Visual Neuroscience

Colour Vision Phenomenology

a guided tour of
colour opponency
&
colour constancy

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<tr>
<th>NAMING SEQUENCE</th>
<th>WAVELENGTH</th>
<th>TRADITIONAL SPECTRUM</th>
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<tr>
<td>Red</td>
<td>R 668</td>
<td>Red</td>
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<tr>
<td>Reddish-yellow</td>
<td>R Y 600</td>
<td>Orange</td>
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<td>Yellow</td>
<td>Y 580</td>
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<td>Yellowish-green</td>
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<td>Bluish-red</td>
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<td>Violet</td>
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TRADITIONAL SPECTRUM

Red
Orange
Yellow
Green
Blue
Indigo
Violet

Isaac Newton 1704

Newtonian 18th century colour-naming

Ewald Hering 1892 - opponent colour theory

Opponent colour response functions

Not-perceived

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Relative response of red or yellow

Relative response of green or blue

Not-perceived

Unique blue: ~ 475
Unique green: ~ 500
Unique yellow: ~ 580
Unique red:~ extraspectral
successive colour contrast

simultaneous colour contrast
Opponent colour perceptual phenomenology

**Appearance**
No hue combines redness & greenness, nor blueness & yellowness

**Induction**
One member of an opponent pair induces its complementary colour:
- successive colour contrast
- simultaneous colour contrast

**Cancellation**
The colours of an opponent pair should cancel to achromatic white (or grey)

‘COLOUR’ is an illusion created by the brain as a perceptual correlate of spectral wavelength.

There is nothing in the nature of the physical universe, nor the physics of light to compel colour-opponency.

Colour-opponency is entirely caused by biology & by the construction of our nervous system.

So what is the PHYSIOLOGY of colour perception?
3 cone types:
LW (‘red’)
MW (‘green’)
SW (‘blue’)
&
1 rod type.

**COLOUR**
comes from cone comparison.

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**principle of ‘univariance’**

Activity of cone (hyperpolarization) is a univariant property that depends on two properties of incident light: wavelength and intensity. Hence cone activity yields no precise information about wavelength.

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**TWO RETINO-GENICULATE CHANNELS FOR CONE COMPARISON**

- **Konio channel**
  - MW ‘green’ cone
  - LW ‘red’ cone
  - SW ‘blue’ cone

- **Parvo channel**

Actually, all cones contribute to RF surround.

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**Schematic ‘wiring’ diagram for receptive fields of K & P retinal ganglion cells**

- **Excitatory**
  - LW
  - SW
  - MW

- **Inhibitory**
  - LW
  - SW
  - MW

**Relative sensitivity**

- **Equal quantum catch**

**wavelength (nanometers)**

400 500 600 700
Cone opponent variants in retina & LGN

Difference of gaussians (‘DOG’) model

excitatory centre

inhibitory surround

K

Koniocellular
Bistratified

P

Parvocellular
Midget

Thalamic (LGN) terminology
Retinal Ganglion Cell terminology

Colour circle, or 2D colour space
Cone opponent colour space

Can calculate the exact ratio of cone activities produced by any given trio of RGB screen settings.

Cone photoreceptor sensitivity

CRT phosphor emission

Cardinal directions of colour space
Krauskopf et al. (1982)
Crimson - Cyan
Violet - Chartreuse

The spectral characteristics of parvo & konio channels are not the basis of our primary colour percepts!
Cone opponent colour space

Waeger et al. (2005)  
Compilation of unique hue judgments of 18 observers

Crimson - Cyan  
Violet - Chartreuse  

The unique blue – unique yellow axes divide cone-opponent colour space into symmetric zones of blueness and yellowness.

The unique red – unique green axes divide cone-opponent colour space into asymmetric zones of redness and greenness.
Unique blue and unique yellow add to give achromatic white

Unique green and unique red add to give a hue that is mainly yellow
Anthropological studies confirm that different languages/cultures (not just English) have primary colour terms for ‘red’, ‘green’, ‘blue’ and ‘yellow’ (and not orange, magenta, cyan & chartreuse, for instance).

The cardinal axes of colour space are (crimson) red-cyan & violet-chartreuse - not red-green & blue-yellow – hence the retinogeniculate parvo and konio cone-opponent channels cannot be the direct basis of human primary colour perception. Instead, we must infer that cortical mechanisms recombine the retinogeniculate channels (much as the parvo and konio channels themselves recombine cone signals), and that these cortical recombinant channels are the basis of primary colour perception.

The location of unique blue, unique yellow, unique red, and unique green in the cardinal axes (i.e. cone-opponent) colour space explains, or rationalises, why blue & yellow cancel to give white, but red and green cancel to give yellow.

Cortical recombination …?

