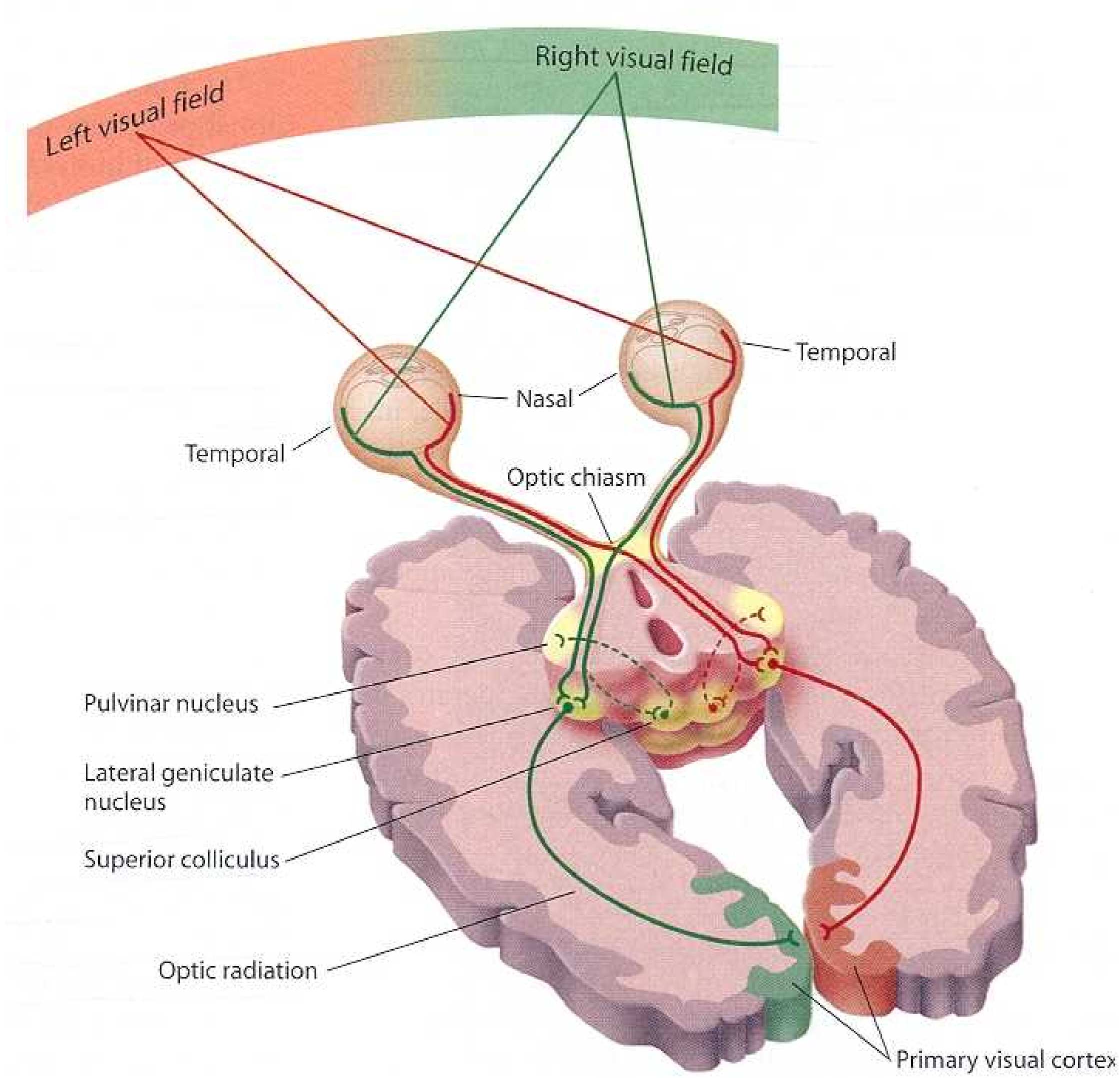


Stages

1. Receptors (input)
2. Retinal Ganglion cells (output to brain)
3. Lateral geniculate nucleus (LGN)
4. Primary Visual Cortex (V1)
5. Seconday Visual cortex. V2

Stage 1: Organization of the Retina: Light Receptor Cells or Photoreceptors

Think of each photoreceptor as a FILTER.

- Electromagnetic energy comes in a wide range of both wavelengths and, over the course of the day, of intensities as well.
- Given the basic laws of chemistry, however, no single receptor cannot respond to all possible wavelengths or light intensities.
- Moreover, there is a limit, due to the size of the photoreceptors, on how small a space (how many degrees of visual angle) each photoreceptor can monitor.

So, for every ‘monitor’ standing ready to receive light, the receptor will act as a filter — that is, it will be sensitive to only certain properties of the light and a certain portion of visual space.

LIGHT SENSITIVITY: What does it take to get a response —very little light or LOTS of light? (high or low sensitivity)

RANGE OF LIGHT WAVELENGTH: What range of light will you respond to?

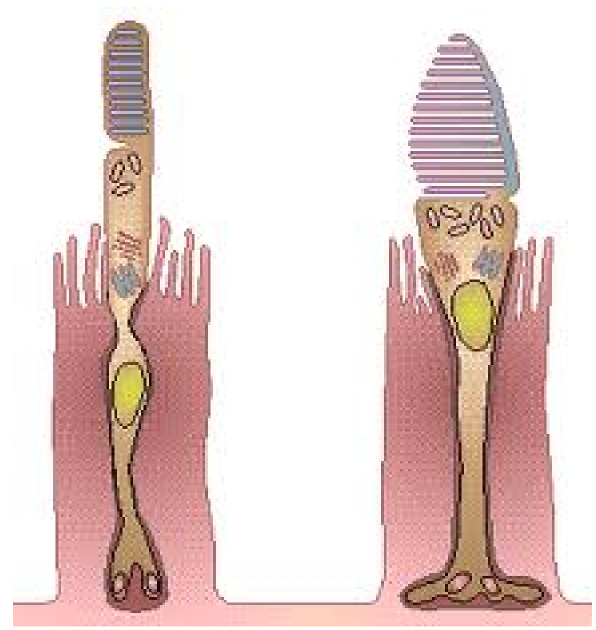
SPACE: Are you monitoring a big space or small space? (high or low spatial resolution)

There are two basic kinds of photoreceptors in the human eye, rods and cones. Here, the central difference between a rod and a cone is NOT that cones can ‘see’ colour.

