Achromatic and chromatic vision, rods and cones.

Outline

- Introduction
- Rod and cone vision
- Rod vision is achromatic
- How do we see colour with cone vision?
- Vision and visual pathways
- Achromatic and chromatic cone vision (colour and luminance)
Achromatic and chromatic vision, rods and cones.

400 - 700 nm is important for vision.
Achromatic and chromatic vision, rods and cones.

The retina is carpeted with light-sensitive rods and cones.

An inverted image is formed on the retina.

Rods and cones

Fig1b: Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.
Human photoreceptors

**Cones**
- Daytime, achromatic and chromatic vision
- 3 types
  - Long-wavelength-sensitive (L) or “red” cone
  - Middle-wavelength-sensitive (M) or “green” cone
  - Short-wavelength-sensitive (S) or “blue” cone

**Rods**
- Achromatic night vision
- 1 type

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Achromatic and chromatic vision, rods and cones.
Why do we have rods and cones?

Our vision has to operate over an enormous range of $10^{12}$ (1,000,000,000,000) levels

To cover that range we have two different types of photoreceptor...
Achromatic and chromatic vision, rods and cones.

**Sensitive ROD SYSTEM**
- Lower range

**Cone System**
- Upper range

**Typical ambient light levels**

- **Moonlight**
- **Starlight**
- **Indoor lighting**
- **Sunlight**

**Visual function**

- **Absolute rod threshold**
- **Cone threshold**
- **Rod saturation begins**
- **Damaging levels**

**Two systems**

**Photopic levels**
- **Photopic levels** (above rod saturation) where cone vision functions alone.
  - A range of $> 10^6$

**Scotopic levels**
- (below cone threshold) where rod vision functions alone.
  - A range of $c. 10^{15}$

**Mesopic levels**
- where rod and cone vision function together.
  - A range of $c. 10^4$

**Photopic retinal illuminance**
- (log phot td)

- [-4.3, -2.4, -0.5, 1.1, 2.7, 4.5, 6.5, 8.5]

**Scotopic retinal illuminance**
- (log scot td)

- [-3.9, -2.0, -0.1, 1.5, 3.1, 4.9, 6.9, 8.9]
Achromatic and chromatic vision, rods and cones.

**Rod vision**
- Achromatic
- High sensitivity
- Poor detail and no colour

**Cone vision**
- Achromatic and chromatic
- Lower sensitivity
- Detail and good colour

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**Facts and figures**

There are about 120 million rods. They are absent in the central 0.3 mm diameter area of the fovea, known as the *fovea centralis*.

There are only about 6 to 7 million cones. They are much more concentrated in the fovea.
Achromatic and chromatic vision, rods and cones.

Rod and cone distribution

0.3 mm of eccentricity is about 1 deg of visual angle

Rod density peaks at about 20 deg eccentricity

At night, you have to look away from things to see them in more detail
Achromatic and chromatic vision, rods and cones.

During the day, you have to look at things directly to see them in detail.

Cone distribution and photoreceptor mosaics.
Achromatic and chromatic vision, rods and cones.

The human visual system is a foveating system

Simulation of what we see when we fixate with cone vision...

Visual acuity gets much poorer with eccentricity
Achromatic and chromatic vision, rods and cones.

The foveal region is magnified in the cortical (brain) representation.

ROD AND CONE DIFFERENCES
Rod and cone differences can be demonstrated using several techniques, including visual psychophysics.

What is visual psychophysics?

Psychophysicists study human vision by measuring an observer’s performance on carefully chosen perceptual tasks.

The idea is to work out what is going on inside the visual system from the relationship between the stimulus at the input and the response of the observer.
Rod-cone threshold sensitivity differences

How might we measure them?

Rod and cone threshold versus intensity curves

Rod-cone break

Achromatic and chromatic vision, rods and cones.
Rods are about one thousand times more sensitive than cones. They can be triggered by individual photons.

Spectral sensitivity differences
Threshold versus target wavelength measurements

Incremental flash

10-deg eccentric fixation

Intensity

Space (x)

Achromatic and chromatic vision, rods and cones.
Threshold versus target wavelength measurements

Incremental flash

10-deg eccentric fixation

Intensity

Space (x)
Achromatic and chromatic vision, rods and cones.

Rod and cone spectral sensitivity curves

Plotted as “thresholds” versus wavelength curves

Fig. 2. Spectrum sensitivity curves for rod and cone vision on a real energy basis. The data for the separate curves are from the same sources as in Fig. 1. The position of the two curves on the ordinates corresponds to the fact that after complete dark adaptation, any region of the retina outside the cone new red light of 650 mµ in relative standard as thresholds, and as colored only above the threshold. The precise energy increment above the threshold for the appearance of color (cone function) varies for different parts of the retina; in the parafovea it lies between 0.1 and 1.0 log unit.

