Seeing Colour

“… 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”

Sir Isaac Newton (1730)

Light and Colour

• Visible light occupies the electromagnetic spectrum from approx. 400-700 nm

![Visible Light Spectrum](image)

• The wavelength of the light is correlated with the colour we experience

Sir Isaac Newton
The Founder of Colour Science

• Before Newton, colour was thought of as a fundamental property of objects

• Newton made several crucial discoveries:
  – that colour was a subjective experience
  – that white light was made of a mixture of many different wavelengths of light
  – that the colour experience is determined by the combination of wavelengths that reach the eye

Newton’s Prism Experiments (1)

• Newton’s classic experiment was to show that white light could be broken down into its spectral components by passing it through a prism

![Newton’s Original Experiment](image)
Newton’s Prism Experiments (2)

- He also showed that:
  - once broken down into a spectrum, single components could not be broken down further
  - it was possible to recombine several wavelengths to produce white

Seeing Rainbows

- The colours of a rainbow are determined by prismatic refraction in rain drops

What is colour for?

- Some form of colour vision is almost universal across species
- Colour vision capacity varies a great deal across species
- Colour vision capacity is related to the visual environment
- No definitive answer as to why colour vision evolved, but it seems likely that it provided an advantage in the identification of food sources or in mate selection

Things to know about colour vision

- What are the phenomena of colour?
- How do we describe colours? Colour specification
- How do we produce colours? Colour mixing
- Colour matching. The psychophysics of colour
- Colour vision theory. Trichromacy vs opponent processing
- How is wavelength information processed by the visual system?
- Why do some people not see colours normally? Colour deficiencies
- Is colour experience universal across species? Comparative colour vision

The Phenomena of Colour

Coloured afterimages
The Phenomena of Colour
Coloured afterimages

The Phenomena of Colour
Colour assimilation

The Phenomena of Colour
Coloured afterimages

The Phenomena of Colour
Colour assimilation

The Phenomena of Colour
Colour Contrast
The Phenomena of Colour

Colour Contrast

The Phenomena of Colour

Saturation Adaptation

The Phenomena of Colour

Saturation Adaptation

The Phenomena of Colour

Colour Deficiencies

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How do we describe colours?

Colour Specification

The Dimensions of Colour

- Although we tend to think of colour in terms of colour names, colour is a multi-dimensional experience.
- Each of these dimensions is associated with a different physical property of light
- There is a need for a system that allows for colours to be described accurately and reproduced reliably

Dimensions of Colour

Subjective  | Physical
---|---
• Hue
  – the “colour” of the target
• Saturation
  – the degree of whiteness in the target
• Brightness
  – the perceived intensity of the target
• Wavelength
• Spectral purity
• Luminance

What colours do we see?

Hue

- All discriminable colours can be described in terms of 4 colour names:
  - Blue; Yellow; Green; Red

  e.g. purple = red + blue
  brown = dark yellow
cyan = blue + green
  etc.

How many colours can we see?

- Can calculate the theoretical maximum based on the number of jnds for each colour dimension
  - Wavelength Discrimination - 200 jnds
  - Saturation - 20 jnds
  - Brightness - 500 jnds
- Therefore total range of possible colours
  \[200 \times 20 \times 500 = 2 \text{ million}\]
Saturation and Brightness

- All colours can vary in saturation and brightness

The Specification of Colour

- The Colour Wheel
  - Only gives information about hue

The Specification of Colour

- The Colour Disk
  - Gives information about hue and saturation

The Specification of Colour

- The Colour Solid
  - Gives information about hue, saturation and brightness

The Specification of Colour

- The colour shapes provide a qualitative description of colours
- There is a great need for a precise quantitative system to ensure consistency in paints, dyes, inks, etc.
- Several systems in use

The CIE System

- The CIE system was developed to provide a description of any given colour using a set of “primary” wavelengths and a “standard” observer.
- Based on the fact that different wavelength mixtures produce different colour sensations
- A colour is defined by the relative amounts of each of the primaries needed and can be plotted as shown
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How do we produce colours?

Colour Mixing

Producing Colours

Although hue is determined by wavelength, we are very rarely exposed to single wavelengths

Most of the time, what we see is a mixture of many different wavelengths

Colour and Wavelength

- Typical wavelength mixtures for colours we see

Determining the colours we see

- Ultimately, the wavelength composition of the light that strikes the retina determines the colour we see.

BUT

- The wavelengths that reach the eye depend on several factors.

