly, all the calculations are achieved automatically and subconsciously.

For example, in a room in which the ceiling is white but one wall is red, a predominance of long wavelengths will be reflected from that wall onto the ceiling, making the light coming from the ceiling pink (ie containing more long wavelengths than short wavelengths). But we still perceive the ceiling as white because our visual brain takes account of the spatial arrangement of the ceiling and coloured wall, and automatically ascribes any pinkness coming from the ceiling to reflected light from the red wall, rather than to the properties of the ceiling itself.[14]

With clever tricks like this, our colour system continuously attempts to make colour represent the physical properties of an object itself, rather than the spectrum of light that happens to be reaching us from the object in any given circumstance. Thus what we see is actually our brain's interpretation of objects, rather than any simple representation of the light entering our eyes. It is this automatic interpretation that makes colour vision so useful for detecting and recognising objects despite changes in their environment.

**References**

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