More Than Mere Colouring

Spectral Information

in

Human Vision

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Talk Outline

I. The “Good For” Question

II. Recasting the question: The basic nature of vision

III. Beyond phototaxis. Spectral information for object vision

IV. Practical Implications

What is human colour vision “good for”?

Colour-for-Colouring: The Seminal Statement

Livingstone MS, Hubel DH. (1987) *Journal of Neuroscience*. Nov;7(11).

Psychophysical evidence for separate channels for the perception of form, color, movement, and depth.

Segregation of form, color, and stereopsis in primate area 18

Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey.

Livingstone & Hubel (1988) “Segregation of Form, Color, Movement and Depth: Anatomy, Physiology, and Perception.” *Science*, vol 240, No. 4853, pp. 740-749.

Colour-for-Colouring: The Seminal Statement

- Their primary question was “what kinds of visual information is used for which visual tasks — and in which pathway is that information carried (parvocellular or magnocelluar)?

- Conducted a set of psychophysical experiments to determine the informational parameters of a multitude of visual processes — e.g. depth from stereopsis, depth from occlusion, shape from shading….

- One of the informational parameters tested was luminance versus colour information, experiments which used *equiluminant* images as stimuli.

Colour-for-Colouring

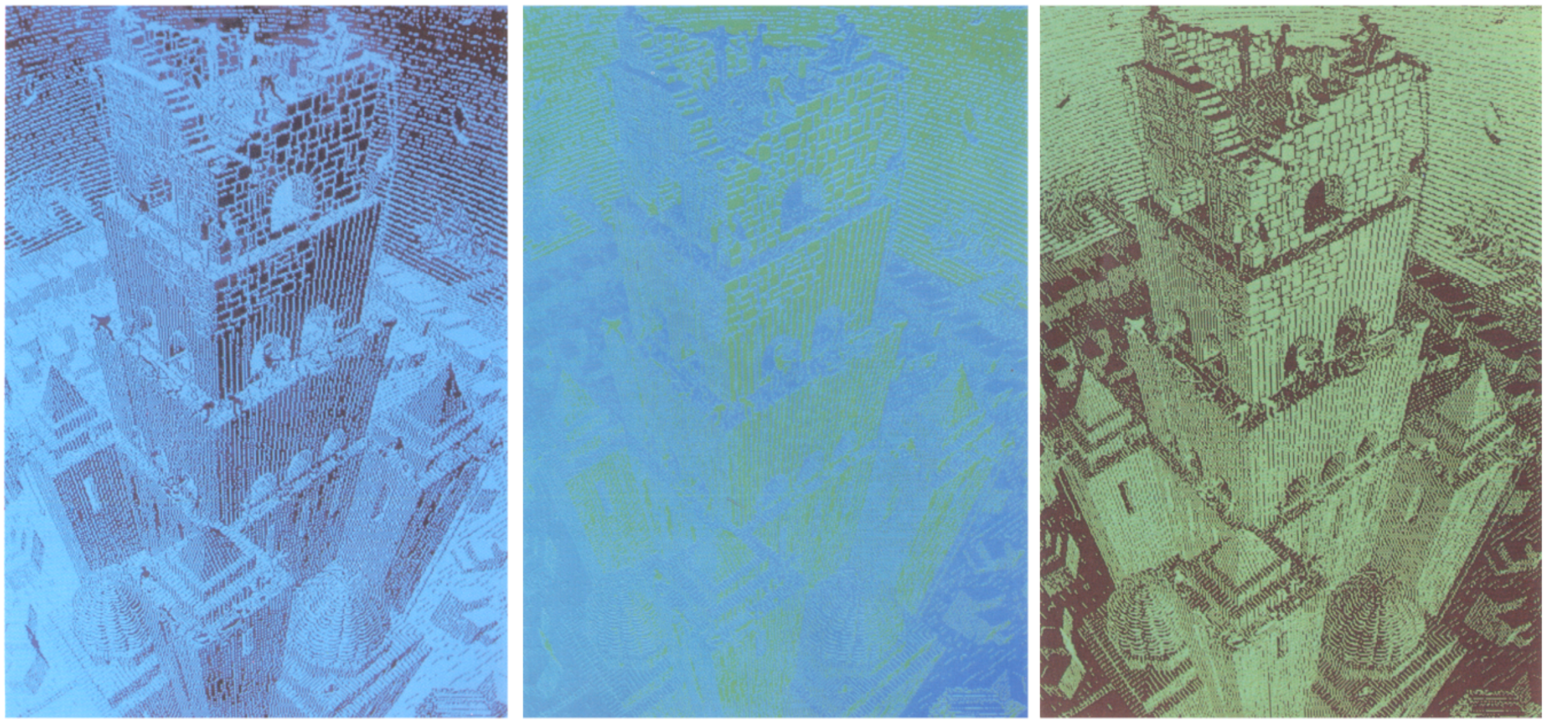
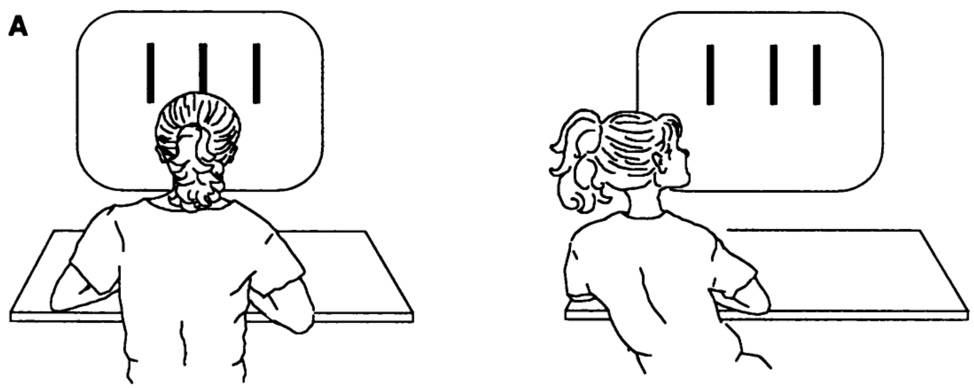
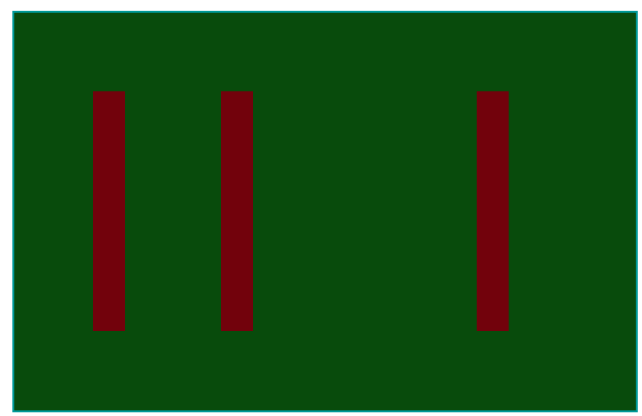


Figure 39. Tower of Babel, by M. C. Escher. Demonstration of loss of depth from perspective, figure/ground discrimination, and linking with equiluminant blue and green, even though either color alone gives a much better impression of organization and three dimensionality. To convince yourself that the same information is present in the blue/green version as in the other two, try looking at it through a yellow or orange piece of plastic.

Colour-for-Colouring





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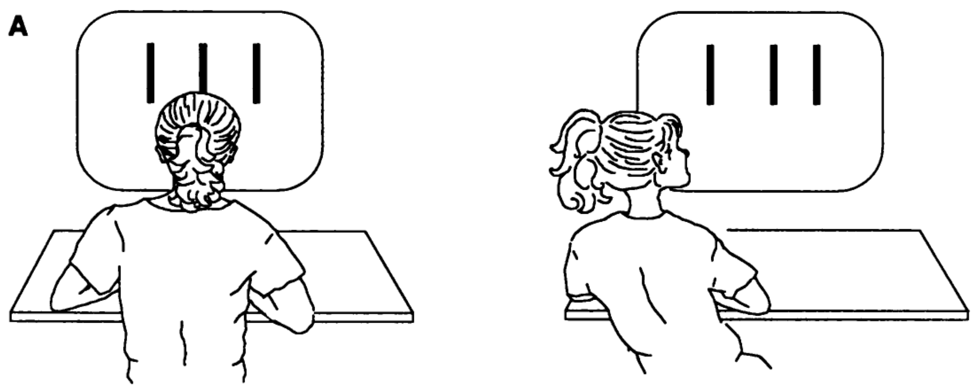

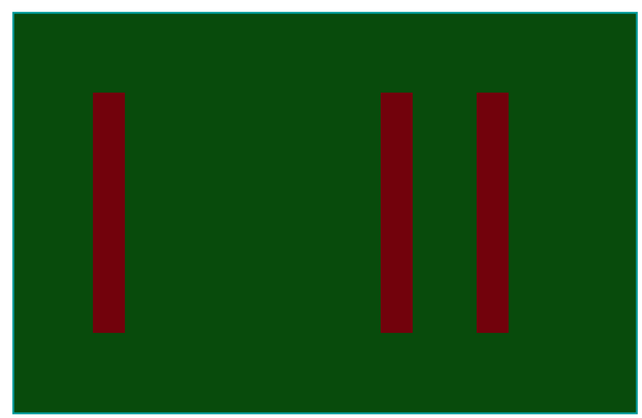

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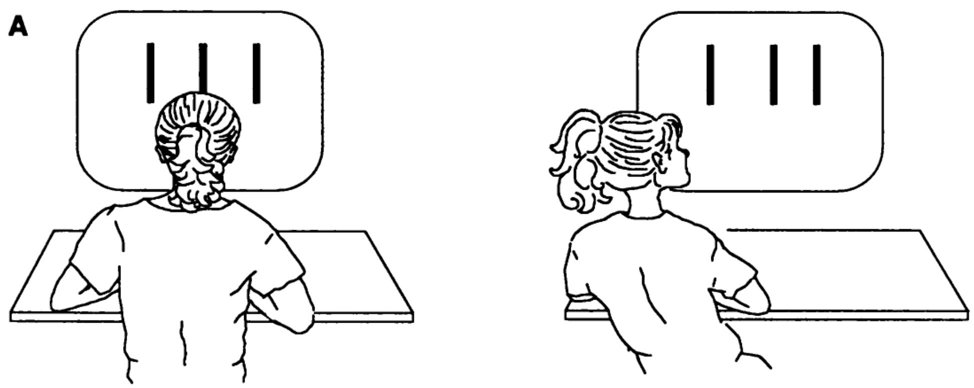

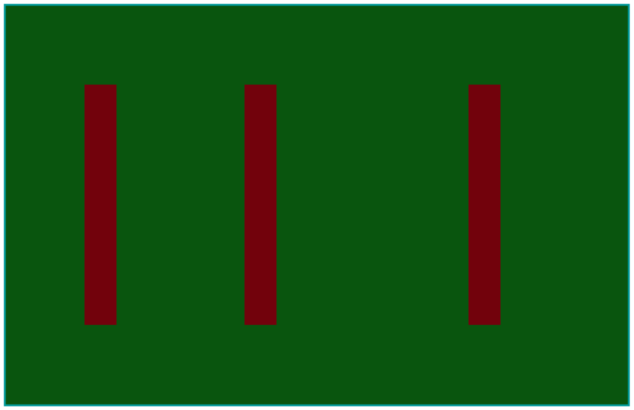

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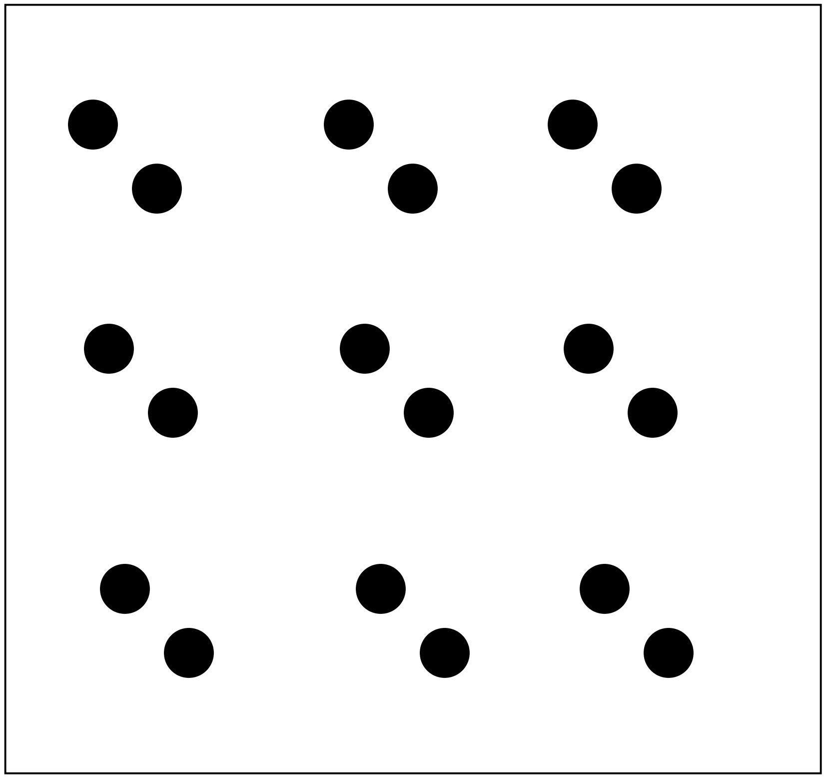

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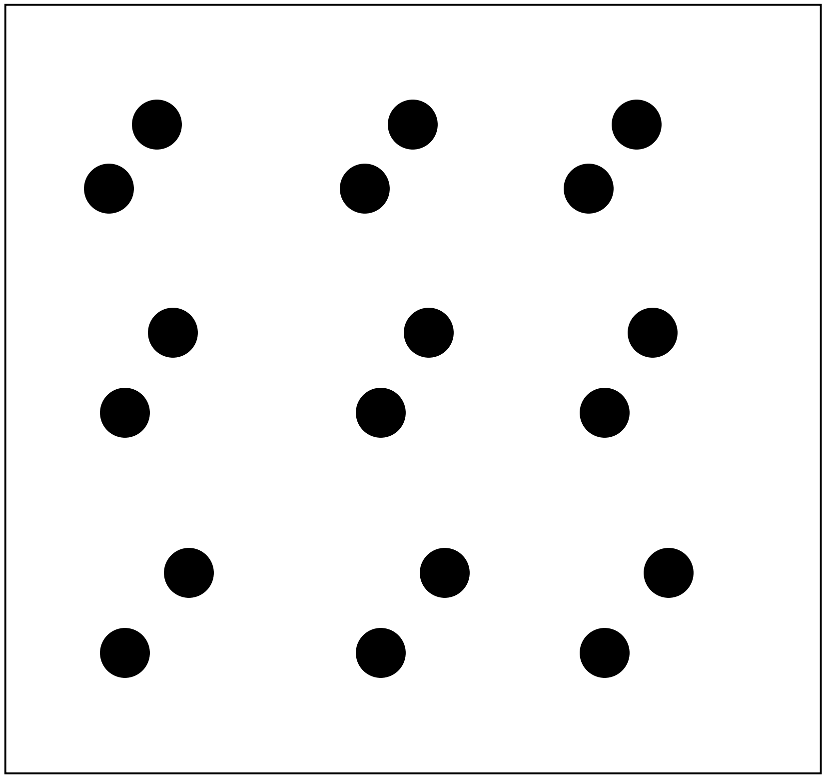

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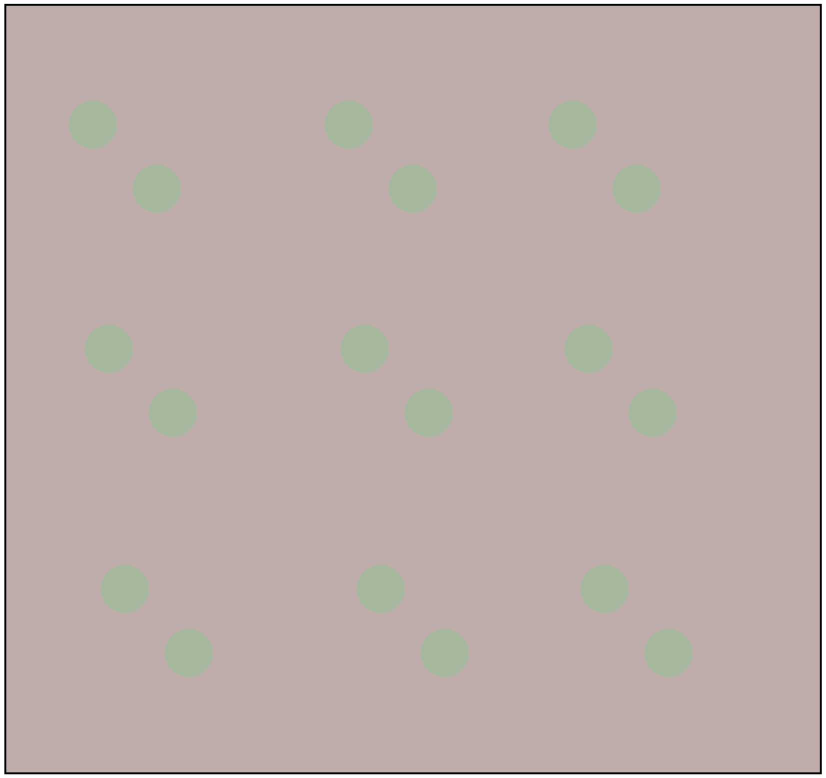