Sensitivity = 1/threshold
or
\log (\text{sensitivity}) = -\log(\text{threshold})

Plotted as the more conventional spectral “sensitivity” curve
Achromatic and chromatic vision, rods and cones. 18

**Approximate dark-adapted photoreceptor sensitivities.**

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**Rods**

Approximate dark-adapted photoreceptor sensitivities.

A change in the relative brightness of colours as the light level changes because of the difference in spectral sensitivity between rod and cone vision (e.g., reds and oranges become darker as rods take over)

**The Purkinje Shift**

A change in the relative brightness of colours as the light level changes because of the difference in spectral sensitivity between rod and cone vision (e.g., reds and oranges become darker as rods take over)

Simulated: Dick Lyon & Lewis Collard at Wikimedia

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Rod-cone dark adaptation curves

From Hecht, Haig & Chase (1937)

Rods take much longer to recover after a bleach than cones.
Temporal differences

Suction electrode recording

4.15 MEASURING CONE PHOTOCURRENTS. The image shows a portion of macaque retina suspended in solution. A single photoreceptor from this retinal section has been drawn into a micropipette and is being stimulated by a beam of light passing transversely through the photoreceptor and micropipette. Courtesy of Denis Baylor.

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Greater temporal integration improves rod sensitivity (but reduces temporal acuity).

Highest flicker rates that can just be seen (c.f.f.)

Photopically (cone) equated scale

Fig. 16.6 Relation of CFF to log retinal illuminance for seven spectral regions. (Hoch and Shlaer, 1936. Reproduced by permission of The Rockefeller Institute Press from The Journal of General Physiology, 1936, 19, 955–979; Fig. 33.)
Achromatic and chromatic vision, rods and cones.

Spatial differences (visual acuity)

The acuity here is defined as the reciprocal value of the size of the gap (measured in arc minutes) that can be reliably identified.

Rod and cone visual acuities

König (1897)

1/1 = 1

1/1.6 = 0.63

1/2 = 0.5

Fig. 11.14 König's data for the relation between visual acuity and illumination, as replotted by Hacht (1936). The lower limb of the data is an equation for rods, whereas the upper curve is for cones. The task is one of recognizing the orientation of a hook form of test object.
Achromatic and chromatic vision, rods and cones.

Rod and cone visual acuities

Greater spatial integration improves rod sensitivity but reduces acuity

The loss must be postreceptoral because the rods are smaller than cones in the periphery.

Rod vision is achromatic

Why?
Vision at the photoreceptor stage is relatively simple because the output of each photoreceptor is:

**UNIVARIANT**

What does univariant mean?

**UNIVARIANCE**

Crucially, the effect of any absorbed photon is *independent of its wavelength.*

*Once absorbed* a photon produces the *same* change in photoreceptor output whatever its wavelength.

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Crucially, the effect of any absorbed photon is independent of its wavelength.

So, if you monitor the rod output, you can’t tell which “colour” of photon has been absorbed.

All the photoreceptor effectively does is to count photons.
What does vary with wavelength is the **probability** that a photon will be absorbed.

This is reflected in what is called a "spectral sensitivity function".

### Achromatic and Chromatic Vision, Rods and Cones

**Rod spectral sensitivity function** (also known as the scotopic luminosity curve, CIE $V'_\lambda$)
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

So, imagine you have four lights of the same intensity (indicated here by the height). The green will look brightest, then blue, then yellow and lastly the red will be the dimmest.

We can adjust the intensities to compensate for the sensitivity differences. When this has been done, the four lights will look completely identical.
Achromatic and chromatic vision, rods and cones.

Changes in light intensity are confounded with changes in colour (wavelength)

Rod

UNIVARIANCE

A change in photoreceptor output can be caused by a change in intensity or by a change in colour. There is no way of telling which.

Colour or intensity change??

Each photoreceptor is therefore ‘colour blind’, and is unable to distinguish between changes in colour and changes in intensity.
A consequence of univariance is that we are colour-blind when only one photoreceptor operates...

Examples: SCOTOPIC VISION, cone monochromacy

![Spectral sensitivities and the Purkinje shift](image)

Achromatic and chromatic vision, rods and cones.
With three cone photoreceptors, our colour vision is chromatic.

Achromatic and chromatic vision, rods and cones.
So, if each photoreceptor is colour-blind, how do we see colour?

Or to put it another way: How is colour encoded?

A change in colour from green to red causes a relative increase in the L-cone output but causes a decrease in the M-cone output.

A change in colour from red to green causes a relative increase in the M-cone output but causes a decrease in the L-cone output.