1. The spectral composition of the source

Different light sources have very different spectral compositions
2. The spectral reflectance of the surface

Achromatic surfaces

Common pigments

Reflectance of some common objects

Determining the colours we see

The wavelengths that reach the eye represent the product of the source and the object wavelength distributions

Metamers

- It is possible to produce the same colour sensation using a variety of wavelength combinations
- When two colours with different wavelength compositions generate identical colour sensations they are said to be metameric

Colour Mixtures

- Colour mixing refers to the way in which wavelength combinations may be delivered to the eye
- Most of the time we are aware simple of the end result and are not concerned with the process of producing specific colours
- However, sometimes we wish to ensure that we can create a specific colour by mixing wavelengths

4.11 Metameric Lights. Two lights with these spectral power distributions appear identical to most observers and are called metamers (A) An approximation to the spectral power distribution of a tungsten bulb (B) The spectral power distribution of light emitted from a commercial television monitor whose three phosphor intensities were set to match the light in panel A in appearance.
Mixing Colours

• There are two ways in which we can alter the wavelength composition of light reaching the eye

• For subtractive mixtures, the source produces a wide range of wavelengths, some of which are eliminated

• For additive mixtures, wavelengths from different sources are combined

Primary and Complementary Colours

• Primary Colours
  – are those colours that will give the widest range of colours when mixed together.
  – these are different for additive and subtractive mixtures

• Complementary Colours
  – colour “opposites”
  – have different effects when mixed additively or subtractively

Subtractive Colour Mixing

• Applies to paints, dyes, inks, etc., and to light passing through filters

• Begin with broad range of wavelengths then take away some away
  – resultant colour is always darker than the components

• Primaries are blue, yellow and red

• Mixing complements produces black

Subtractive mixtures

Through selective reflection
Through selective absorption

Colours from subtractive mixtures

Reflective Surface
Single filter
Multiple filters
Additive Colour Mixing

- Applies when light is coming from more than one source; e.g. spotlights, TVs, magazine images
- Light reaching the eye is the sum of the wavelengths of the sources – final result is brighter than the components
- Primaries are blue, green and red
- Mixing complements produces white

Additive colour mixing

Print and TV colours are produced additively because the individual colour elements are too small to be resolved

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Colour matching

The psychophysics of colour

- Colour mixing experiments showed that many colours could be produced by varying the relative proportions of the component wavelengths
- Colour matching experiments were designed to quantify the component mixtures
- These data were then used to infer something about the underlying mechanisms
Colour matching experiments

- A metameric match means that two different sets of wavelengths are having identical effects on the visual system
- To understand this, we need to understand the conditions under which metamerism occurs
- But natural metamers have complex spectral distributions

Metameric matches

Need to use a simpler arrangement with only a limited range of wavelengths

Two important findings from colour matching:

1. All spectral lights could be matched by mixing several other wavelengths (primaries) together in varying proportions
2. A maximum of three primaries was needed to match all spectral lights

This result led to the conclusion that there must be three classes of receptor responding to light of different wavelengths.

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Trichromatic Vision

- Why should the fact that we need three wavelengths to make all spectral matches mean that we have three receptors?
- Can understand this if we understand why rods are colour blind
The Purkinje effect: Rods are colour blind

• The Purkinje effect shows that the transition from cone to rod vision results in a loss of colour sensation

• As light levels decrease:
  – colours begin to fade and eventually everything looks grey
  – reds and yellows look very dark, while blues and greens look relatively bright

Why are the rods colour-blind?

• The spectral luminosity functions show only that the rods are more sensitive at shorter wavelengths.

Question: Why do the rods not permit colour vision?
Answer: There is only one photopigment in the rods.

Explanation: Receptors can only signal that they have been stimulated by light, not what wavelength has stimulated them (The Principle of Univariance)

The response of a single receptor system to light of different wavelengths:

• The output of a photoreceptor is a product of the intensity of the light and the sensitivity of the receptor to that particular wavelength

  Output = Intensity * Relative Sensitivity

• This means that two lights of different intensity can produce the same effect if their intensities are adjusted appropriately

...
The response of a dual photoreceptor system to light of different wavelengths

• If there are two photopigments with overlapping spectral sensitivities, then it is impossible to adjust the relative intensities of two single wavelengths to produce a match.

The response of a dual photoreceptor system to light of different wavelengths - single primary

• To produce identical outputs from two detectors with different, but overlapping, sensitivity functions, one has to adjust the intensities of two different wavelengths simultaneously to match any other wavelength.

• Because two primaries are required to make a match, the system is said to be dichromatic.