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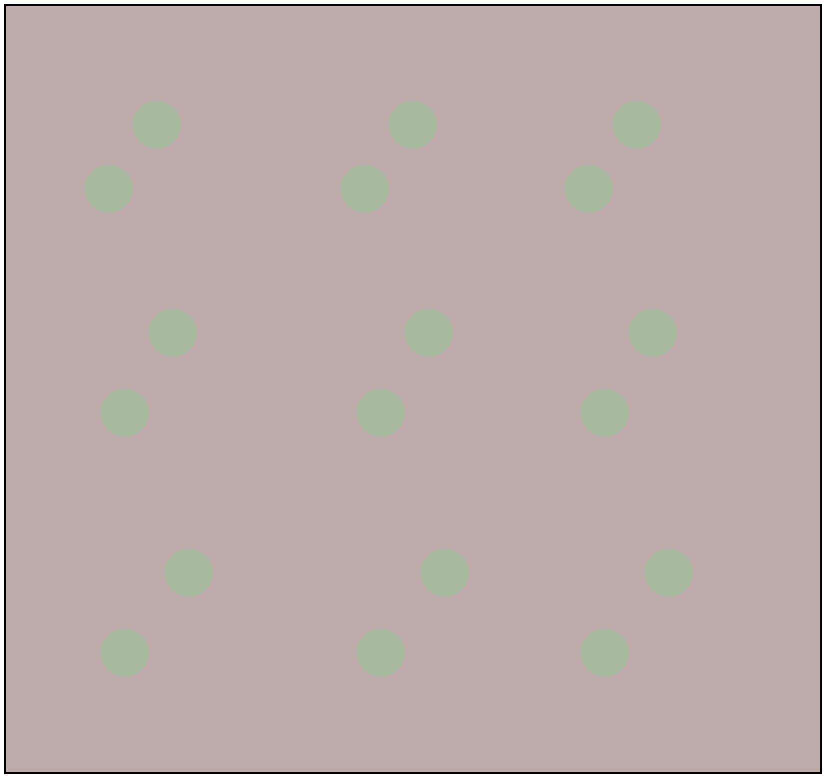
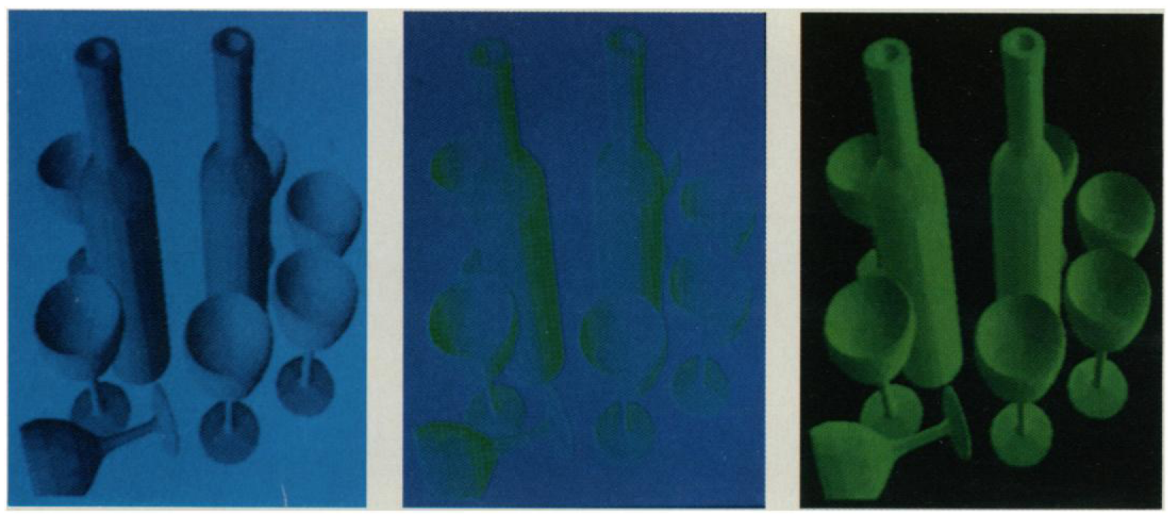


Colour-for-Colouring

Fig. 7. Computer-generated images in which shape is generated by shading. In the middle image the two colors are equiluminant, and the three-dimensional shape is harder to discern than in the other two images, which have luminance-contrast.



Colour-for-Colouring

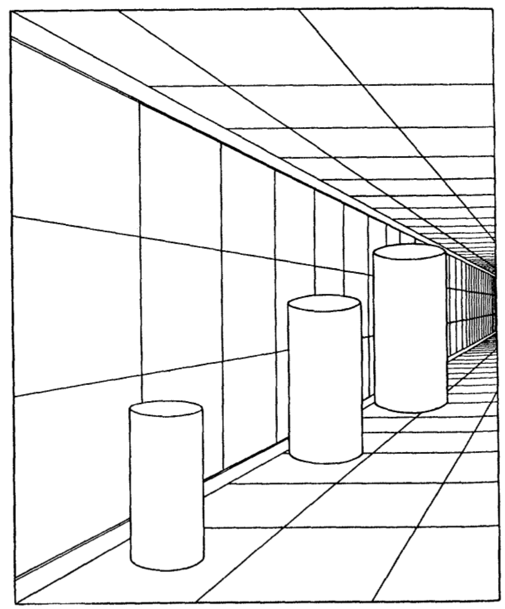


Fig. 8. Gibson's corridor illusion. [From (*47*) with permission, copyright 1950, Houghton Mifflin] At equiluminance the image no longer appears to recede into the distance, and the cylinders all appear to be the same size, as indeed they actually are.

Luminance Info.

Movement detection

Apparent motion

Depth Cues….

- Stereopsis
- Parallax
- Shading
- Contour Lines
- Occlusion
- Perspective
- Interocular Rivalry
- Depth from motion

Linking Cues

- Figure/ground discrim.
- Colinearity
- Movement

Chromatic Info.

Shape discrimination

Orientation

Lum. & Chrom.

Surface colour

Flicker fusion

What is colour vision "good for"?

Evolutionary answers to the question of what colouring is "good for" have been in terms of the advantages of *colour* to foraging…

What is human colour vision "good for"?

•Camouflaged fruit among leaves

(Osorio D, Vorobyev M. 1996)

•Ripest or most sugar-rich food.

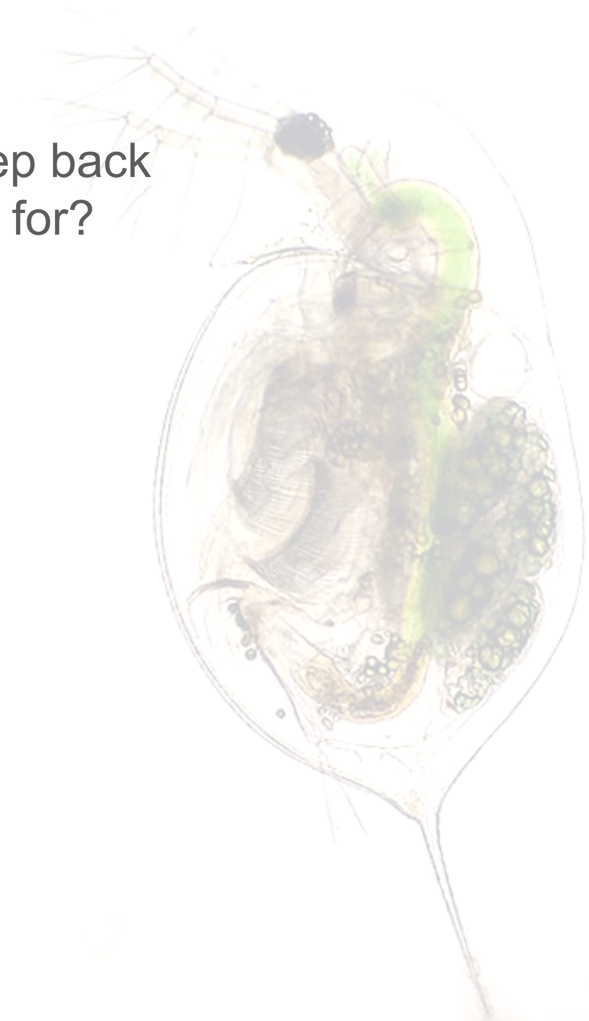
(Riba-Hernandez P, Stoner KE, Lucas PW. 2005; Sumner P, Mollon JD. 2000)

•Most tender shoots and leaves

(Lucas et al. 2003)

Recasting the Question

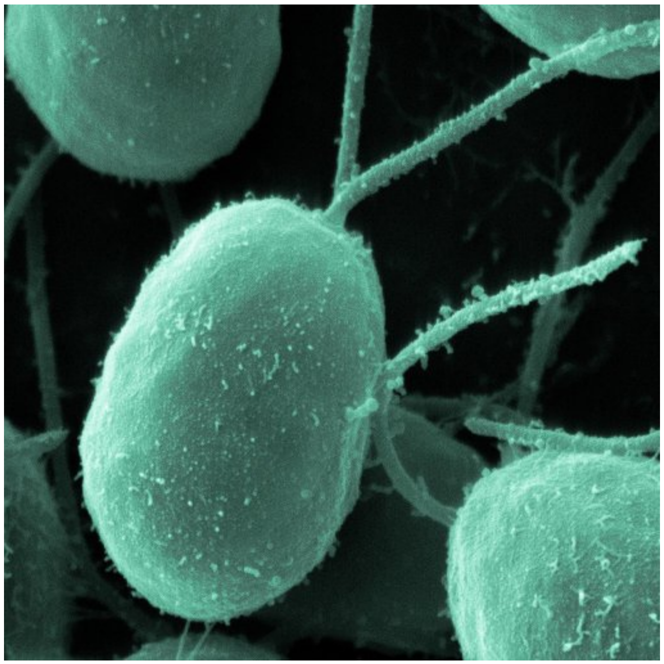
In order to recast the “good for” question, let us step back and ask a far more basic one: what is **vision** good for?



Recasting the Question

In order to recast the “good for” question, let us step back and ask a far more basic one: why **vision**?

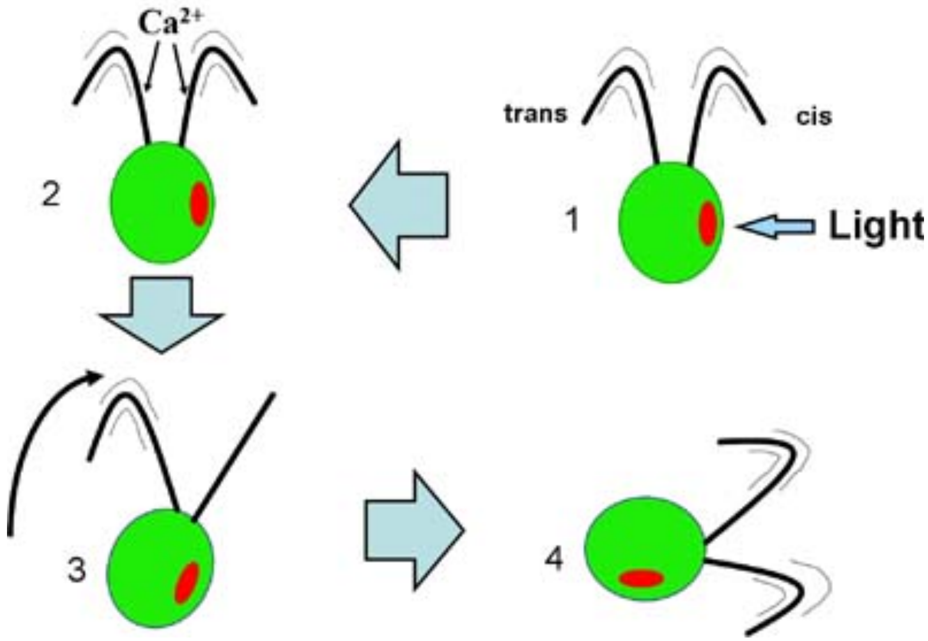
Photoreceptors that influence behaviour are found in virtually every living organism exposed to light, including single cell algae and multi-cellular plants of all kinds.



Green algae *chlamydomonas*

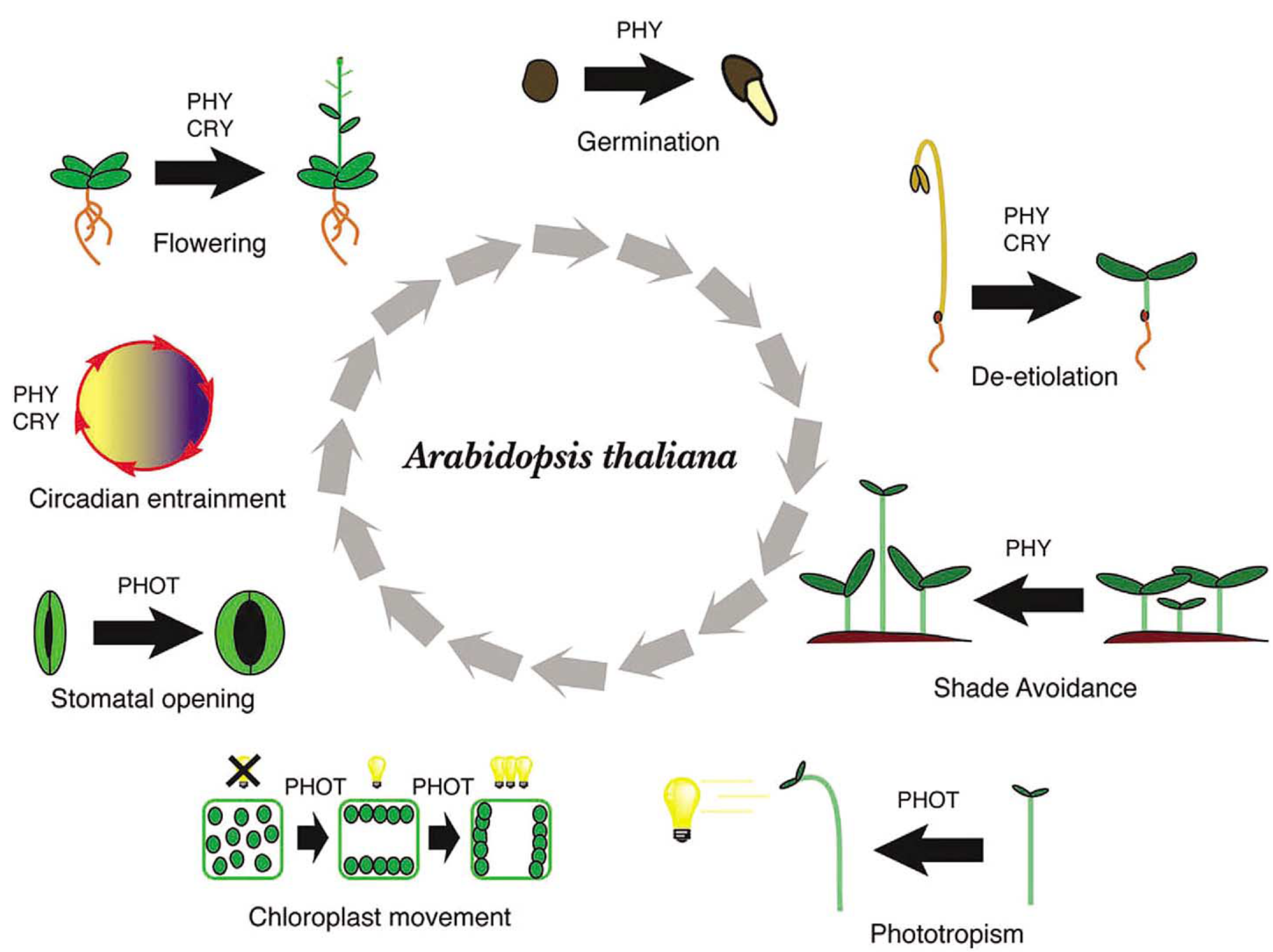
Bright orange eyespot that is connected directly to the flagella.

Eyespot information about intensity directly drives a beating response of the flagella in three dimensions so as to keep the eyespot centered on the light source.



Phototaxis: Chlamydomonas sense the direction of light by a single eyespot (red in the figure). The position of the eyespot relative to the two flagella is always the same. If a cell swimming toward the top of the screen (1) senses light coming in from the right, this causes an influx of Ca2+ into the flagella (2). The 2 flagella respond differently to this increase in Ca2+; one flagellum becomes more active, and the other becomes less active (3). This difference in activity causes the cell to turn toward the light (4). Cells can be either positively phototactic (turn toward the light) or negatively phototactic (turn away from the light).

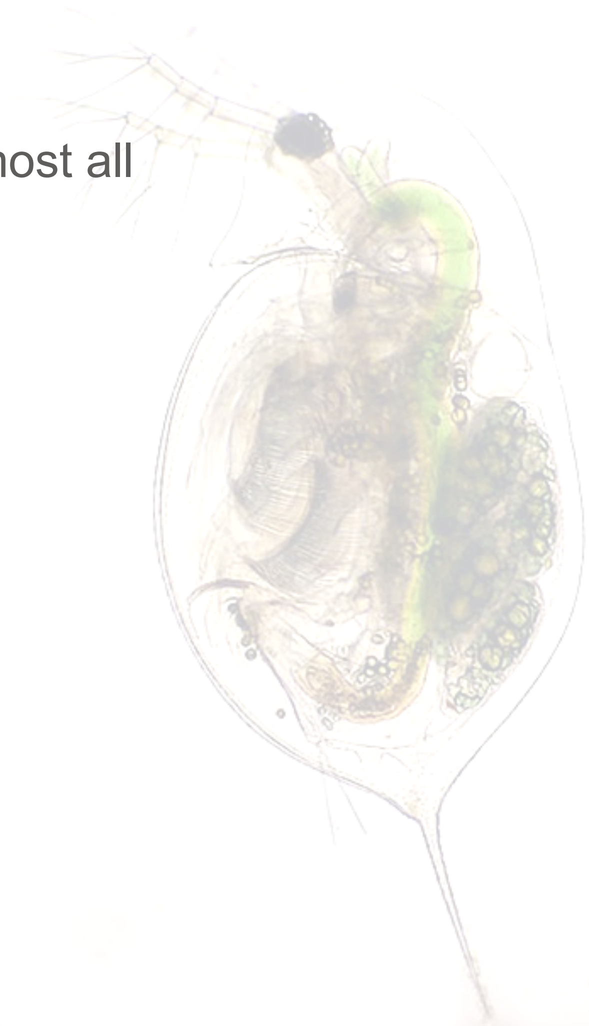
Light activated “behaviors” in plants



Recasting the Question

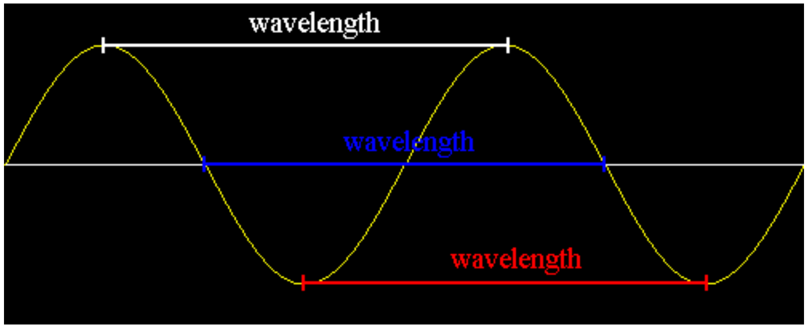
So clearly “light sensing” is profoundly useful to almost all living organisms.