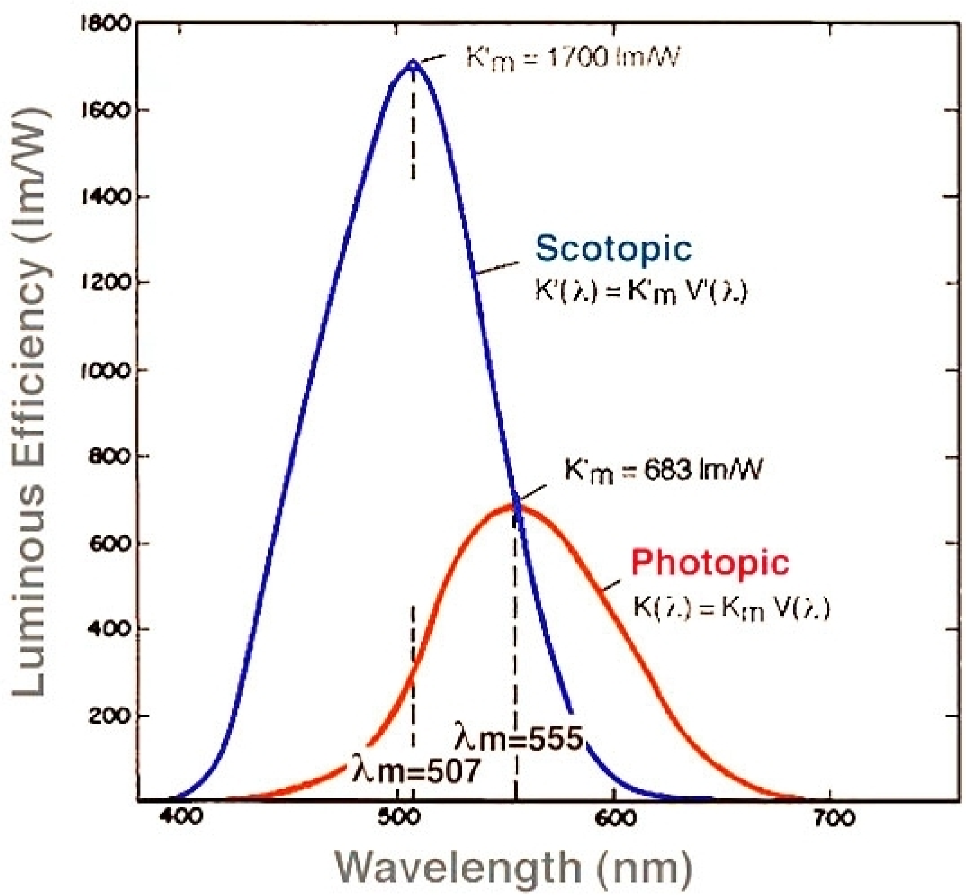
Rather they differ in their *light sensitivity*: rods are need very little light in order to react; cones are far less sensitive—they require more light in order to respond.

Daylight range of illumination = cone response

Evening/dawn/night illumination = rod response



Light sensitivity



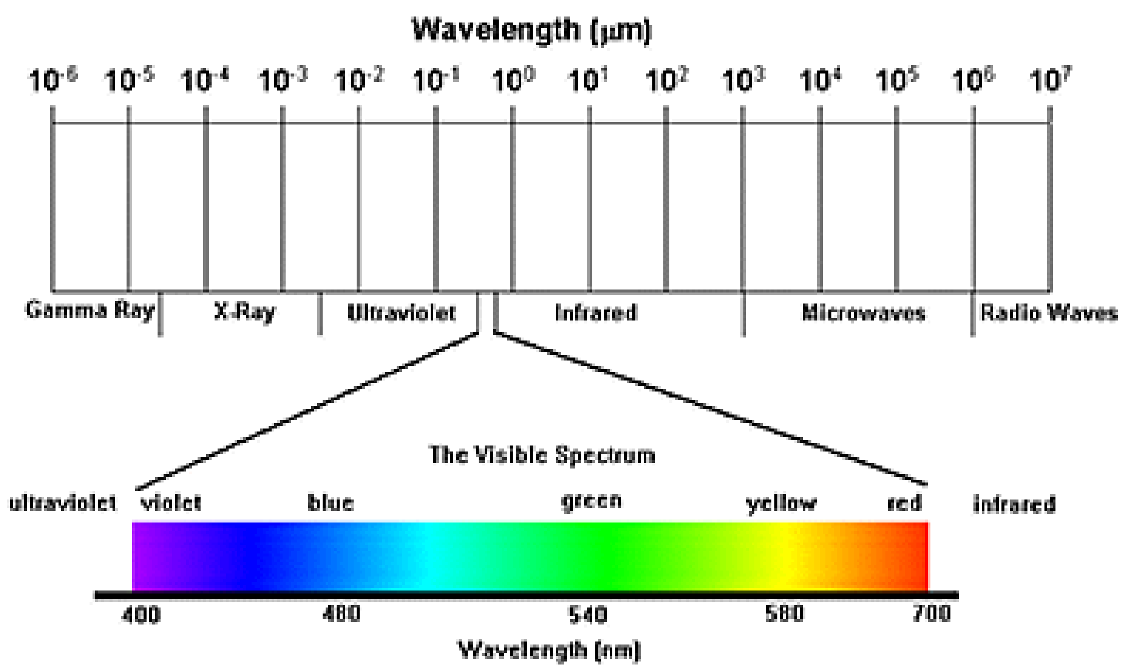
The luminance efficiency of rod versus cones.

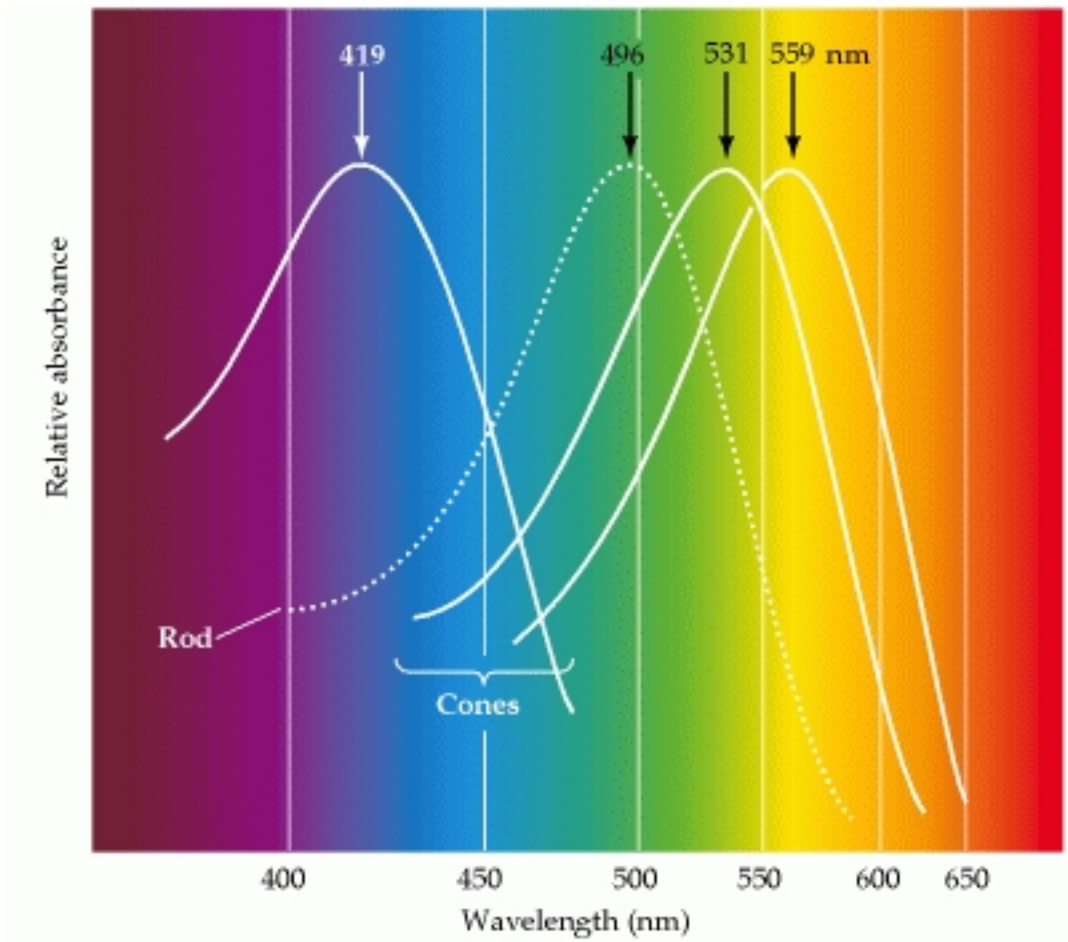
Light sensitivity (how much light?)