Going by the colour phenomenology, we would infer that:
Redness is supported by L-M and S-(L+M) [the latter component rationalising the violet colour of light at the SW end of the spectrum];
Greenness is supported by M-L and (L+M)-S;
Yellowness is supported only by M-L;
Blueness is supported by S-(M+L) and M-L, plus a minor contribution from L-M !

BUT – direct physiological evidence to support such a systematic cortical recombination of the retinogeniculate colour channels has yet to be obtained.
Colour constancy

The computational principles of colour constancy can be understood by first examining achromatic lightness constancy…

Two forms of opponency in retinal ganglion cell & lateral geniculate nucleus (LGN) receptive field organisation:-

1. cone opponency (‘K’ & ‘P’)
2. spatial opponency (‘M’ & ‘P’)

<table>
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<tr>
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<th>P</th>
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<tr>
<td><strong>Koniocellular</strong></td>
<td><strong>Parvocellular</strong></td>
<td><strong>Magnocellular</strong></td>
</tr>
<tr>
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Thalamic (LGN) terminology

Retinal Ganglion Cell terminology
achromatic simultaneous contrast

If the retina were to signal absolute intensity, much of this sensitivity would be lost.

If the retina signals contrast, it allows small differences in brightness to be distinguished over a wide range of illumination intensity.

If the retina were to signal absolute intensity, much of this sensitivity would be lost.
How do the responses of a RGC (e.g. ON centre, OFF surround) vary at different positions across a light dark edge?

Apparent surface brightness is reconstructed from contrast across edges; - but there is no guarantee that absolute perceived brightness is veridical: does the brain guess?
The retinal ganglion cell centre-surround RFs are not efficient at detecting intensity gradients...

Apparent surface brightness is reconstructed from contrast across edges... - Problem for detecting fuzzy edges (lightness gradients) ..?
Is this an illusion, or an example of ‘lightness constancy’?
The goal of brightness perception is to perceive the reflectance of the surfaces in view.

Different coloured surfaces have different spectral reflectance curves, including fish...

The goal of colour perception is to perceive the spectral reflectance of the surfaces in view.
Colour constancy depends on 'discounting the illuminant'

Think of this as being not an image on a screen, but a real-world situation, in which a multi-faceted (Rubik’s cube) type object is illuminated by very yellowish or blue-ish light, in which case it would be advantageous to see the real blue (left) or yellow (right) colours of the elements, as opposed to the achromatic (grey) spectral composition of the light actually reaching the eye.

It all depends upon a subjective (& individually variable) interpretation of lighting conditions. Objects viewed in shade have excess blue light, hence the brain’s percept tends to discount some blueness from the retinal image. People differ in thinking that the dress is or is not in the shade! - Shows how prior assumptions can influence perception (predictive coding).
If colour constancy depends on ‘discounting the illuminant’ …

…how might the brain do this?
Colour constancy depends on ‘discounting the illuminant’

How does the differential blue detector respond with an excess of blue illumination?

Perceived blueness/yellowness

Differential blue detector

Blueness profile

Retinal image

In theory, the brain might reconstruct a blue/yellow profile from chromatic edge signals, and then adjust for overall excess of blue (or yellow) light.
Edwin Land (d.) … pictured with his multicoloured display

Piet Mondrian 1872 - 1944
Multiple visual areas in prestriate cortex of macaque monkey

Recordings of colour cells in area V1 and V4, using Mondrian stimuli

**LW illumination**

**White light’ illumination**

- **V1** ‘red’ neuron responds well to red area
- **V1** ‘red’ neuron responds mildly to red area
- **V1** ‘red’ neuron: responds whenever LW light is dominant within RF - i.e. when LW:MW cone ratio > 1
LW illumination  'Greenish-White light' illumination

same ratio; differing intensity
differing ratio; differing intensity

V1 red neuron responds well to red area
V1 red neuron unresponsive to red area

V1 red neuron: responds when LW light is dominant within RF; - Fails to respond when LW:MW cone ratio < 1

V4 red neuron unresponsive to red area
V4 red neuron responds well to red area – that has maximal ratio of LW:MW cone activity

V4 red neuron with hypothetical centre-surround RF:
- responds when centre LW:MW cone ratio is greater than average surround LW:MW cone ratio
LW illumination

G MW MW LW
same ratio; differing intensity

V4 'red' neuron unresponsive to red area

V4 'red' neuron with hypothetical centre-surround RF: still responds in greenish-white illumination, as centre LW/MW cone ratio remains greater than average surround LW/MW cone ratio.

Greenish-White light ’ illumination

differing ratio; differing intensity

V4 'red' neuron is responsive to red area – that has maximal ratio of LW/MW cone activity

V4 'red' neuron is responsive to red area – that has maximal ratio of LW/MW cone activity.