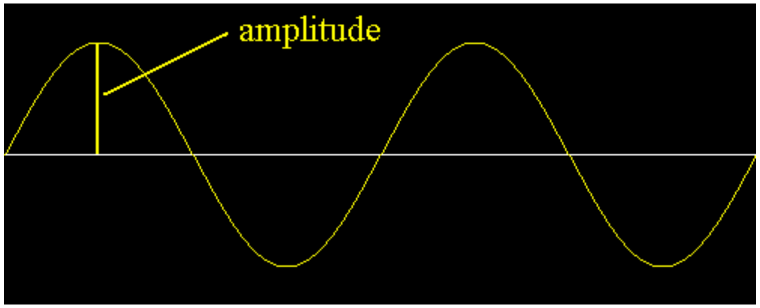
The questions is: why?



The Stimulus: Light

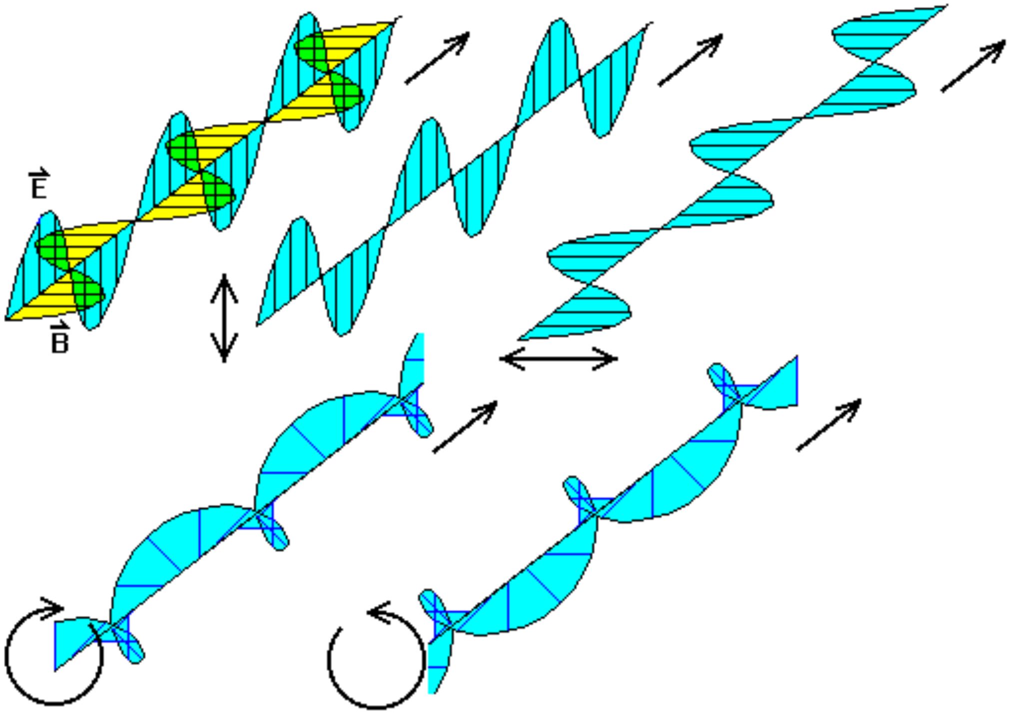
Light is a multi-dimensional stimulus—direction of propagation, velocity, wavelength, amplitude, frequency, polarity.





The nature of vision

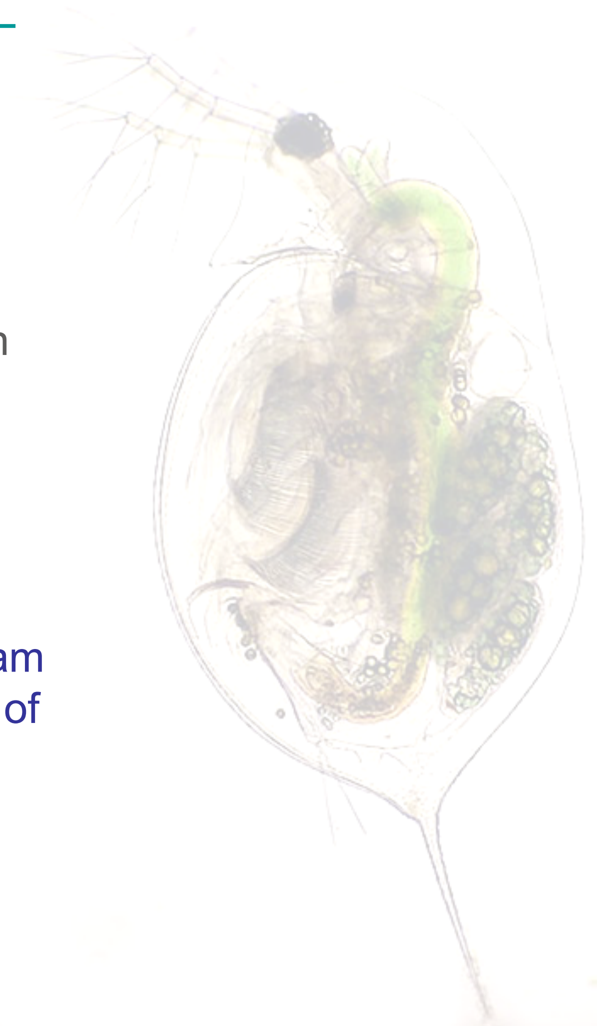
Polarity



The nature of vision

As light interacts with the furniture of the world, all three dimensions of light both *affect* and *are effected* by these interactions—by absorption, transmission and reflection—in law-like ways.

“each interaction of light with bulk matter can be viewed as a *co-operative event* arising when a stream of photons sails through and interacts with an array of atoms suspended (via electromagnetic radiation) in the void…” *Hecht, Optics.*



The nature of vision

The net result is that each and *every* dimension of light is a potential source of information about the distal world.

The nature of vision

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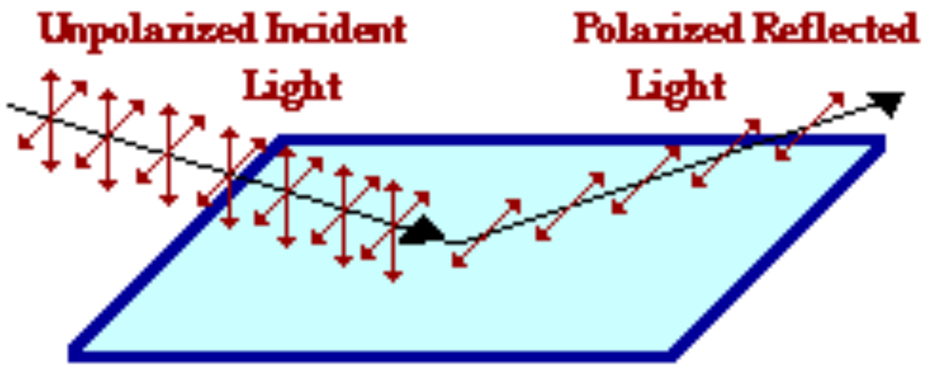
An Example: Polarity

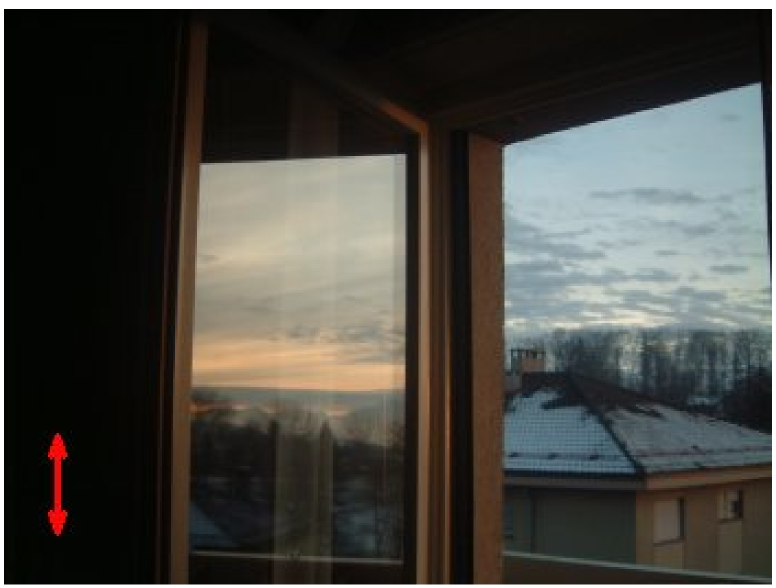
Although natural sunlight is not polarized, sunlight is partially polarized through transmission, reflection, refraction and scattering.

The nature of vision

Polarization by Reflection



Reflection of light off of non-metallic surfaces results in some degree of polarization parallel to the surface.



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POLARIZATION CONTRAST VISION IN OCTOPUS

SHASHAR & CRONIN The Journal of Experimental Biology199, 999–1004 (1996)

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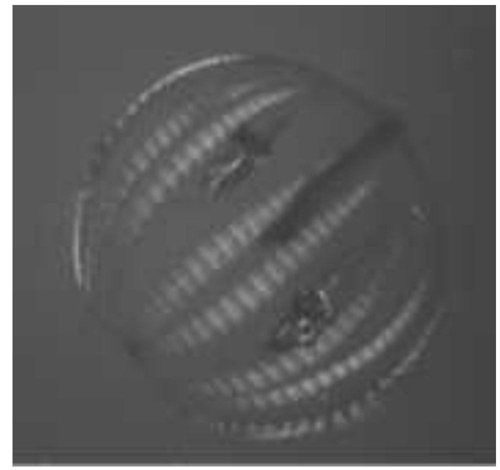
Luminance image

Crossed polarization



Combined

Ctenophor plankton

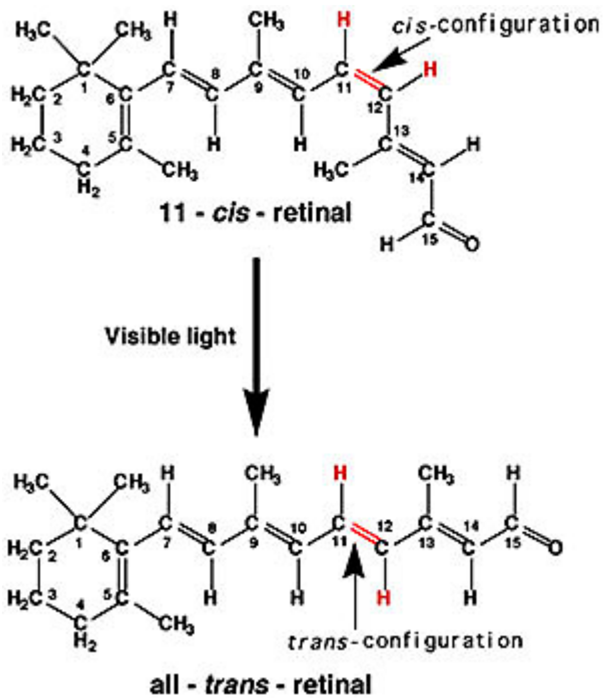
The nature of vision

The Receptor: A Chromophore (pigment) + An Opsin

The Chromophore

- Responsible for the molecule's colour
- Well-known chromophores: chlorophyll, heme, & β-carotenes
- A conformational change in the molecule is induced when it absorbs a photon.

The nature of vision



- In animals, the chromophore at issue is *retinal* — a derivative of Vitamin A.
- Highly sensitive to light and absorption peak readily shifted into the visible spectrum
- Very stable in the absence of light …no false images!
- Structural change produced is sufficient to break the opsin bond

www.physics.utoledo.edu/~lsa/_color/18_retina.htm

The nature of vision

Opsins

An Opsin: A protein chain that forms a “cage” around the attached chromophore, and snakes back and forth across the membrane of a cell in seven segments.

The type of amino acids in certain key locations in the opsin chain segments have a profound effect upon the *wavelength sensitivity* of the receptor .

Any retinal + any opsin = a rhodopsin, the photoreceptors of all multi-cell animals.

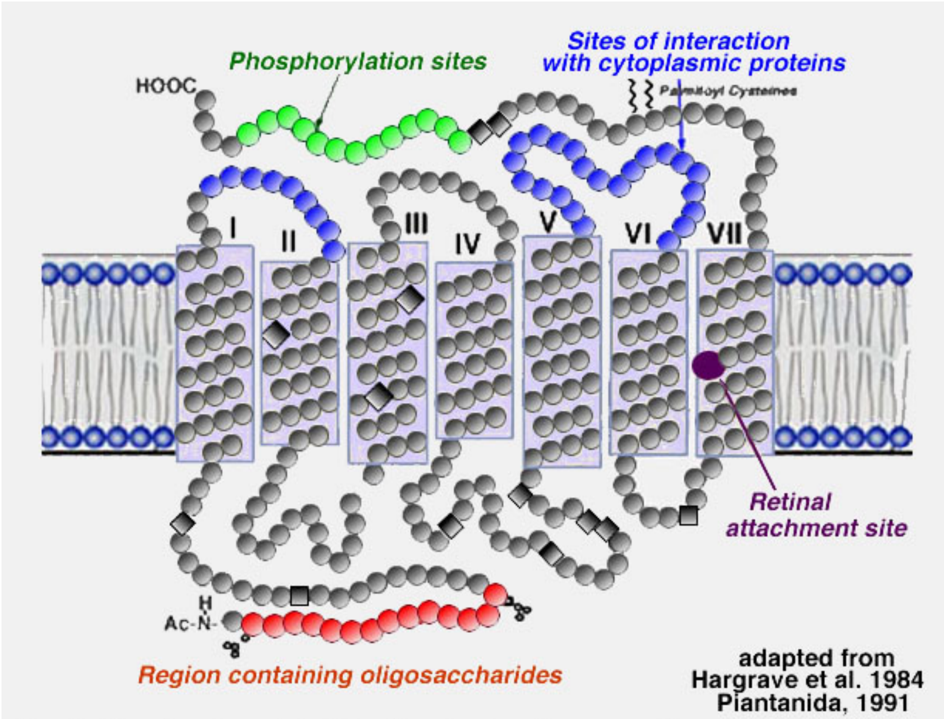


Fig. 9. Structural model of rhodopsin showing seven transmembrane components and the attachment site for retinal.