Spectral range

Each photoreceptor —whether a rod or a cone—responds over a limited portion of the spectrum, to light of a certain *range* of wavelengths.

If we add together the ranges of ALL our photoreceptors—rods and cones—we still see only a very limited range of wavelengths. This I the range of ‘visible’ light for humans (but not for other creatures).





This shows the spectral range for each photoreceptor—how likely the receptor is to absorb light at each wavelength of light. NOTE: this is the response for a single intensity of light at each wavelength.

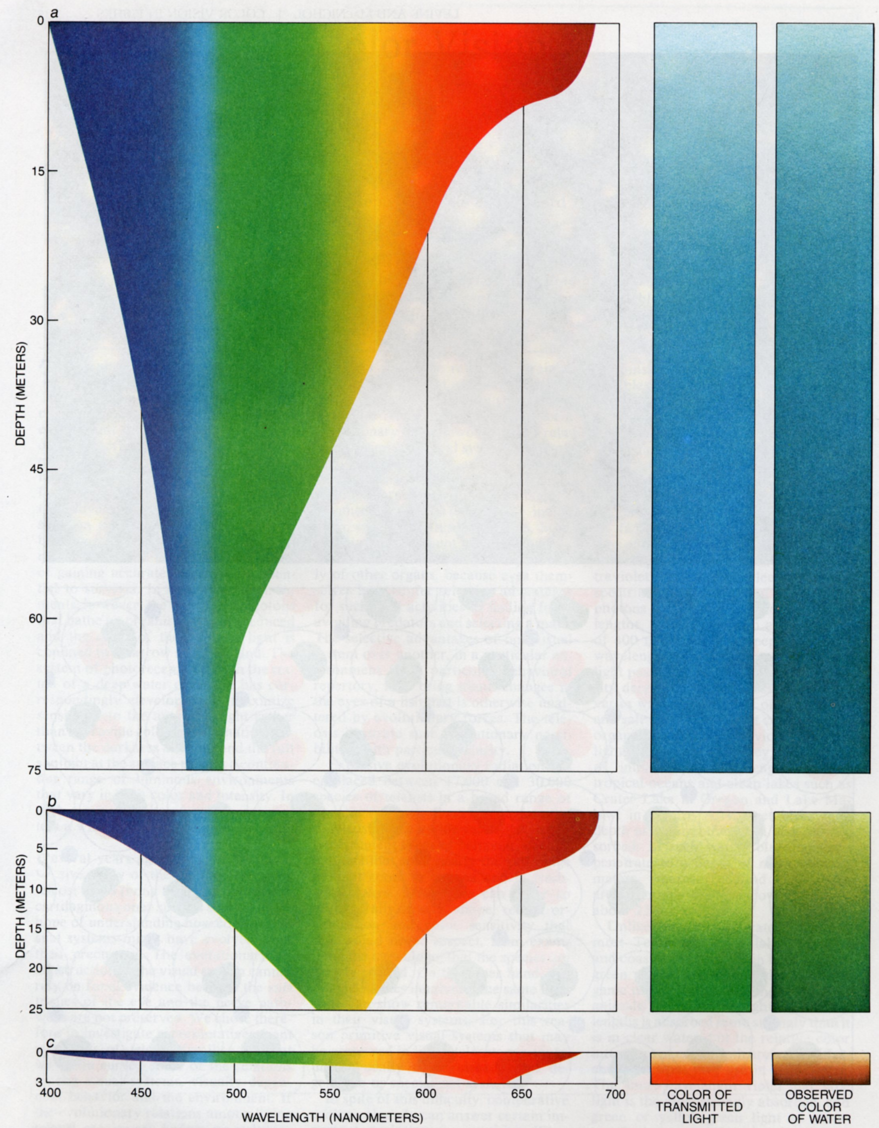
Spectral range

Spectral range

Fresh & Salt Water Condition

Lakes & Streams Water Condition

Marshes & “Black Water” Condition



TRANSMISSION OF LIGHT by water is dependent on the color or wavelength of the light. In clear oceans and lakes (*a*) the light becomes increasingly monochromatic and blue as its path length increases. In fresh water that carries green organic matter (*b*) light at all wavelengths is absorbed more quickly than it is in clear water, but the light becomes greener with path length. In rivers, swamps and marshes that carry large amounts of the products of plant and animal decay (*c*) absorption is rapid and the spectral distribution of the light shifts to the red. Such waters are called black because the human eye is relatively insensitive to light at long wavelengths; a less anthropomorphic name would be infrared water. The depths given for the maximum penetration of light are typical, but they vary widely.

The spectral range of light, in a natural environment, varies hugely from niche to niche. The ‘colour’ of the ambient light—in under a forest canopy, on the open savannah, under two meters of water in the Mediterranean, or 3 meters of water in a Canadian lake—is highly variable.

General rule: In order for anything to be visible—for you to see it—you must have photoreceptors that respond to whatever wavelengths of light are reflected from objects. And in order for the light to be reflected, it must be **present** — contained in the light source (I.e. sunlight).

To take advantage of the available light, you need sensors that are most sensitive to whatever wavelengths of light are most abundant.

Some consequences of this fact about photopigments…

1. Photoreceptors do not respond to a single light intensity.
2. Photoreceptors do not respond to a single light wavelength.
3. Rather, all photoreceptors have a continuous response that conflates the intensity and the wavelength of the stimulus. (From the ‘inside’, given a single type of receptor response— ‘red cones responding like crazy’— you cannot tell the wavelength of light of the stimulus.)
4. In the evolution of a visual system, the photopigments of a species come to reflect the light conditions of the past environment, **both the intensity and wavelength ranges of the available light**.

This is the evolutionary ‘choice’ of what will be, for that species ‘visible light’.

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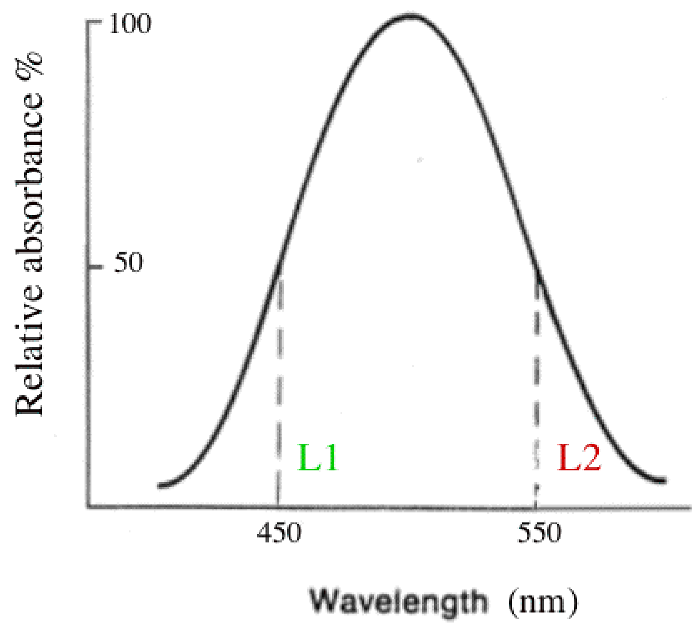
A single type of photoreceptor cannot signal colour



The problem here is not merely that lights of two distinct wavelengths (at the same intensity) will both produce the same response.