The response of a dual photoreceptor system to light of different wavelengths - two primaries

Trichromacy

• It follows from the results of the colour matching experiments that if three primaries are necessary to make a match, then there must be three receptors.

• For colour matching, the number of primaries needed to match all spectral lights implies the number of underlying receptor systems.

• By plotting the relative intensities of the primary wavelengths needed to make a spectral match, it is possible to derive the shape of the underlying receptor sensitivity functions.

• These data provided evidence in favour of the trichromatic theory of colour vision.

Trichromatic Theory

Young-Helmholtz Theory

• The original suggestion that we have only a limited number of photoreceptive mechanisms was based on logic rather than experiment.

• Thomas Young (1802) realised that we could not individual receptors for all the colours we see.

• He proposed that there were only three types of receptor, each responding to a wide range of wavelengths.
Trichromatic Theory

Young-Helmholtz Theory

- The original suggestion that we have only a limited number of photoreceptive mechanisms was based on logic rather than experiment.
- Thomas Young (1802) realised that we could not have individual receptors for all the colours we see.
- He proposed that there were only three types of receptor, each responding to a wide range of wavelengths.
- Helmholtz provided the psychophysical evidence to support this theory with his colour matching experiments.

Opponent-Process Theory

- Although colour matching experiments could be explained easily by trichromatic theory, there were a number of colour phenomena that did not seem to fit with this theory.
  - afterimages
Opponent-Process Theory

- Although colour matching experiments could be explained easily by trichromatic theory, there were a number of colour phenomena that did not seem to fit with this theory
  - afterimages
  - simultaneous colour contrast
  - “fundamental” character of blue, green, red, and yellow
- Hering suggested that these colours were linked in some way

Opponent-Process Theory

- Hering proposed that red-green, blue-yellow, and black-white were organised in some opponent fashion so that the activation of one would suppress the other
- On this basis it was possible to explain many colour phenomena
- Immediate difficulty was that there was no candidate mechanism as there was for the Trichromatic Theory

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The Physiological Basis of Colour Vision

- For many years there was disagreement about which colour vision theory was correct
- Until the 1960s, virtually all of the available data were psychophysical and they supported Y-H
- A new technique, micropspectrophotometry (MSP) allowed for direct measurement of cone photopigments
- First measurements of cone absorption curves made by Brown and Wald in 1964. Showed presence of three cone pigments
The Molecular Basis of Colour Vision

- Research over the past 15 years has shown that the absorption spectrum of a photopigment is determined by the sequence of amino acids in the opsin protein
- Small differences in the sequence shift the peak of the absorption curve along the spectrum

Trichromatic vs Opponent Process Theory
Was Helmholtz right?

- MSP appears to vindicate Y-H theory
  - But
  - Some psychophysical evidence in favour of opponent process (mainly from colour cancellation experiment)
- Then
  - Physiological data began to appear that showed neurons responding in an opponent fashion

Neural processing beyond the receptors

- Advances in technology allowed for recording from single neurons
- One characteristic of neurons is that they have a spontaneous rate of firing. This means that they can respond by increasing or decreasing their firing rate
- Recordings from the lateral geniculate nucleus showed spectrally opponent responses

Svaetichin recorded from the horizontal cells of fish and found some cells that responded by hyperpolarizing to some wavelengths and depolarizing to others.

This was the first evidence for an opponent system
Receptive Fields

- A receptive field is the area on the retina that feeds into a single neuron.

- If this area is stimulated by light the neuron will change its firing rate

Opponent Process

Receptive Field

Responses of a colour opponent cell
Was Helmholtz right?
Both the trichromatic and opponent process theories are necessary to explain most of the phenomena of colour vision.

How do trichromatic cones become opponent processing ganglion cells?

- While Y-H and opponent theories together explain most colour phenomena, Land’s experiments show that other factors need to be taken into account.
- Opponent cells can signal the wavelength of an object efficiently but don’t account for spatial effects like such as simultaneous contrast, coloured shadows, etc.
- One class of neuron that might be involved is the double-colour-opponent cell.

Centre-Surround Receptive Field

A double opponent receptive field
A cell with this receptive field arrangement would respond well to a red object on a green background.

Colour Processing in the Visual Cortex
- Double colour opponent cells are found in specific areas of the visual cortex.
- Because of their appearance they are known as “blobs”.