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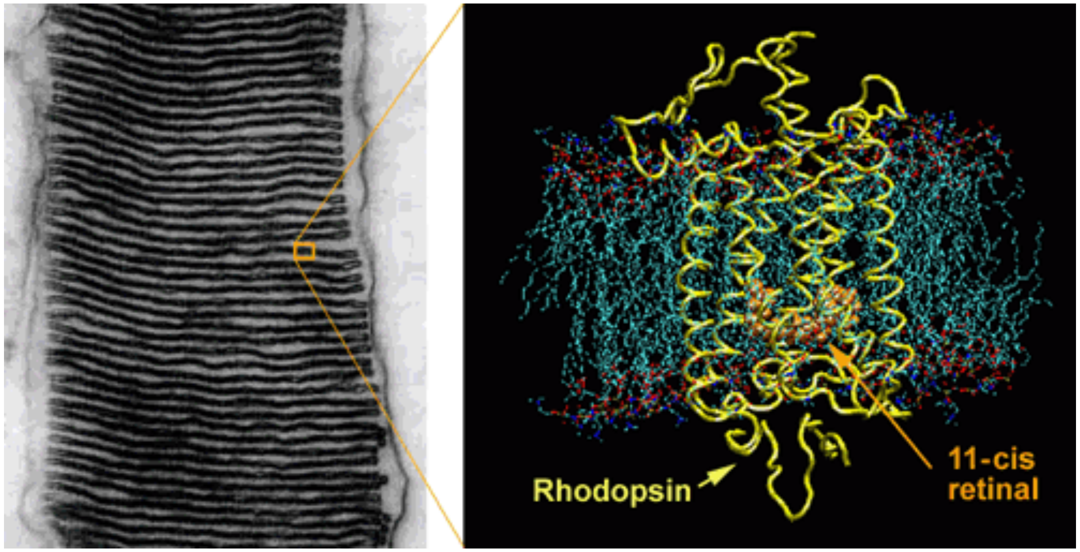


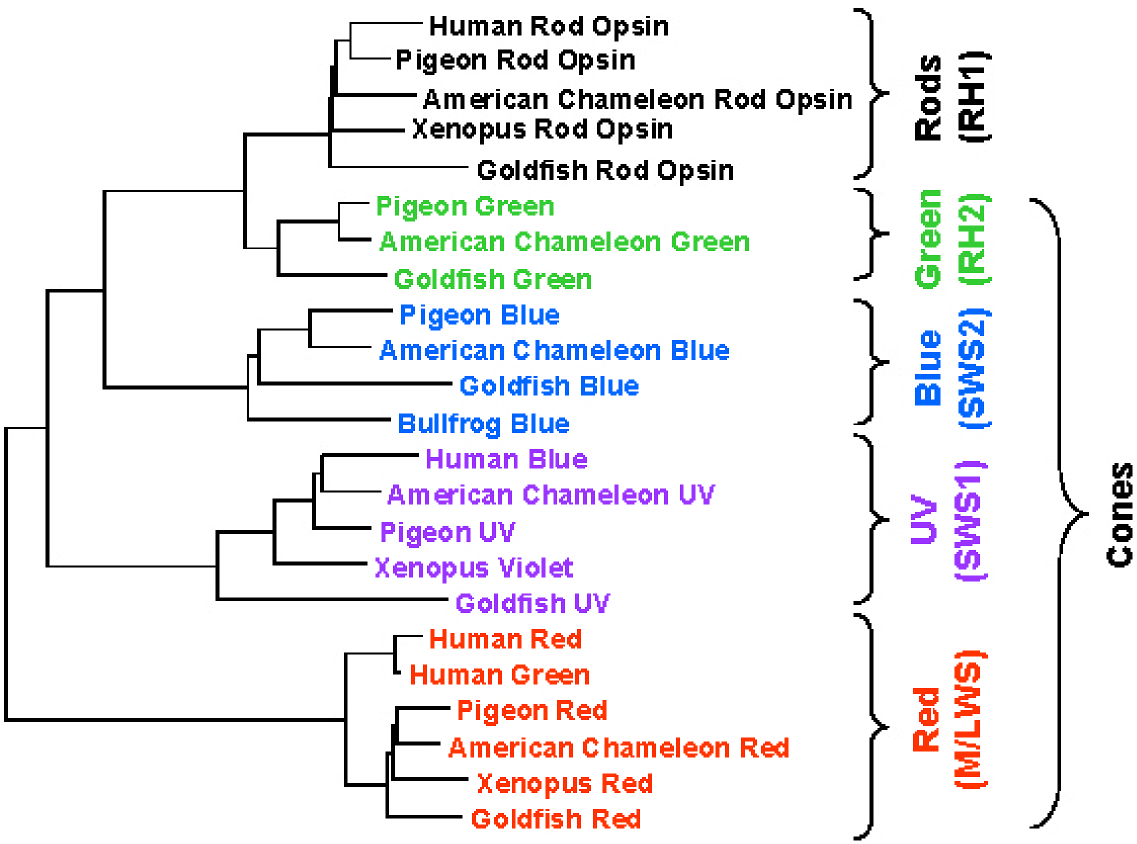
• Left: cross section of the photosensitive end of a rod consisting of stacked disks penetrated by many rhodopsin proteins.

• Right: diagram of the trans-membrane protein rhodopsin; the chromophore is bonded to a lysine residue in α-helix 7

www.physics.utoledo.edu/~lsa/_color/18_retina.htm

The nature of vision

Vertebrate Vision



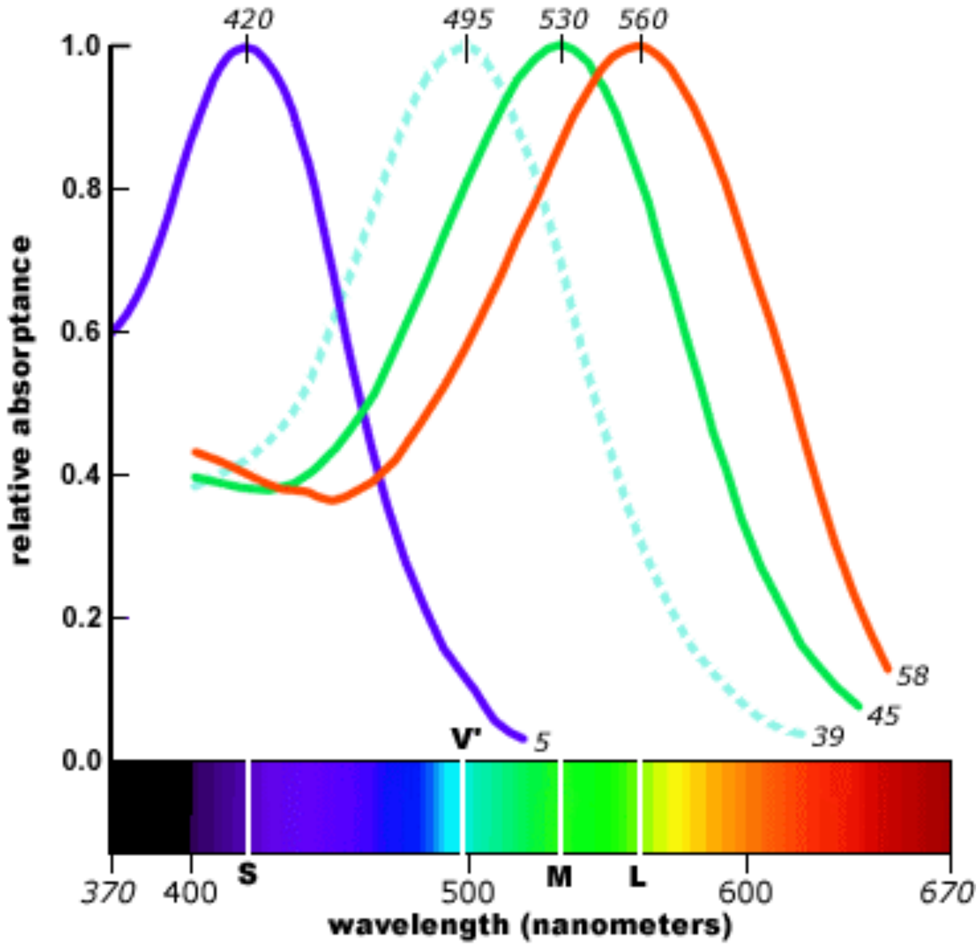
There are only five types of opsins for all vertebrates— I.e. five different genetic differences that account for the five different receptor types in all vertebrates.

The nature of vision

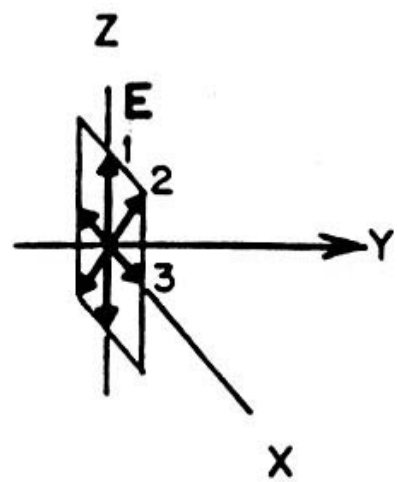
The Receptor: Photopigments

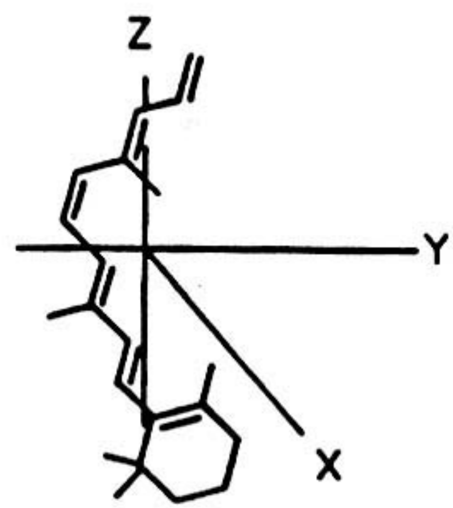
Given this basic structure, all photopigments respond selectively to three dimensions of light—wavelength, amplitude and polarity (if the photopigment is anchored at a single orientation).

Wavelength and Amplitude



Polarity





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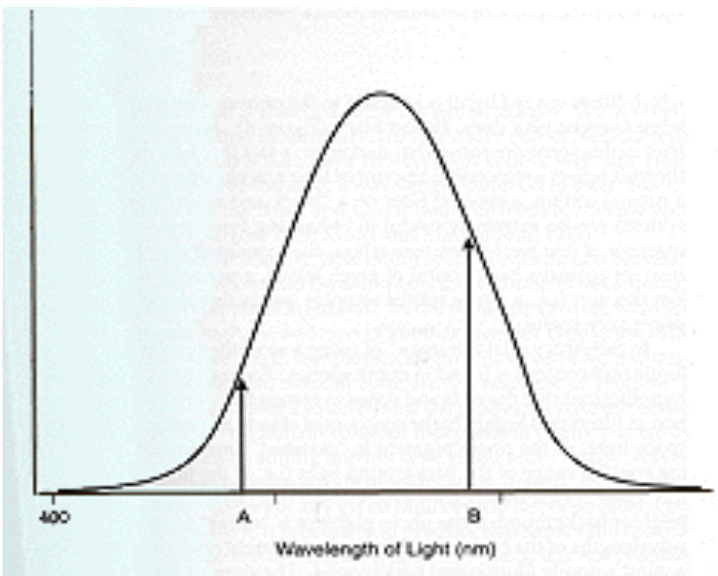
The Receptor: Conflation of Light Properties

Unfortunately, all three of these properties conflated at the receptor level by the response of the photopigment.



Receptor response: Conflation of wavelength and amplitude in a photoreceptor (for a given polarity).

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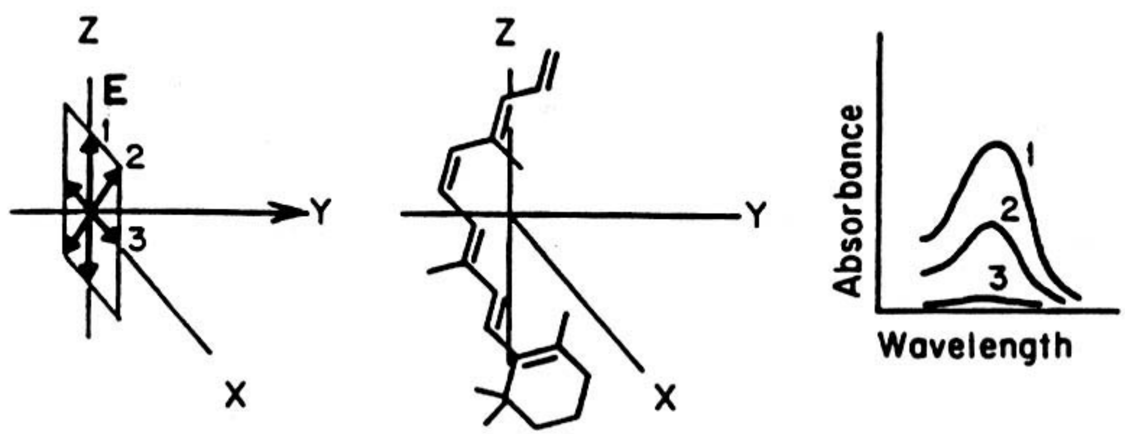
The Receptor: Conflation of Light Properties

Conflation of polarity and wavelength (at a given intensity).



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Evolutionary Consequences

Any evolved visual system will have “solved” the problem of which of these three dimensions of light—polarity, amplitude, or wavelength—to disambiguate or make explicit, given the specific properties of light in the environment of the organism and that organism’s specific behavioral repertoire,

Because all three dimensions of light are effective stimuli, all three dimensions will influence which adaptations. Hence the complex facts about the light environment—any regularities (or the lack thereof) in all three dimensions of light—will have profound adaptive consequences.

The nature of vision

daphnia pulex

Behaviors (Baylor 1953)

"Colour Dances". "Under red light the population appears calm, the individuals dancing upright in the water… Under blue light…the population is distinctly agitated, the individuals leaning well forward in their dance and roaming about with a large horizontal vector to their location. Prolonged exposure to this light has literally driven populations to death."

Polarization Response. Swim towards large areas of diffuse, polarized light, but only if e-vector approximately horizontal.

Intensity Response: Brightening a blue light will cause downwards swimming; dimming light, blue or red, causes upward swimming.

The nature of vision

daphnia pulex

Ecological Significance

Food foraging. *Daphnia* eat plankton which, when aggregated, make the water appear red ("red tide"). When the water appears red, daphnia display the typical "hop and bob" movement, feeding in place; When the water is blue, active foraging occurs.

Diel Vertical Migration. *Daphnia* avoid predators (fish) by migrating downwards during the day. Thus intense blue light causes downward swimming; dimming light causes upward swimming. However, this response is altered by the presence or absence of fish kairomones.

Shoreflight. *Daphnia* avoid shallow, predator-rich waters near the shore. Light reflected from the surface of water will have stronger horizontal polarization.

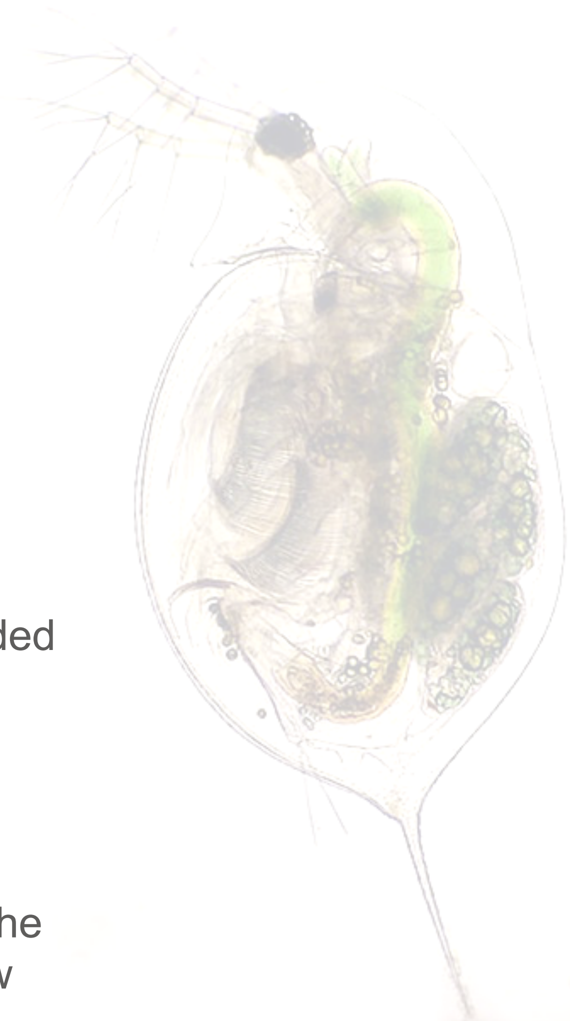
The nature of vision

•Four types of visual pigments: UV, S, M, & L (Smith & Macagno 1990)

•M & L cells are specialized for polarization (Flamarique & Browman, 2000)

•As far as we know, information from these daylight photoreceptors is not used for seeing a coloured world.

The Nature of Vision



Conclusions

•All dimensions of light have the potential to carry information about its distal interactions with the furniture of the world.

•Photopigments react to three dimensions of light—polarity, wavelength, amplitude.

•Thus,each dimension can be used, whether encoded explicitly or not, by a visual system.

•E.g. Wavelength can used in many different ways depending upon the environment and the organism—to signal plankton rich water, to signal the time of day, to signal the direction of shore, to show visual contrast…

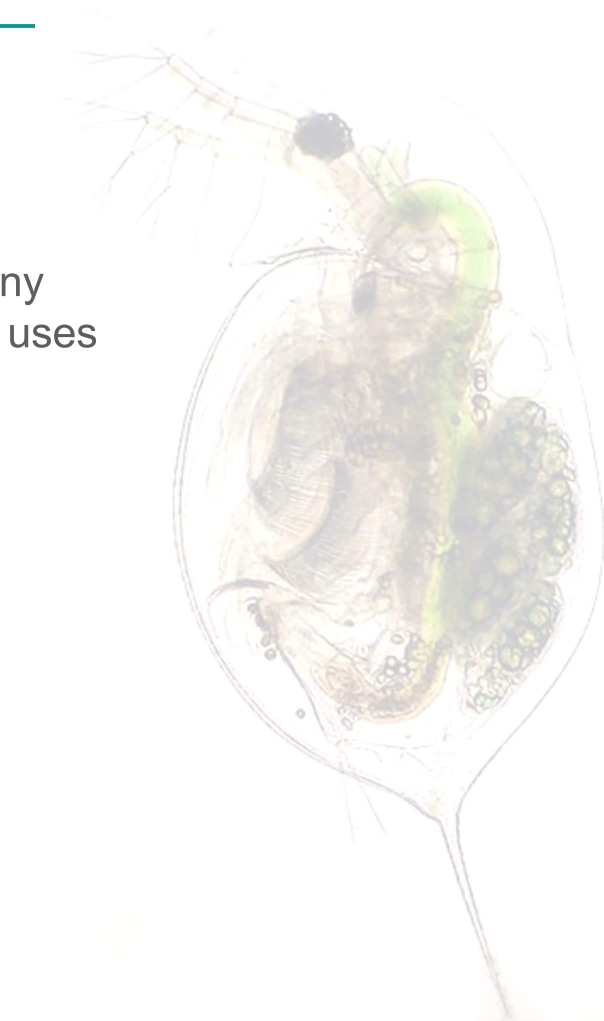
The Nature of Vision

Conclusions…

So the most general question we should ask of any visual system is not about **colour** per se and the uses of colour.