The problem is that, given that light across the visible spectrum can have a wide range of intensities, any given receptor response could be caused by a light of ANY wavelength (within with the receptor's range) with a suitable adjustment of light intensity.

E.g. A light of 450 nm. with a high intensity will have the same result as a light of 500 nm at a lower intensity.

The Principle of Univariance.

Once a photo is absorbed, it produces an electrical effect (in photoreceptors, hyper-polarization). At this point, that is all we can say: that an electron was absorbed. The response of the receptor does not distinguish between the wavelength and the intensity of the light.

Bottom line: A visual system with a single receptor is colour/wavelength blind.

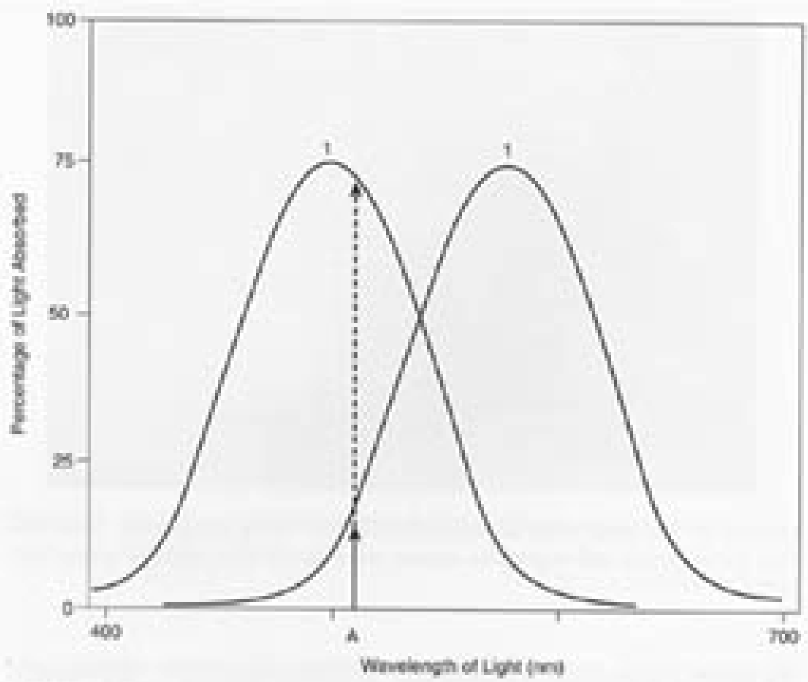


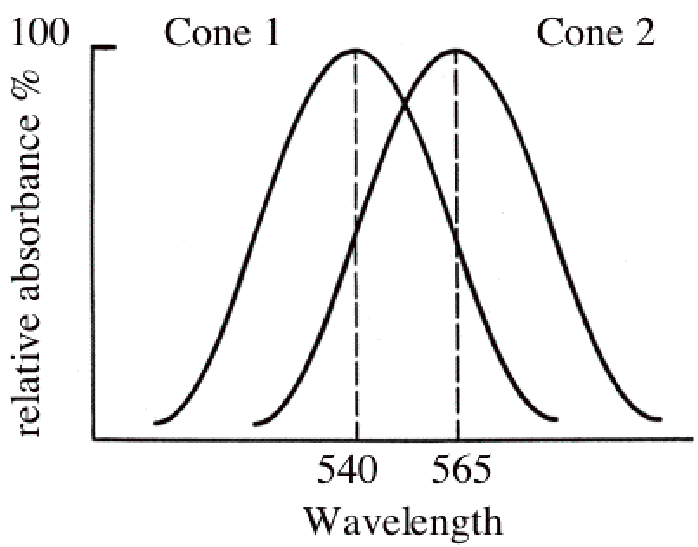
FIGURE 9 In a two-pigment system, the responses of receptors 1 and 2 can be compared to determine the unique wavelength of a stimulus (from Sekuler and Blake, 1990).

However, if another receptor is added, the problem is *partially* resolved.

Any increase or decrease in intensity will effect the receptors to the same extent.

Thus if one compares the results of the two cones, the *ratio of response*, for the two cones, is constant relative to wavelength.

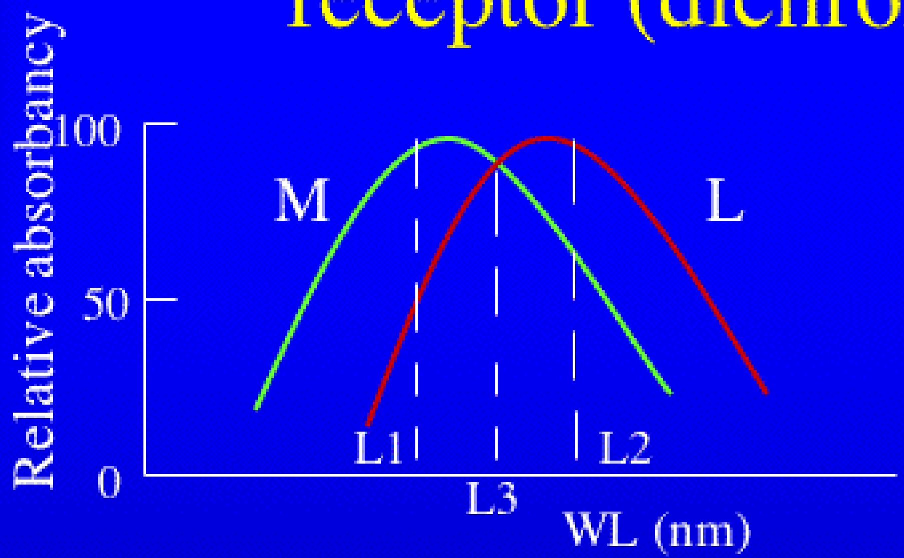
Response curve for a two receptor system



By comparing the electrical potentials of the receptors, a two receptor system can distinguish between two lights, each with a single wavelength, here 540 and 565.

This is only a partial solution to the problem of wavelength discrimination because, in a two cone system, there is always another combination of two light sources that will have exactly the same effect.— i.e produce the same quantum catch.