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Colour Vision Deficiencies

Colour Deficiencies

- The term “colour-blind” is incorrect, except in a very small proportion of cases
- Occurs in about 8% of male population, much less than 1% in females
- Several different forms of colour deficiency
- Most forms are hereditary and sex-linked
- Result from missing a photopigment or having photoreceptors with anomalous spectral absorption characteristics

Characteristics of colour deficiency

- Colour deficiencies classified (formally) in terms of number of primaries needed to make a spectral match
- In practice, diagnosis is based on screening tests
  - Colour test plates
  - Colour sorting tasks
- See colours, but have a wide range of confusion where two colours are indistinguishable

Colour Vision Screening Plate
### Monochromacy
- Very rare; often associated with other problems
- May be considered as “true” colour blindness
- Can match all wavelengths by adjusting intensity of any other single wavelength
- Comes in two forms
  - Rod monochromacy
  - Cone monochromacy

### Total Colour Blindness
- Rod Monochromats
  - No colour vision
  - Poor acuity
  - Photophobic
- Cone monochromats
  - No colour vision
  - Otherwise normal vision

### Dichromacy
- Occurs in about 2% of males and .01% females
- Is not colour “blindness”, rather colour deficiency
- Can match all wavelengths by adjusting intensity of two other wavelengths
- Comes in three forms
  - Protanopia
  - Deuteranopia
  - Tritanopia

### Protanopia
- Missing the long wavelength pigment
- Reds and orange look very dark
- Confuses red and green

### Deuteranopia
- Missing the middle wavelength pigment
- Brightness normal
- Confuses red and green

### Tritanopia
- Missing the short wavelength pigment
- Brightness normal
- Confuses blue and green

### Anomalous Trichromacy
- Occurs in about 6% males, .01% females
- May be thought of as a milder version of dichromacy
- Three wavelengths needed to make a spectral match, but use different proportions of primaries form normal trichromats
- Comes in three forms (characteristics are milder versions of dichromatic defects)
  - Protanomaly
  - Deuteranomaly
  - Tritanomaly

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Comparative Colour Vision

What do other species see?

• We tend to think of our colour vision as being the norm, but it is certain that sensitivity to different wavelengths varies across species and it seems likely that colour experience varies too.

• Traditional thinking has tended to downplay the role of colour in other species

One indication that an animal may have a different colour experience is if the cone absorption curves are different

But this does not tell us what use they might make of these mechanisms

Measuring colour vision in other species

• With the possible exception of parrots, one cannot simply ask an animal what colour it sees

• To assess colour vision in animals, we must devise techniques that will allow us to infer the presence of colour vision

The Colour Blindness Myth

• ‘Within the mammals, color vision is by no means widespread’ G.L. Walls (1942). The Vertebrate Eye

• ‘most of them are practically colour blind.’ L.H. Matthews (1969). The Life of Mammals


• ‘On the whole, mammals appear not to have colour vision, except for the primates where it is well developed and almost certainly trichromatic’ K. Tansley (1965). Vision in Vertebrates

Criteria for Chromatic Vision

• Two (or more) cone classes with different spectral sensitivities

• The requisite neural architecture for interpreting these differences

• The ability to make use of the information in a discrimination task
Assessment Techniques

- **Anatomical**
  - microspectrophotometry

- **Physiological**
  - electroretinograms

- **Behavioural**
  - discrimination tasks

The potential for colour vision can be demonstrated using anatomical or physiological techniques.

But

- Colour vision must be demonstrated behaviourally.

Behavioural Assessment of Colour Vision

- “The brightness problem”

  Most important to ensure that animal is making a judgement on the basis of the hue information and not some other attribute of the stimulus.

  If one target is brighter than another, then animal may be using this attribute, rather than hue.

  Can be dealt with by making brightness irrelevant or by taking it into account directly.

An example: testing horse colour vision

- Horses are very visual animals.

  Conflicting statements in the literature about their abilities.

  Very few studies have been carried out.

- Horses are very visual animals.

  Conflicting statements in the literature about their abilities.

  Very few studies have been carried out.
Dealing with the brightness problem

- First measure how good they are at detecting small intensity differences for non-coloured stimuli.
- Then, for the coloured targets, choose a range of intensities close to the brightness match.
- If they can see the colour, they will perform well, no matter what the intensity differences are.
- If they are basing their judgements on brightness, performance will decline close to the brightness match.

Task is to select the central panel that looks different from the flanking panels.

This technique first used with babies.

Performance declines for an achromatic target on a grey background.
Performance consistently good for the red target on a grey background.

Measuring horses’ ability to detect small differences in luminance.

The data show that as the luminances become more similar, performance declines.

Summary

- Horses are capable of making chromatic discriminations, so they do have colour vision.
- They can easily discriminate red and blue, but have more trouble with green and yellow.
- These results suggest that horses must be at least dichromatic.