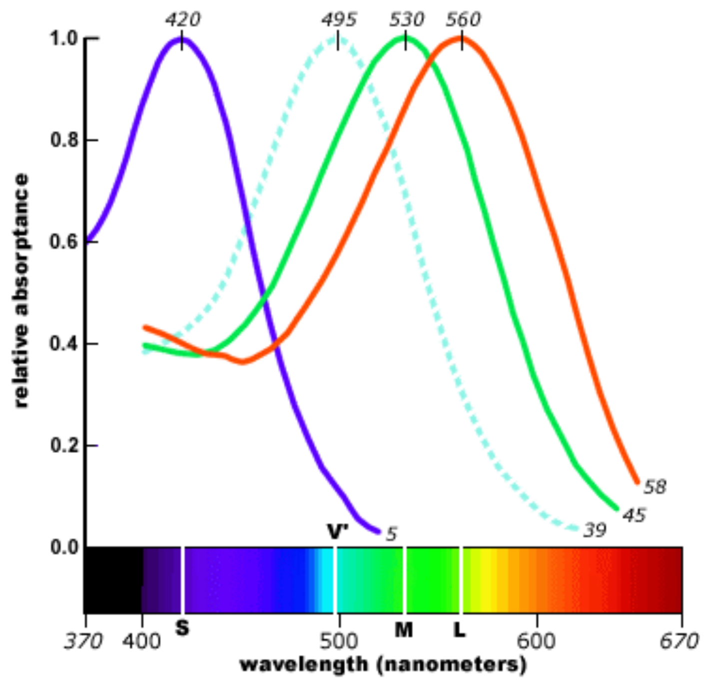
The question is: How does this particular visual system use wavelength information?

I.e. What is **wavelength information** good for?



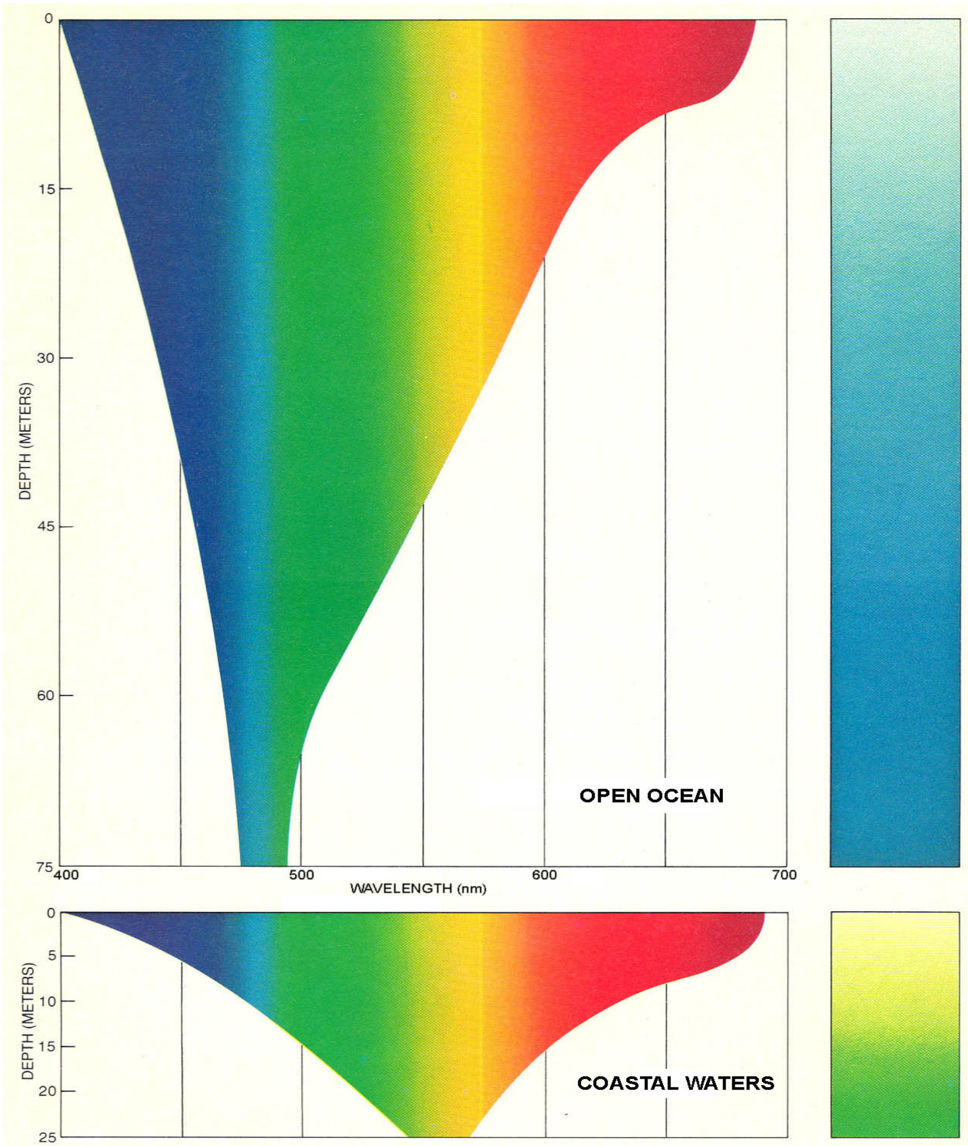
Beyond Phototaxis: Spectral information and object vision.

Every photoreceptor is a wavelength filter.

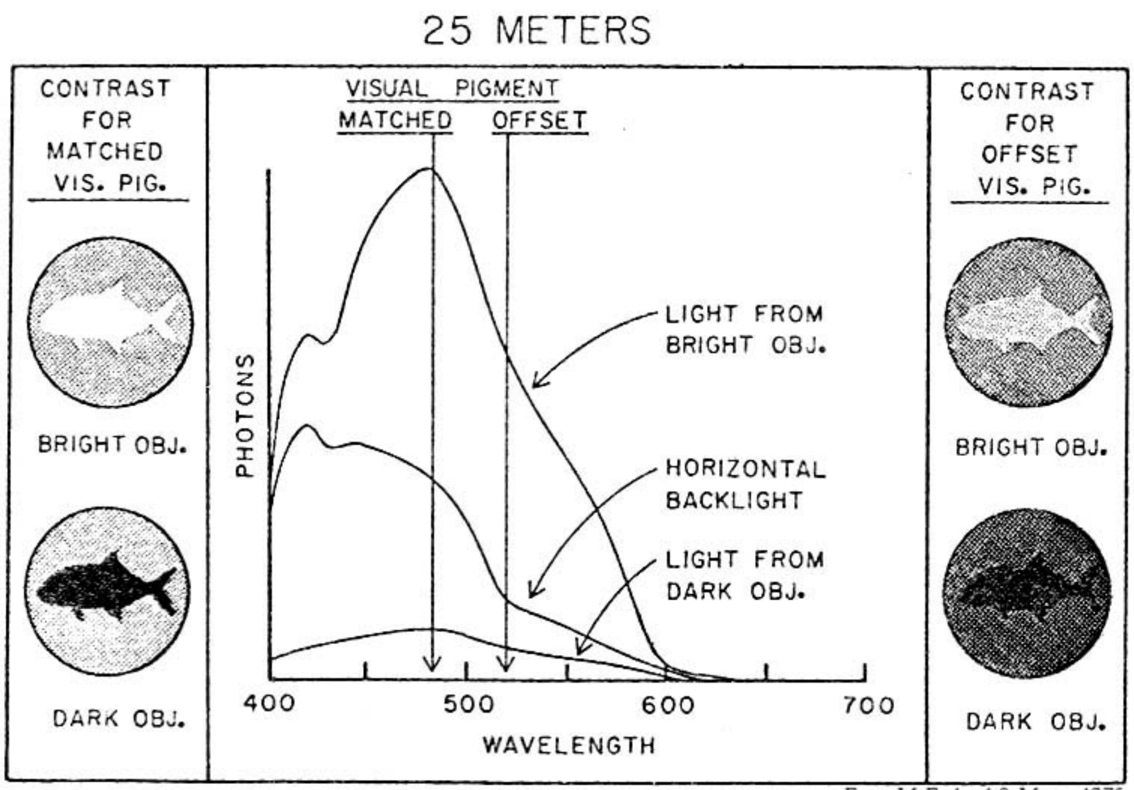


Spectral information and object vision

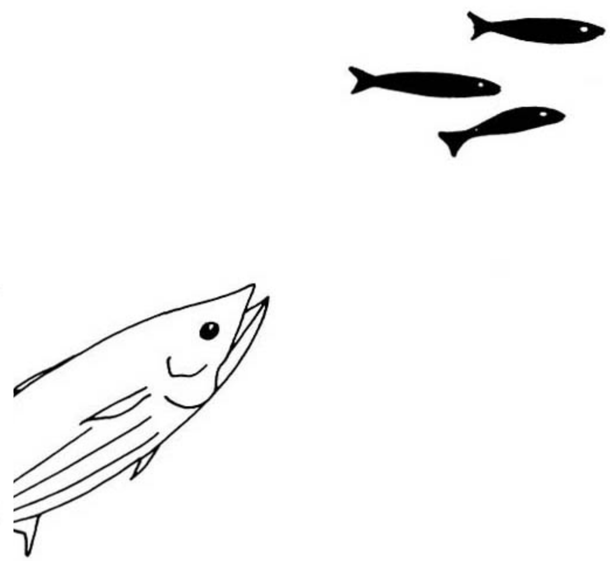
Relative to a specific environment and purpose, filters can be used to heighten contrast—visual contrast—of an object with its background.


0
15
30
45
60
75
DEPTH (METERS)
400
500
600
700
WAVELENGTH (nm)
OPEN OCEAN
0
5
10
15
20
25
DEPTH (METERS)
COASTAL WATERS

Using spectral tuning to enhance contrast of an object with its background



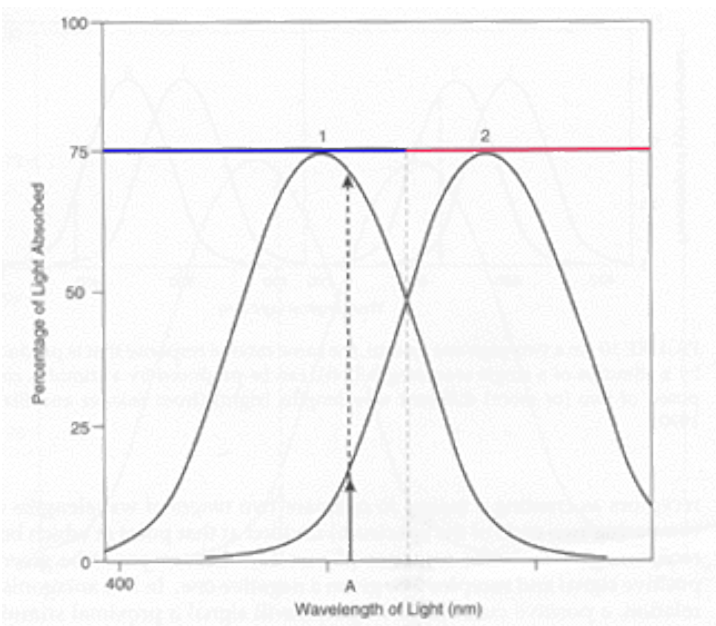
From McFarland & Munz, 1975

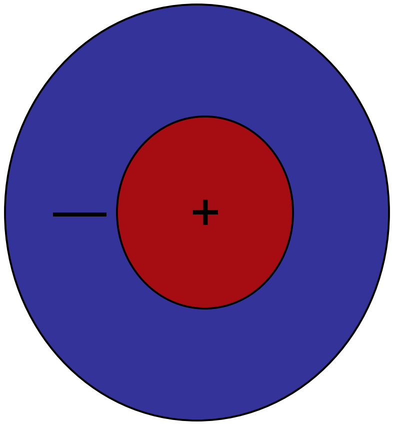


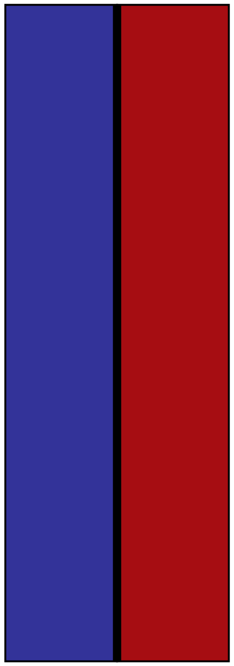
The skipjack tuna strikes upwards.

Spectral Information and Object Vision

Using spectral contrast for edge detection







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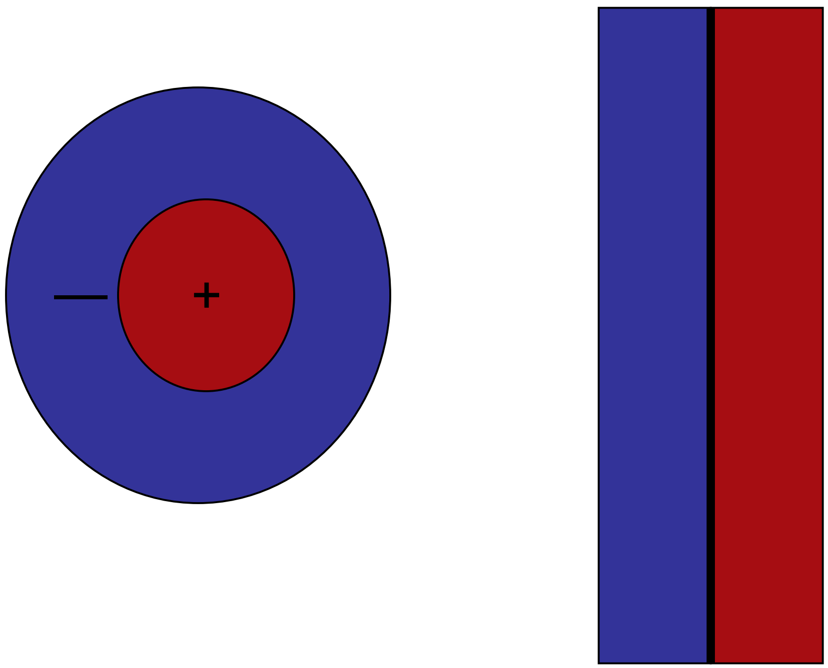

Spectral Information and Object Vision

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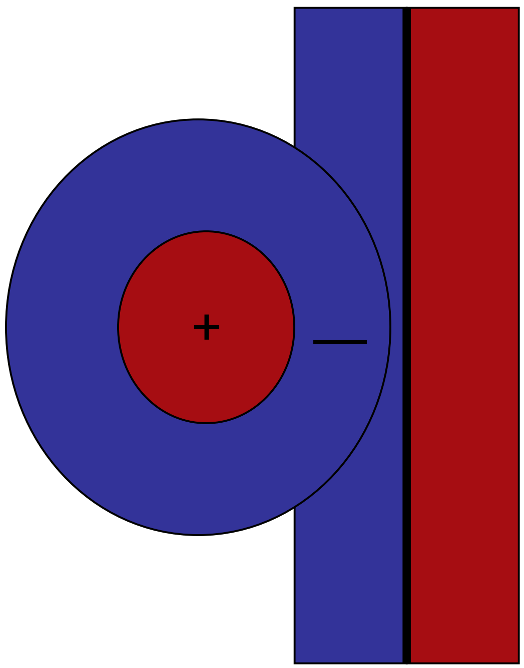

Spectral Information and Object Vision

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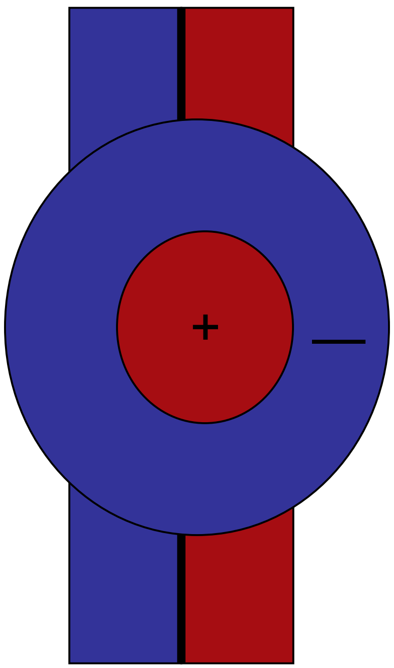

Spectral Information and Object Vision

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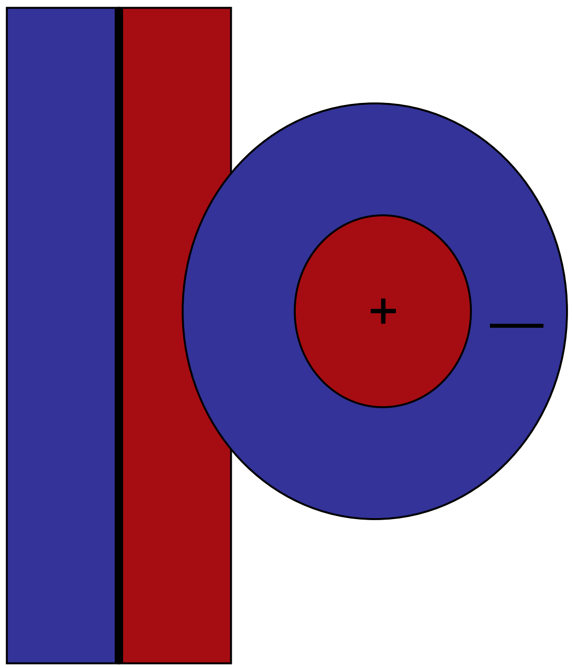
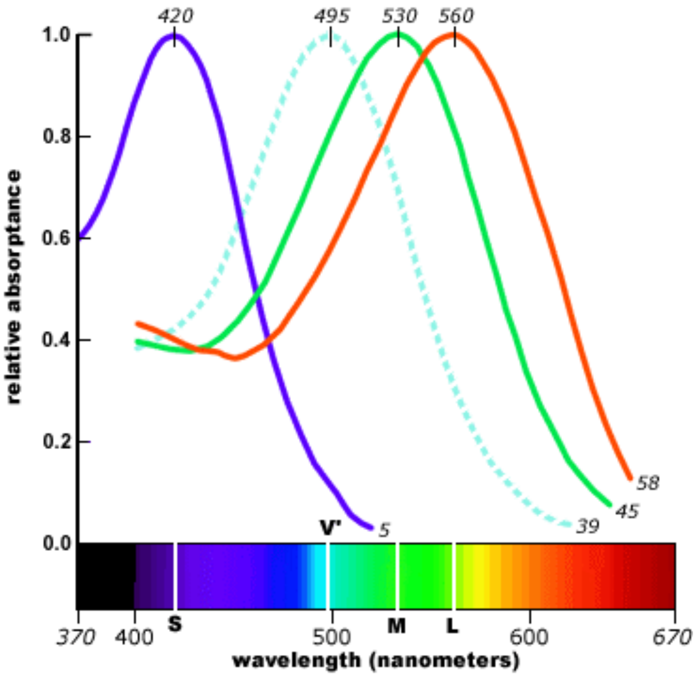
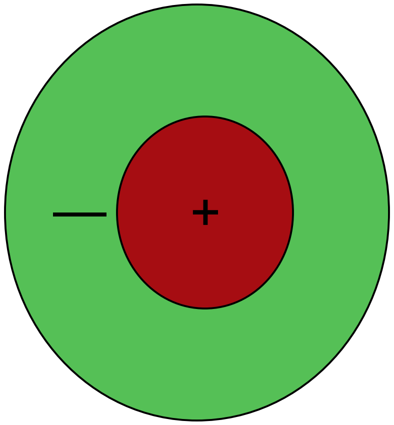
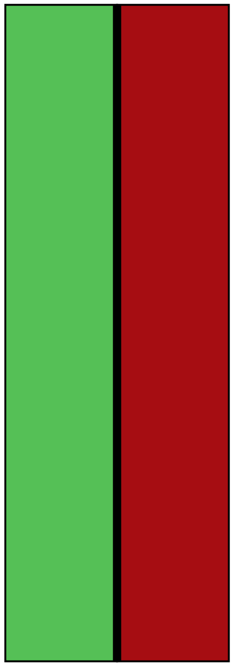


Spectral Information and Object Vision

Using spectral contrast for edge detection







Spectral Information and Object Vision

But why would it be useful to object vision to encode spectral contrast in addition to luminance contrast?