The basis of colour mixing in a two receptor (dichromatic) system



Lights

Receptors

	L1	L2	L1+L2	L3
M	90	55	145	95
L	50	95	145	95
L:M			1:1	1:1

The mixture of red and green light looks the same as the yellow light because the red-green mixture and the yellow produce the same quantal absorptions in the L and M cones

A dichromatic system requires 2 mixing lights

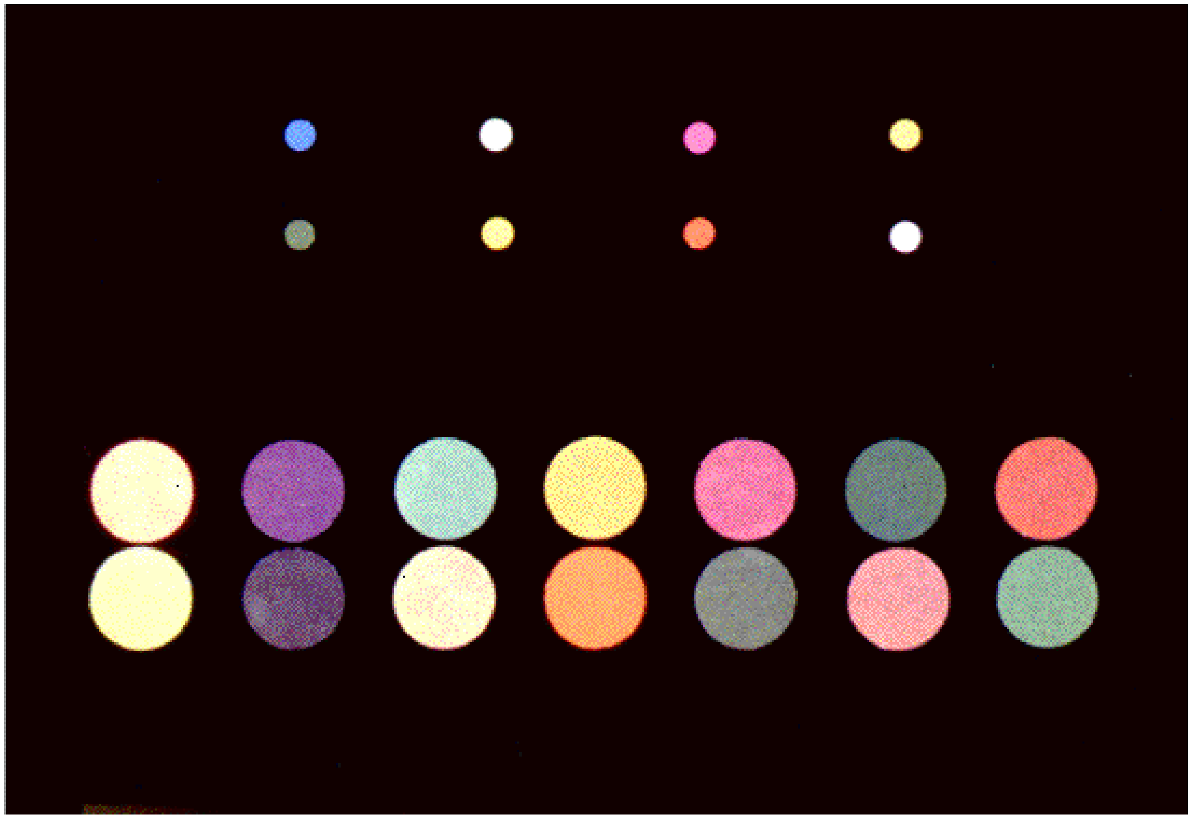
A trichromatic (three receptor) system requires 3 mixing lights (primaries)

Any two lights that produce the same quantum catch in both receptors will be indistinguishable to the system—hence they will appear exactly the same to the dichromat (person with only two receptors).

This principle applies to all colour systems. Thus, for a trichromat, any two stimuli that produce exactly the same ratio of response across the three cones will appear exactly the same—will be indistinguishable.

When two stimuli produce the same ratio of response in the cones, they are called *metamers*.

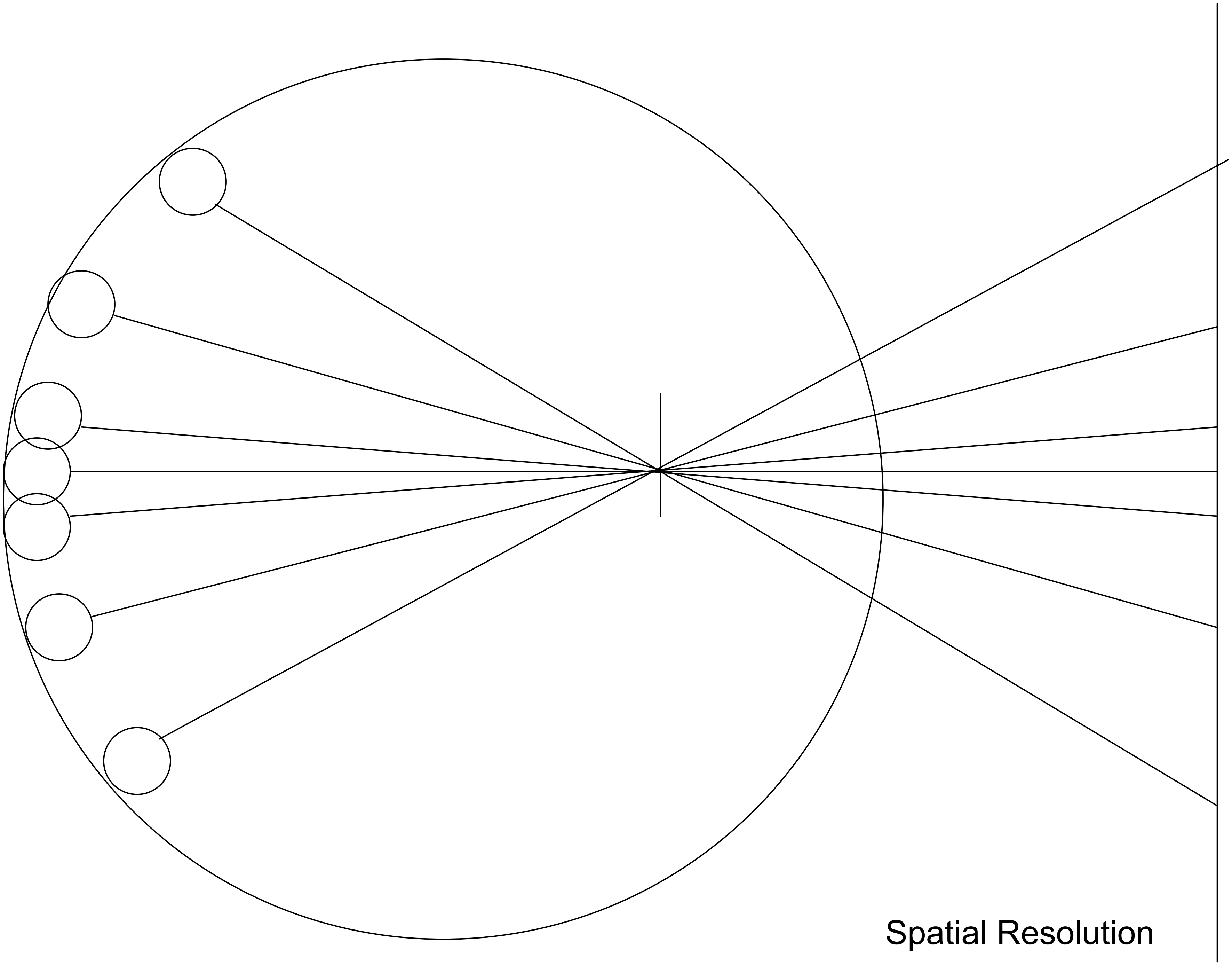
Metameric (matched) colour pairs for colour deficient observers



The closer together the receptors, the less area of visual space each one needs to monitor. (The more receptors, the smaller the space each one can ‘look at’.)

A general constraint on spatial resolution, then, is how tightly the receptors can be packed together —how many receptors per square mm. can be packed together?

Spatial Resolution


Spatial Resolution

How big a part of the visual field should each neuron ‘monitor’? How big is the receptor’s “receptive field”?

High resolution

Low resolution

Spatial Resolution

Rod & Cone summary

Rods

•high sensitivity to light

•low spatial resolution

•single spectral range; they are most sensitive to light in the moonlight range.