Thus, colour can be encoded by comparing the outputs of different cone types...
At the photoreceptors, colour is encoded by the relative cone outputs.

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Blue light

Red light

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Colour is encoded by the relative cone outputs

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Blue light
Green light
Red light

Colour is encoded by the relative cone outputs

Blue light
Red light
Green light
Purple light
Yellow light
White light
POSTRECEPTORAL COLOUR VISION

But what happens next (i.e., how is colour encoded after the photoreceptors)?

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Colour phenomenology

Can provide clues about how colours are processed after the photoreceptors...

Which pairs of colours coexist in a single, uniform patch of colour?  Which pairs never coexist?

WHY?

Reddish-yellows?
Achromatic and chromatic vision, rods and cones.

Reddish-blues?

Reddish-greens?
Achromatic and chromatic vision, rods and cones.

Bluish-yellow?

The colour opponent theory of Hering

Reds can get bluer or yellower but not greener
Achromatic and chromatic vision, rods and cones.

The colour opponent theory of Hering

Yellows can get greener or redder but not bluer

The colour opponent theory of Hering

Greens can get bluer or yellower but not redder
The colour opponent theory of Hering

Blues can get greener or redder but not yellower

The colour opponent theory of Hering

is opposed to R-G

is opposed to Y-B

How might this be related to visual processing after the cones?
Some ganglion cells are colour opponent

Imagine that this is the region of space that the cell “sees” in the external world

A red light falling on the central area excites the cell (makes it fire faster)
Some ganglion cells are colour opponent

A green light falling on the surround area inhibits the cell (makes it fire slower)

Some ganglion cells are colour opponent

RED On-centre
GREEN Off-surround

Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Some ganglion cells are colour opponent

GREEN On-centre
RED Off-surround

Red-green colour opponency

Four variants
Achromatic and chromatic vision, rods and cones.

Source: David Heeger
Achromatic and chromatic vision, rods and cones.

**Summary**

LGN cell responses

Trichromatic stage

Colour opponent stage

Chromatic pathways
Andrew Stockman

So that’s colour (chromatic) vision, but what about “luminance” (achromatic) vision?

Colour...
Achromatic and chromatic vision, rods and cones. By itself chromatic information provides relatively limited information…
Achromatic and chromatic cone vision (colour and luminance)
In addition to neural pathways that signal colour there are also pathways that signal intensity or luminance:

**Chromatic pathways**

Luminance is encoded by summing the L- and M-cone signals:

- **Blue light**
  - L+M
  - Green light
  - L+M
  - **Yellow light**
  - L+M

- **Red light**
  - L+M

- **Purple light**
  - L+M

- **White light**
  - L+M

Achromatic and chromatic vision, rods and cones.
Colour is in many ways secondary to luminance
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.
Achromatic and chromatic vision, rods and cones.

Watercolour effect

A wave-line colour illusion

Seiyu Solmiya
Achromatic and chromatic vision, rods and cones.
Interesting artistic effects occur when vision depends only on colour (and not on luminance)

Achromatic and chromatic vision, rods and cones.
What are the postreceptoral neural substrates of the chromatic and luminance pathways?

Red-green chromatic pathways have been linked to the parvocellular retinal stream for L-M.
Achromatic and chromatic vision, rods and cones.

These cells are chromatically opponent simply by virtue of the fact that they have single cone inputs to the centre of their receptive fields!
Achromatic and chromatic vision, rods and cones.

Blue-yellow chromatic pathways have been linked to the koniocellular stream...

Koniocellular

From Rodieck (1998)
Achromatic and chromatic vision, rods and cones. 62

Koniocellular

From Rodieck (1998)

Luminance pathways, which produce achromatic percepts, have been linked to the magnocellular stream.
The magnocellular pathway, with diffuse bipolar cells and many-to-one cone to bipolar connections, does not.

The parvocellular pathway, with its one-to-one cone to bipolar connections, provides enough samples.

To be able to resolve this E, the image must be sampled at enough points.
The parvocellular pathway must be double-duty supporting finely detailed luminance vision as well as much more coarse colour vision.

Achromatic and chromatic vision, rods and cones.
Chromatic pathways, which produce chromatic percepts, have been linked to the parvocellular retinal stream.

Luminance pathways, which produce achromatic percepts, have been linked to the magnocellular stream, but also depend on the parvocellular stream.
Achromatic and chromatic vision, rods and cones.

Parvocellular pathway:
- High spatial frequencies (spatial detail)
- Low temporal frequencies
- Chromatic
- Lower contrast sensitivity

Magnocellular pathway:
- High temporal frequencies (motion/flicker)
- Low spatial frequencies
- Achromatic
- Higher contrast sensitivity

From Rodieck (1998)