THE AGE OLD DICTUM: Where there is spectral contrast, there is luminance contrast.

Therefore: Spectral contrast is **redundant**.

Therefore: Spectral contrast is **useless**.

Spectral Information and Object Vision

NO.

1. In vision, redundance is a very good thing.

Luminance contrast + spectral contrast = **MORE** contrast

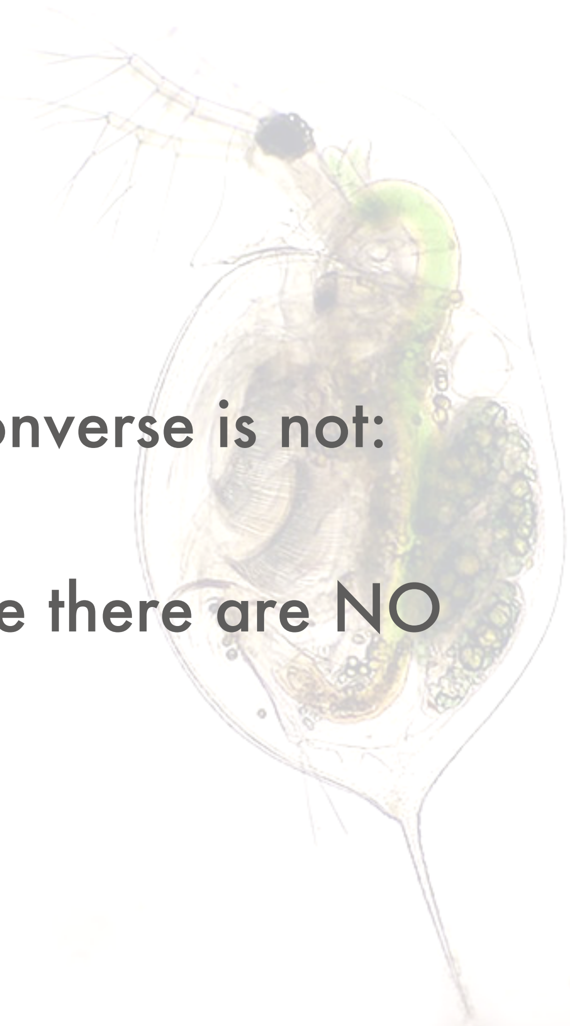
Spectral Information and Object Vision

NO.

2. Although The Old Adage is true, its converse is not:

There are many luminance borders where there are NO spectral borders.

The visual world contains **shadows**.



Spectral vision and object vision

But if could distinguish spectral contrast from luminance contrast, you could solve the problem easily.

OBJECTS are outlined by superimposed spectral and luminance borders.

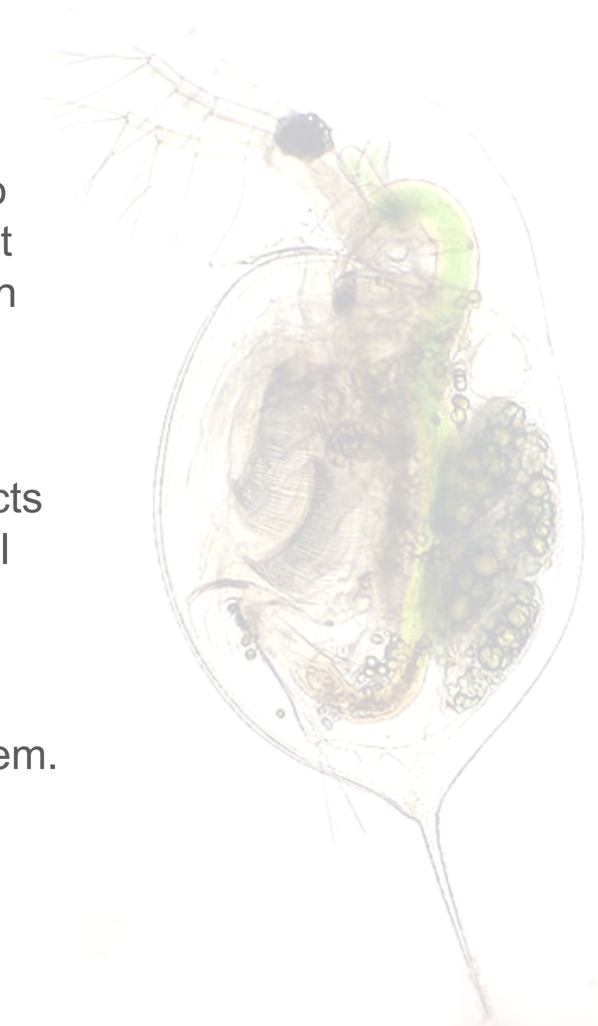
SHADOWS are outlined by ONLY luminance borders

Spectral Vision and Object Vision

On the one hand….Shadows are extremely important to object vision as they provided essential information about shape, depth, texture, transparency, material composition and location.

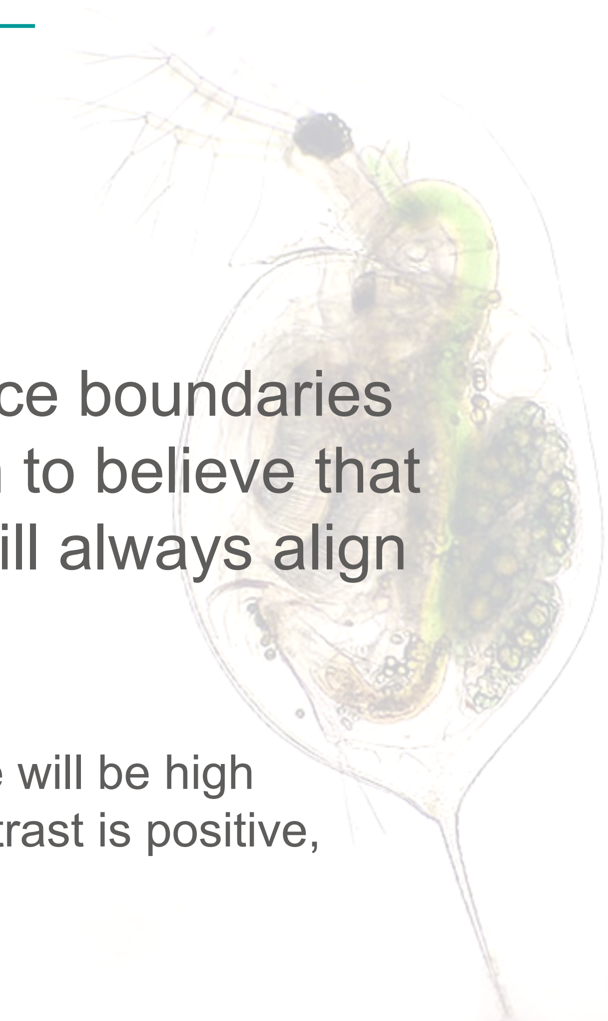
On the other hand….Distinguishing shadows from objects has turned out to be a (ludicrously) difficult computational task.

I.e. You can’t live with them and you can’t live without them.



Spectral Information and Object Vision

Spectral Vision and Object Vision



NO.

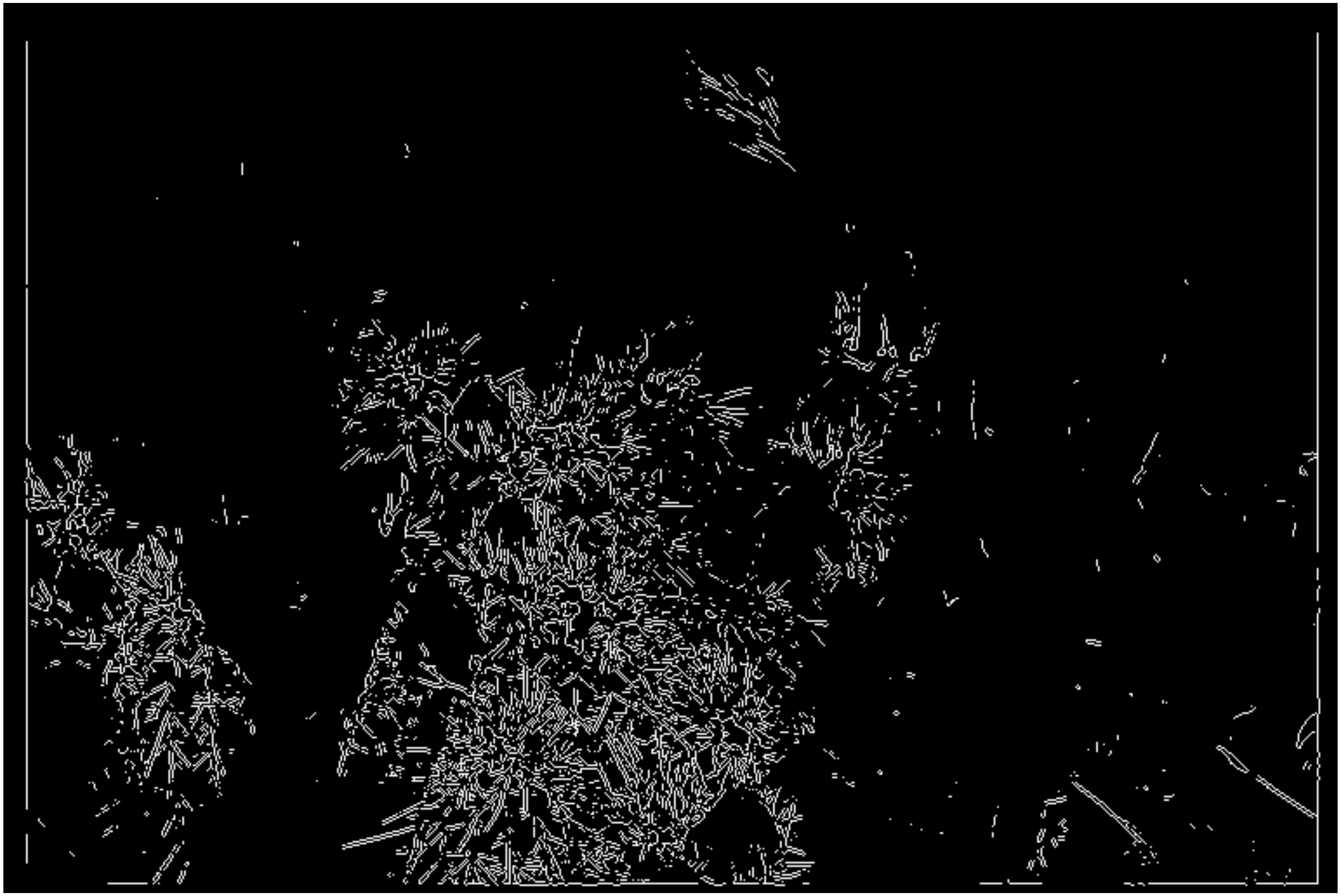
3 Although the spectral and luminance boundaries of objects align, there is no reason to believe that spectral and luminance contrast will always align in value.

E.g. that when there is high spectral contrast there will be high luminance contrast, that when luminance contrast is positive, spectral contrast will be positive.

Full "colour" image:Luminance and spectral information

Luminance Image

Luminance Edges



Red/Green Image (rendered in grayscale)