Cones

•low sensitivity to light

•high spatial resolution

•three different spectral ranges for wavelength. Together they produce a system that is most sensitive to sunlight (at the earth's surface).

How should the rods and cones be arranged in the retina?

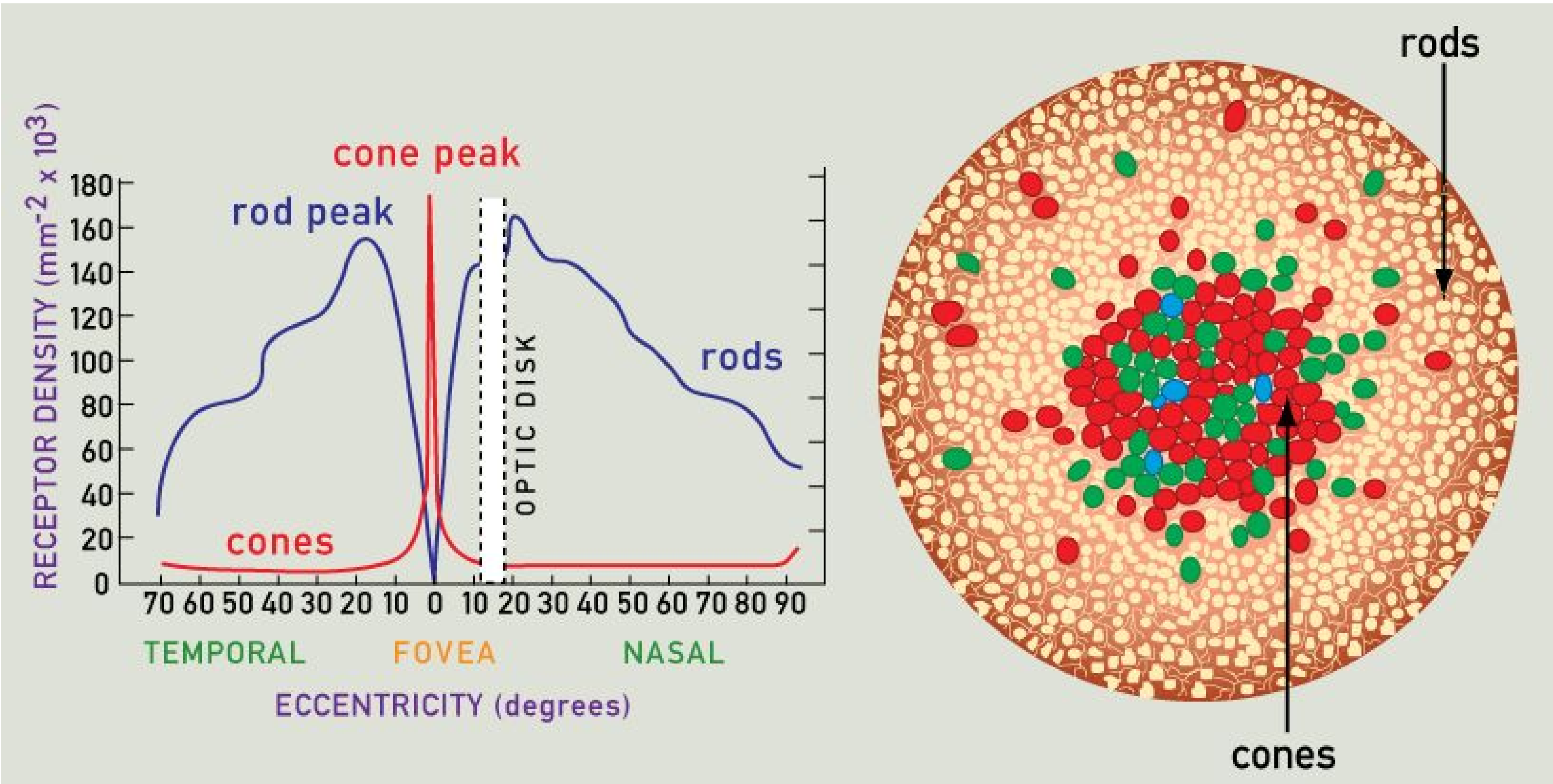
The arrangement of the human retina reflects a *division of labour* between the rods and the cones—”who does what” for human vision.

The Fovea (mostly cones):

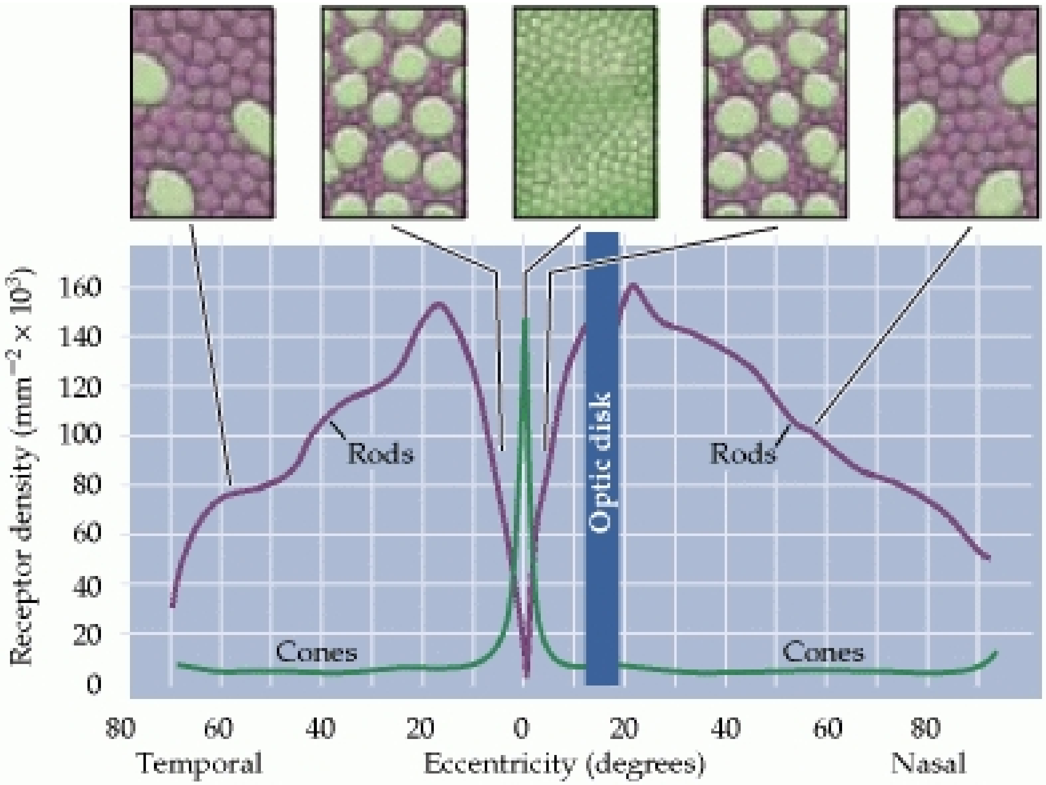
- high spatial resolution (packed together)
- low sensitivity (requires daylight)
- broad range over the spectrum using three different cones (whose responses overlap)

The Periphery (mostly rods):

- high sensitivity (sensitive at night)
- low spatial resolution
- narrower range of wavelengths because there is only one kind of photopigment (most sensitive to moonlight)