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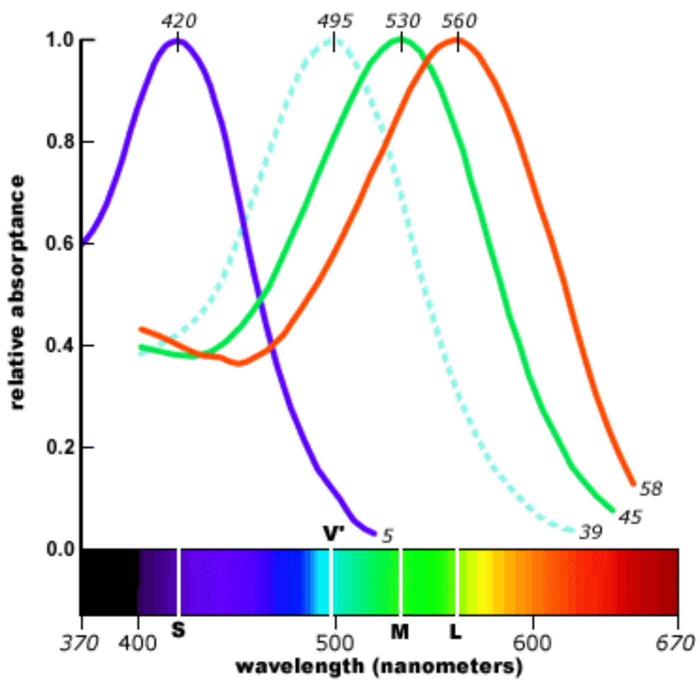
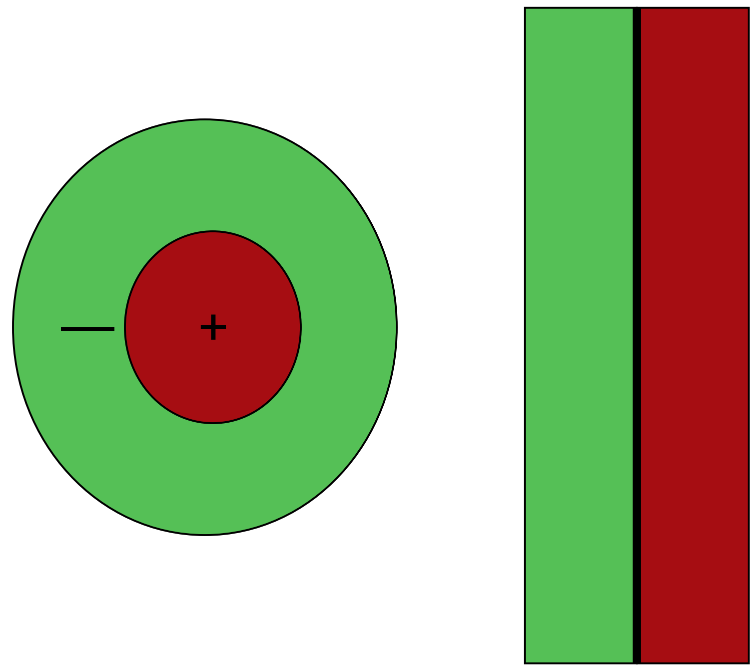
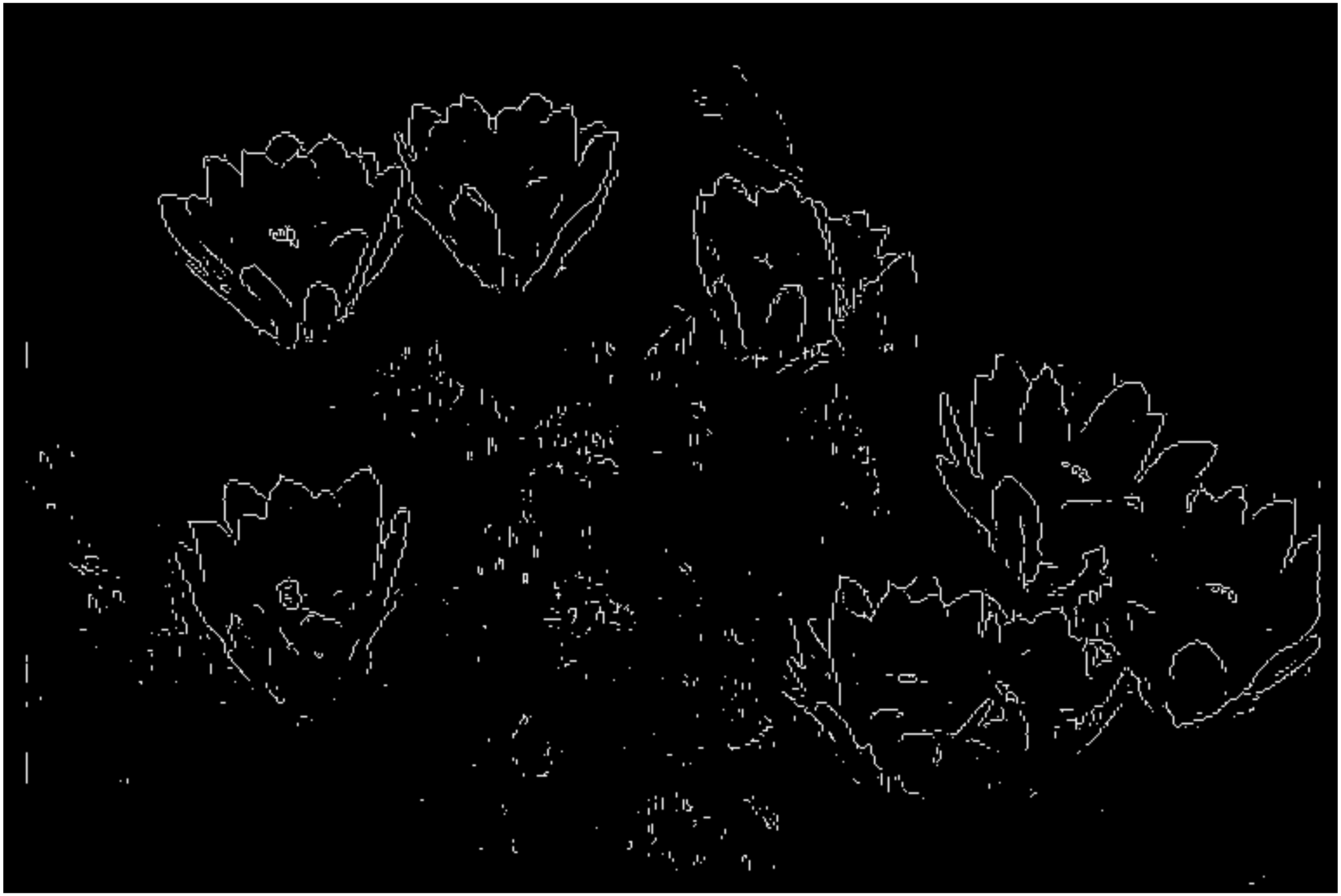
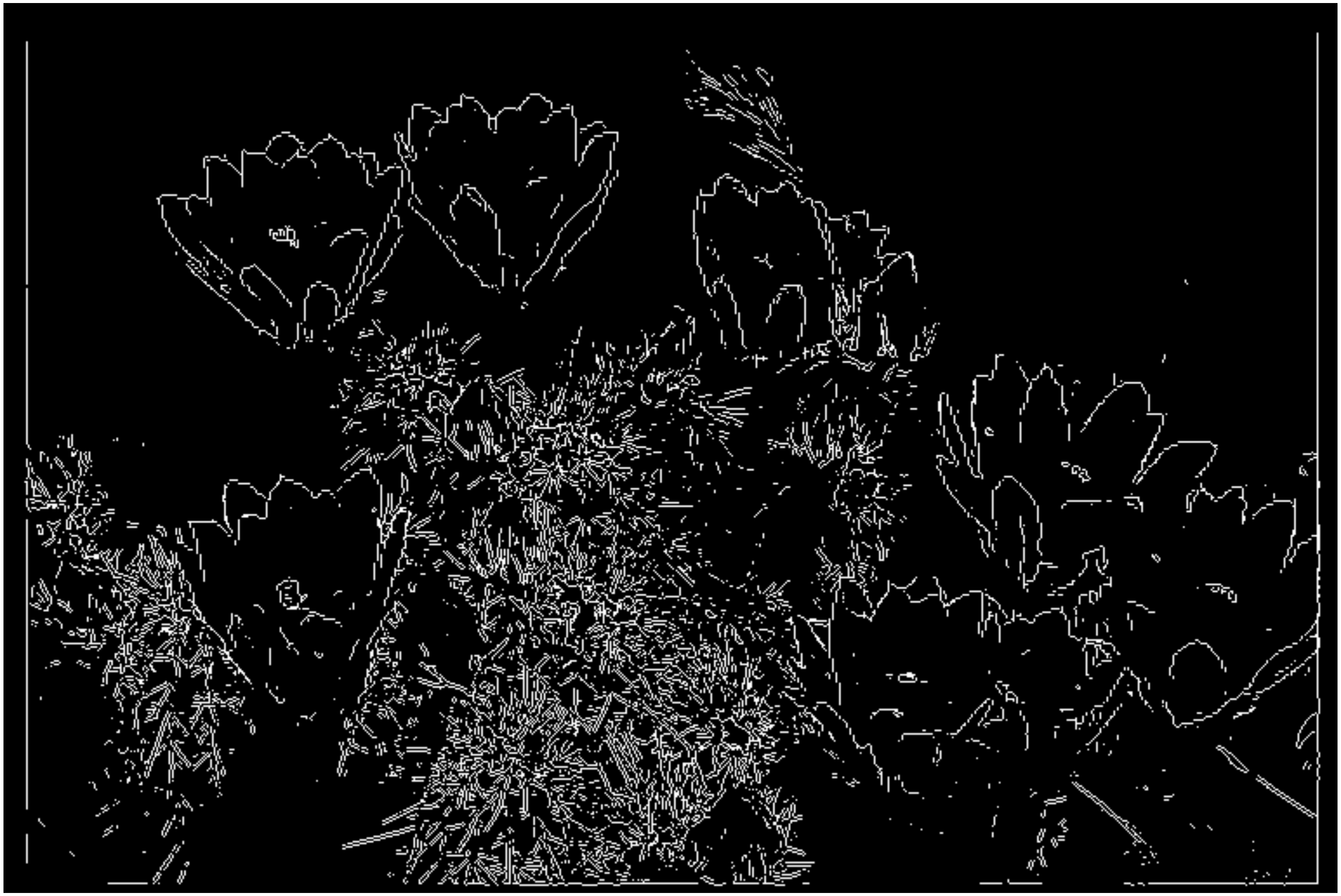


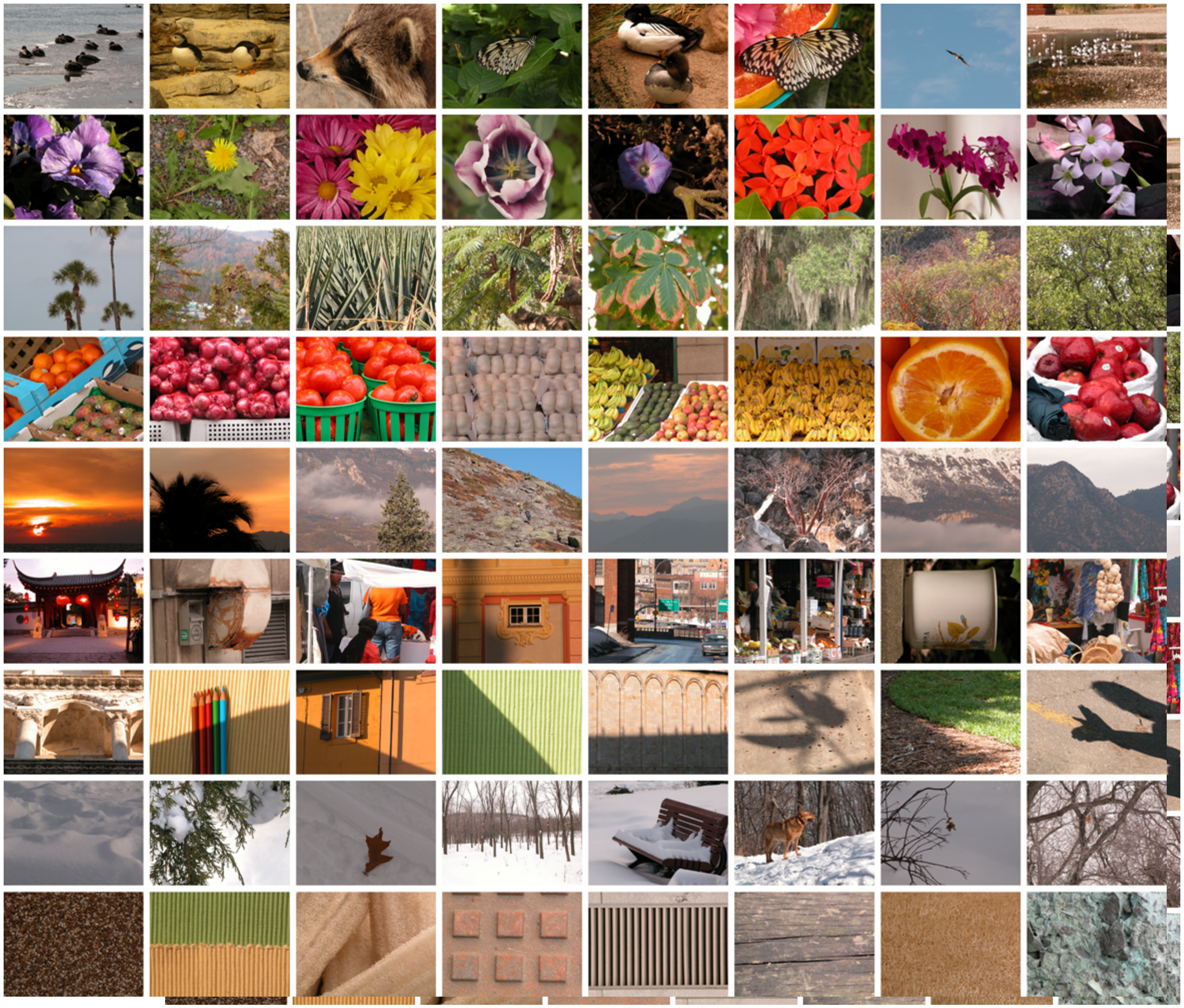


Gred/Green spectral contrast edges



Combined Spectral and Luminance Edges



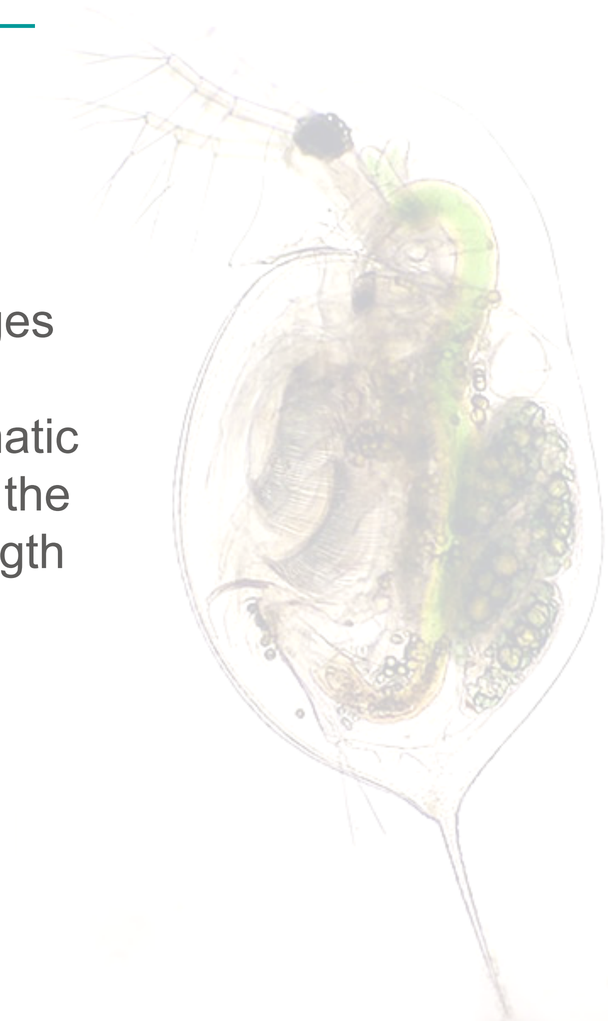


Hansen & Gegenfurtner (2009) "The Independence of colour and luminance edges in natural scenes"
Visual Neuroscience.

Spectral Information and Object Vision

Summary

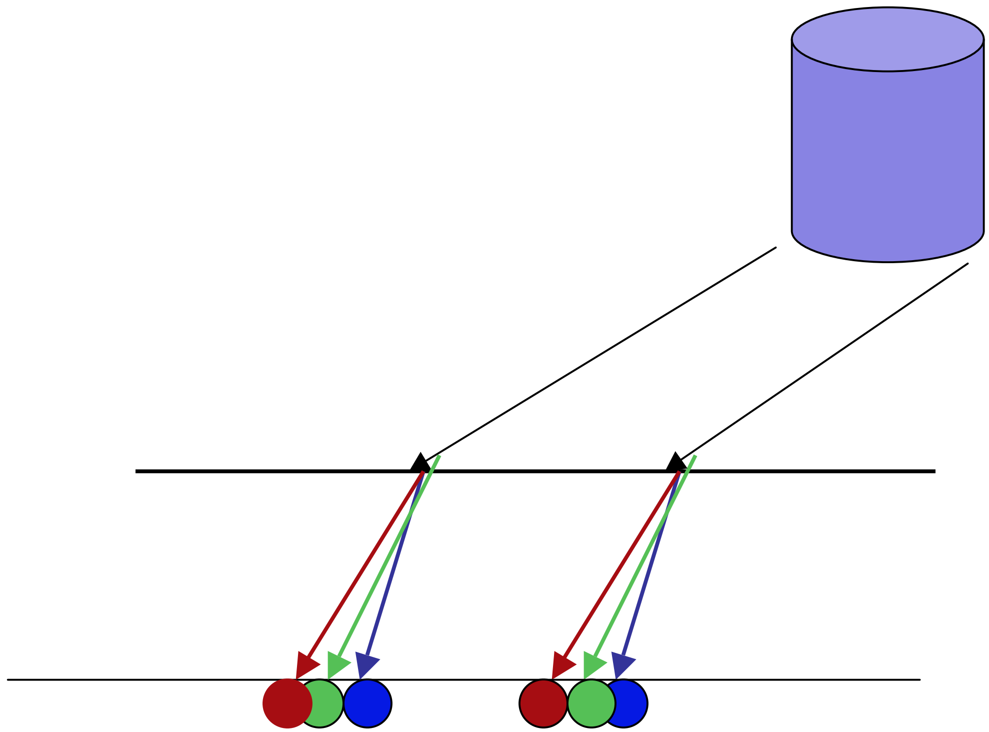
"We have analyzed the distribution of chromatic and luminance edges in natural scenes. Isoluminant edges exist in natural scenes and were not rarer than pure luminance edges….We found chromatic and achromatic edges were statistically independent; the strength of the chromatic edges could not be inferred from the strength of the luminance edge at the same position." (p.11)



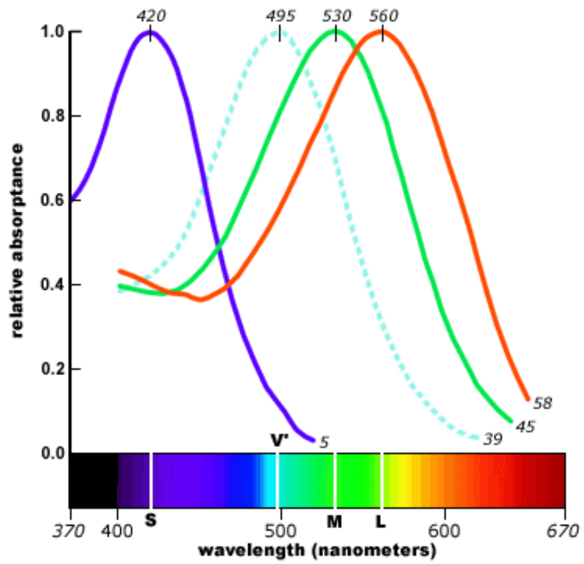
Why three cones for human vision?

Prior to three cones, we had a two cone system, the S-Cone and a “middle wavelength” progenitor cone that was between our current L and M cone in spectral sensitivity.

This old chromatic system appears to have been selectively wired, with blue cones in opposition to M cones. But of necessity this system had a very low spatial resolution because of chromatic aberration.



The facts of chromatic aberration are in direct conflict with the requirement of good "coverage" of the spectrum and spatial resolution. Two cones that have little overlap in their spectral sensitivity, will provide much more wavelength information and be sensitive to a much greater range of light. But the further apart the peak sensitivity of the cones, the greater the chromatic resolution, and hence the less spatial resolution.



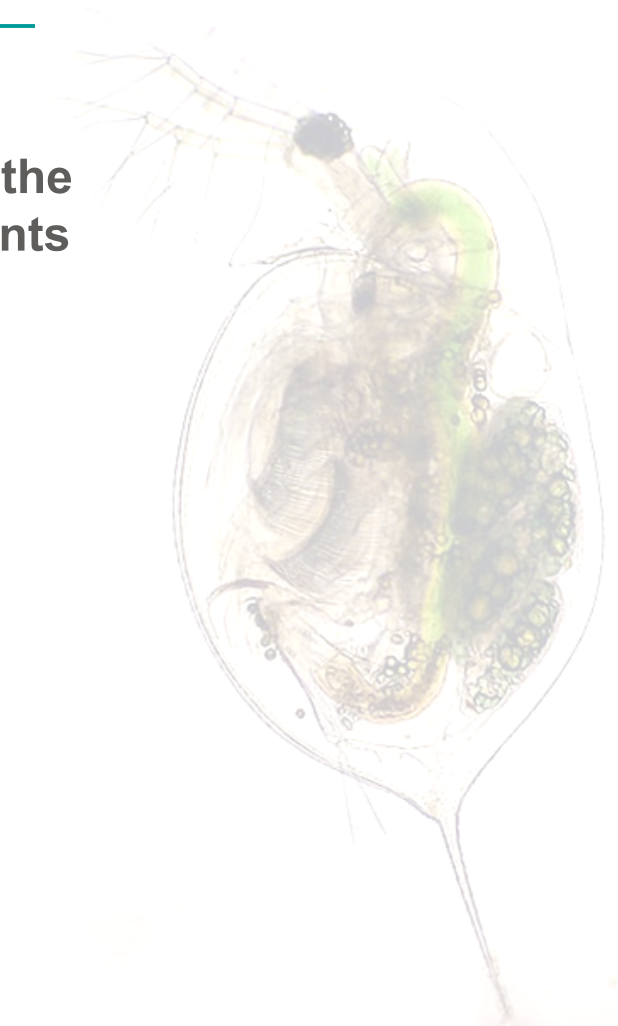
With three cones, there are two different chromatic systems, the older B-Y system and the new M-L system.