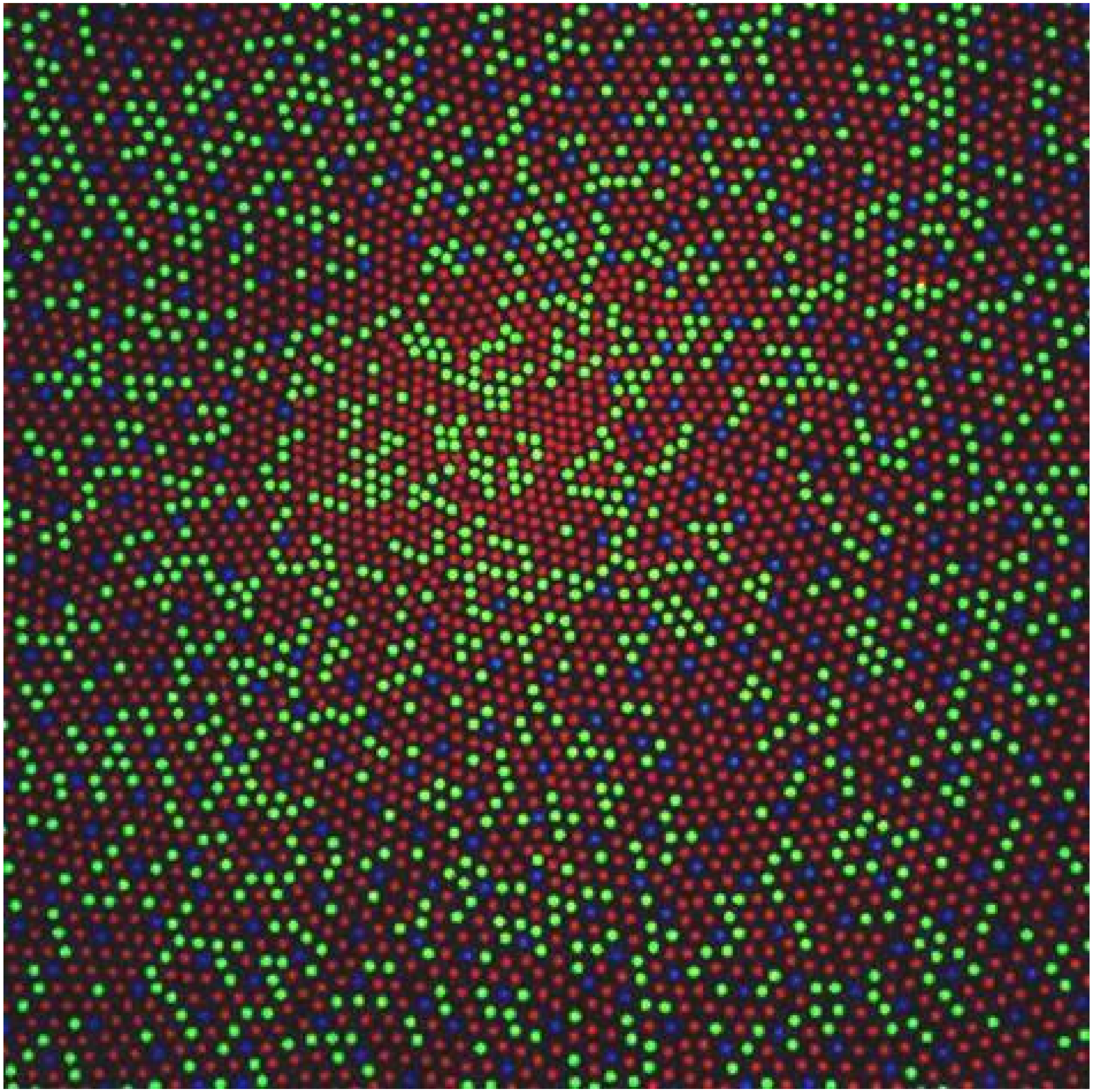
Rod versus Cone Organization in the retina



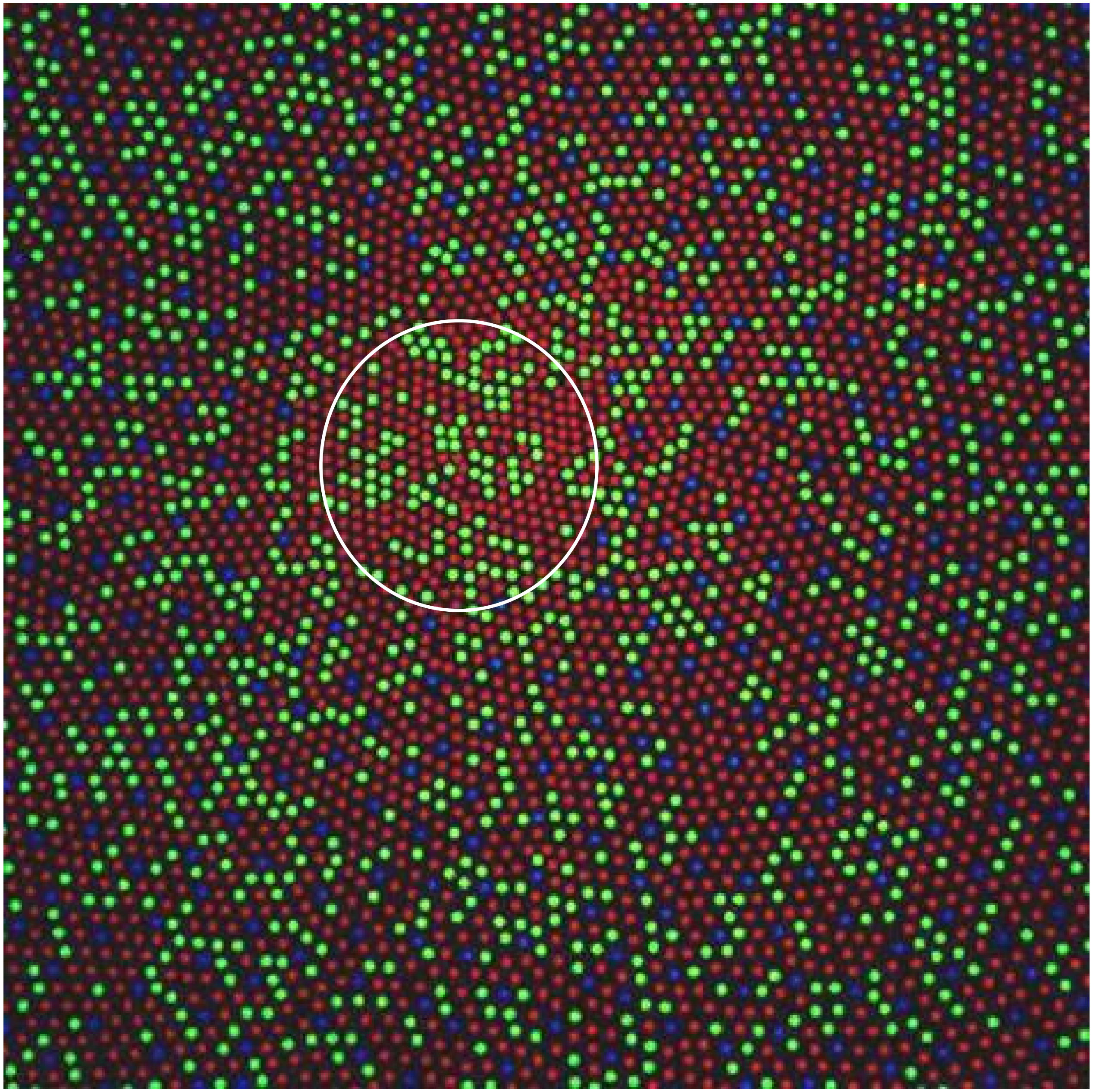
Receptor density (mm^{-2} × 10^3)
160
140
120
100
80
60
40
20
0
Rods
Rods
Cones
Cones
Optic disk
80
60
40
20
0
20
40
60
80
Temporal
Eccentricity (degrees)
Nasal

NOTE: Every person with normal human vision has a retina that is organized in this way. However, even among ‘normal’ subjects, there are large differences.

One of the larger differences between individuals concerns the relative number of red and green cones.



Organization of cones in the fovea. Note the absence of blue cones in the central 2 degrees of the human fovea.



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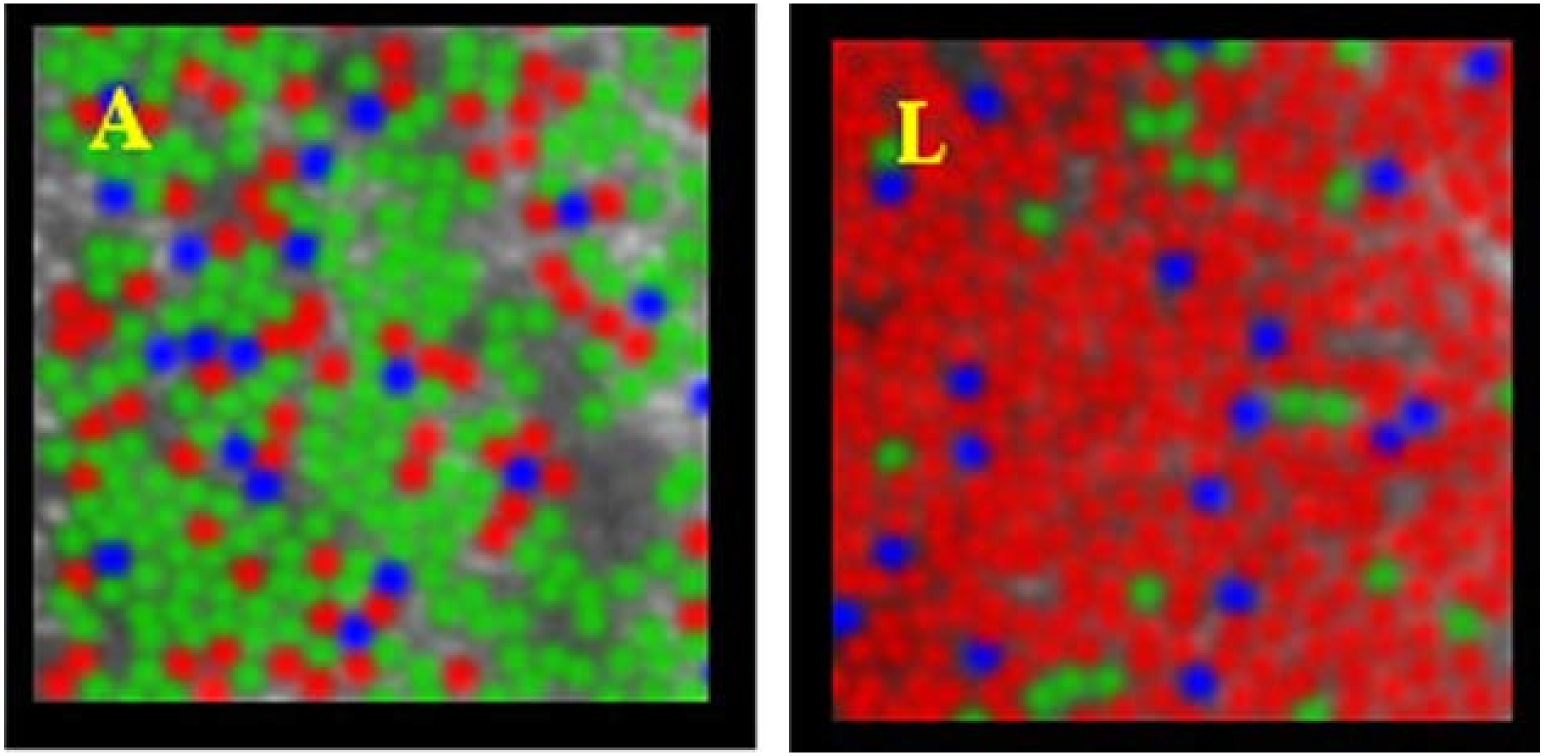
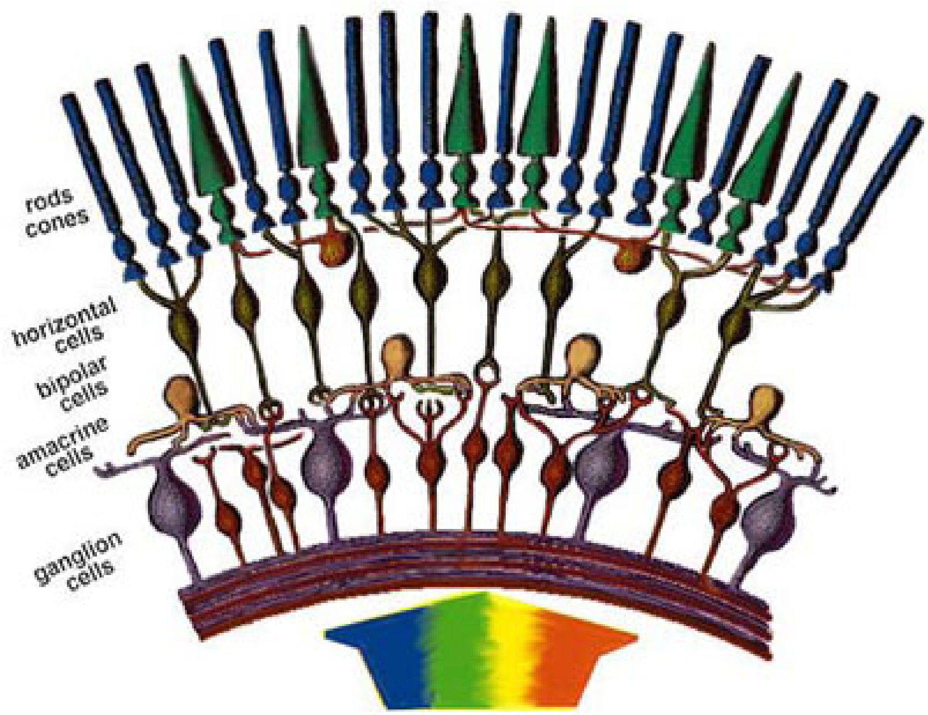


Individual differences: The ratio of red to green cones ranges from 1;1 to 6;1.

Stage 2: The Ganglion Cell. What is the output of a retinal ganglion cell? What information goes beyond the retina?



You can think of ganglion cells as further filtering the image — passing forward, to the LGN, a limited amount of information relative to what has been received.

There are between 18-26 different kinds of ganglion cells. As with the photoreceptors, they form a mosaic over the retina, each type providing a different “take” on the information they receive. (We will talk about 3 kinds in total.)

Most importantly, ganglion cells respond to a **spatially organized pattern of light *contrast***.