The older system provides good coverage of the spectrum of light, plus very rough spatial resolution.

The new system M-L system is chromatically opponent but over a far narrower range. Interestingly, there is NO loss in spatial resolution in the system. This is because somehow or other the system infers the response of other class of cones—I.e. how an M cell would behave if it occupied this location now currently occupied by an L cell with this particular response.

Spectral Information and Object Vision

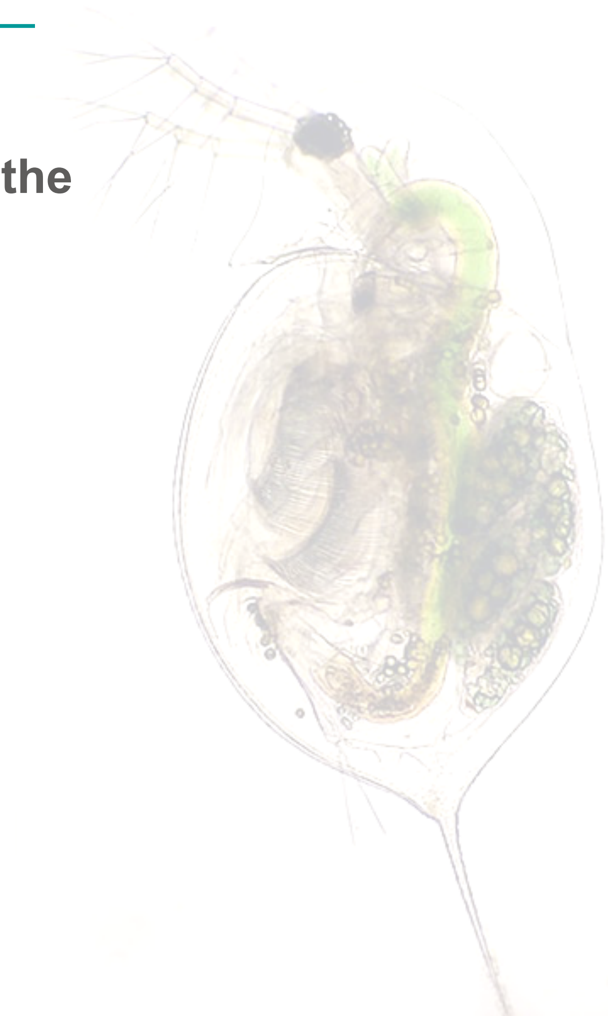
If spectral information is so useful, then why did the Livingstone and Hubel psychophysical experiments come out the way they did?



Spectral Information and Object Vision

If spectral information is so useful, then why did the Livingstone and Hubel psychophysical experiments come out the way they did?

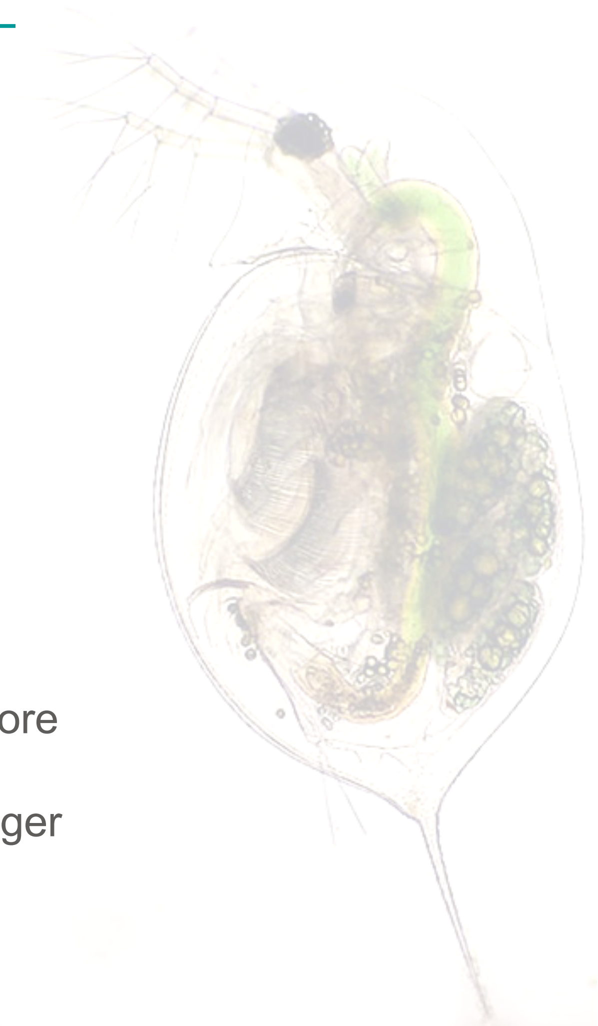
1. The isoluminant spectral stimuli were often not bright enough. The spectral system has a higher intensity threshold.



Spectral Information and Object Vision

If spectral information is so abundant—if spectral contrast presents an independent source of contrast informaton—then why did the Livingstone and Hubel psychophysical experiments come out the way they did?

1. The isoluminant spectral stimuli were often not bright enough. The spectral system has a higher intensity threshold.
2. The H&L experiments did not use stimuli with variable controls for luminance and spectral input. It was therefore not apparent how useful spectral stimuli could be when spectral contrast and intensity were of equal to or stronger (I.e. were more reliable) than luminance stimuli.



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3. The H& L experiments did not measure the *increase* in visibility for combined stimuli with combined luminance and spectral information.

Spectral Information and Object Vision

A General Principle: You cannot discern how a system deploys two independent sources of information simply by *removing* one or the other.

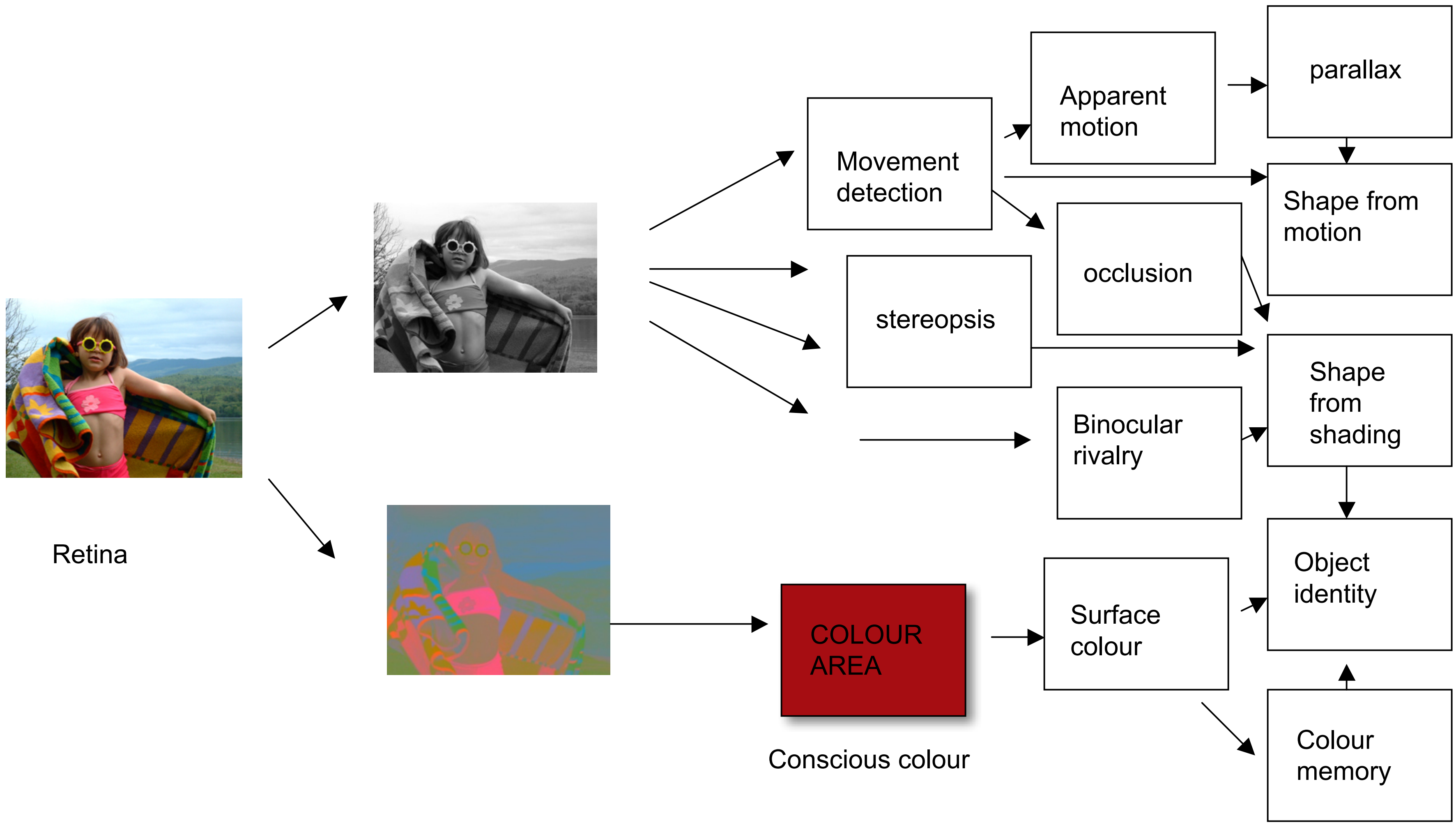
Where are we and why does it matter?

Colour is NOT for colouring *per se*.

Rather, spectral information information is useful for seeing—for discerning properties of many kinds.

Among those properties are depth from a huge number of cues, motion, shape, and of course, surface colour.

Consciousness and Colour-for-colouring



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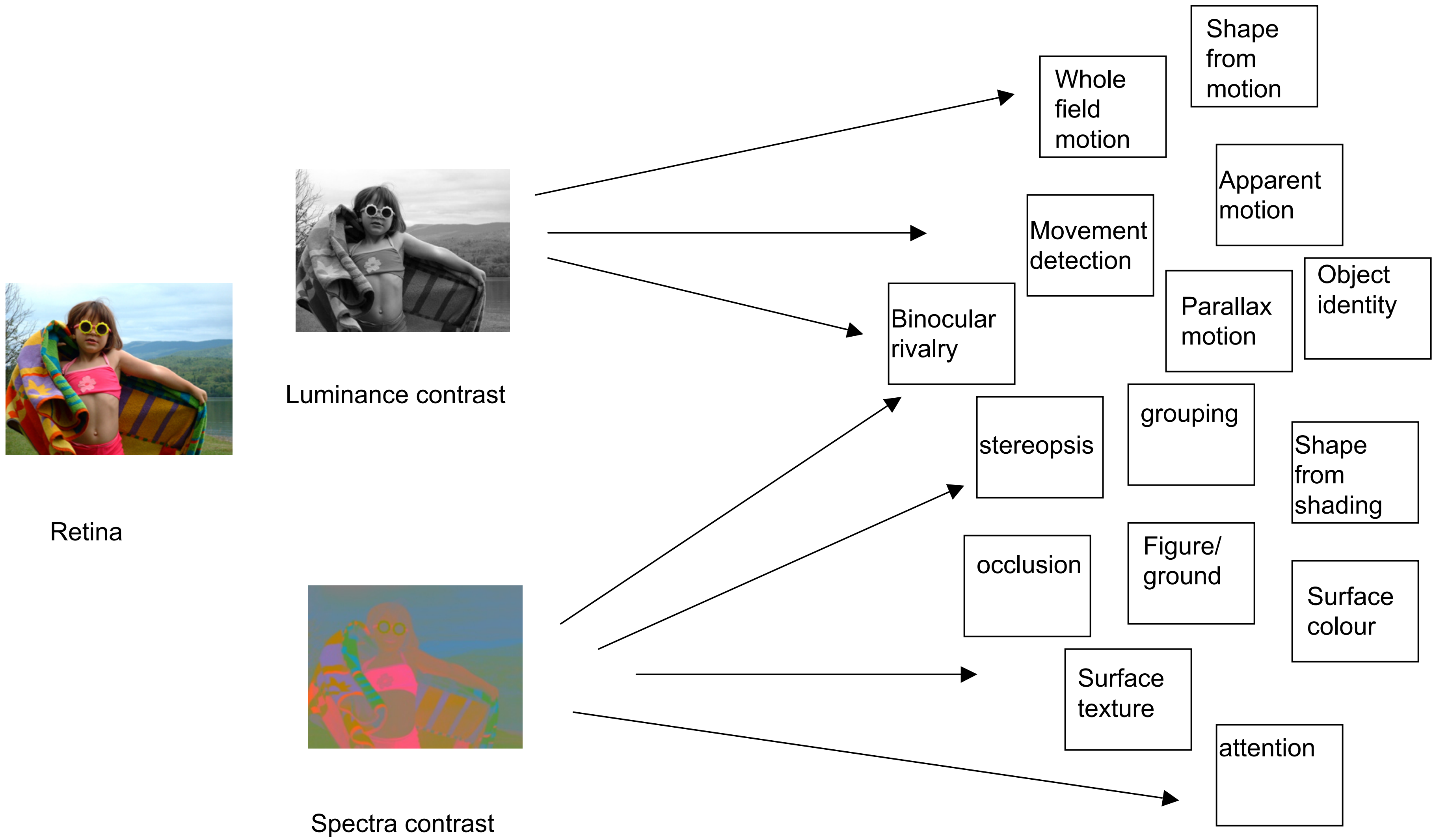

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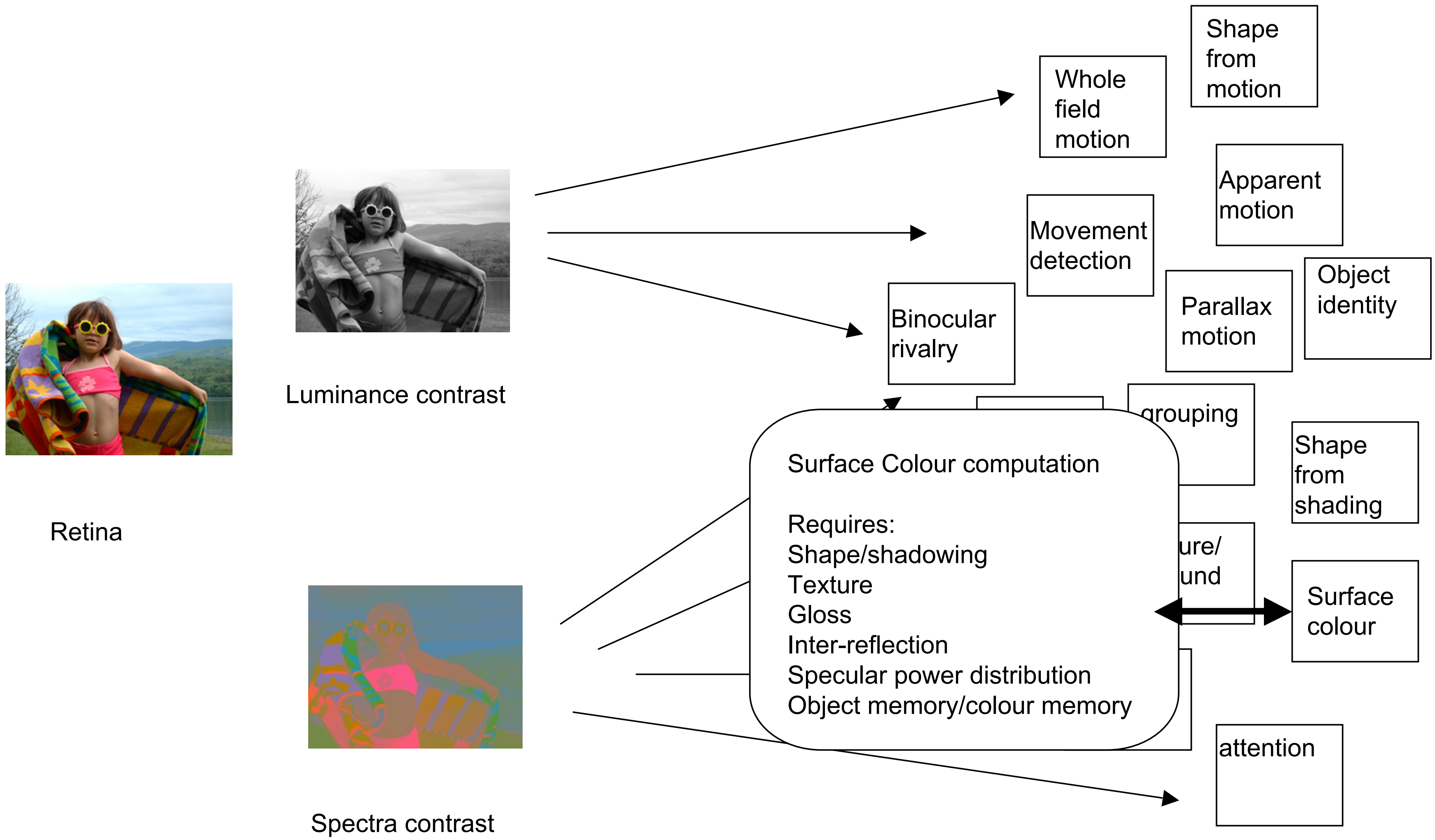
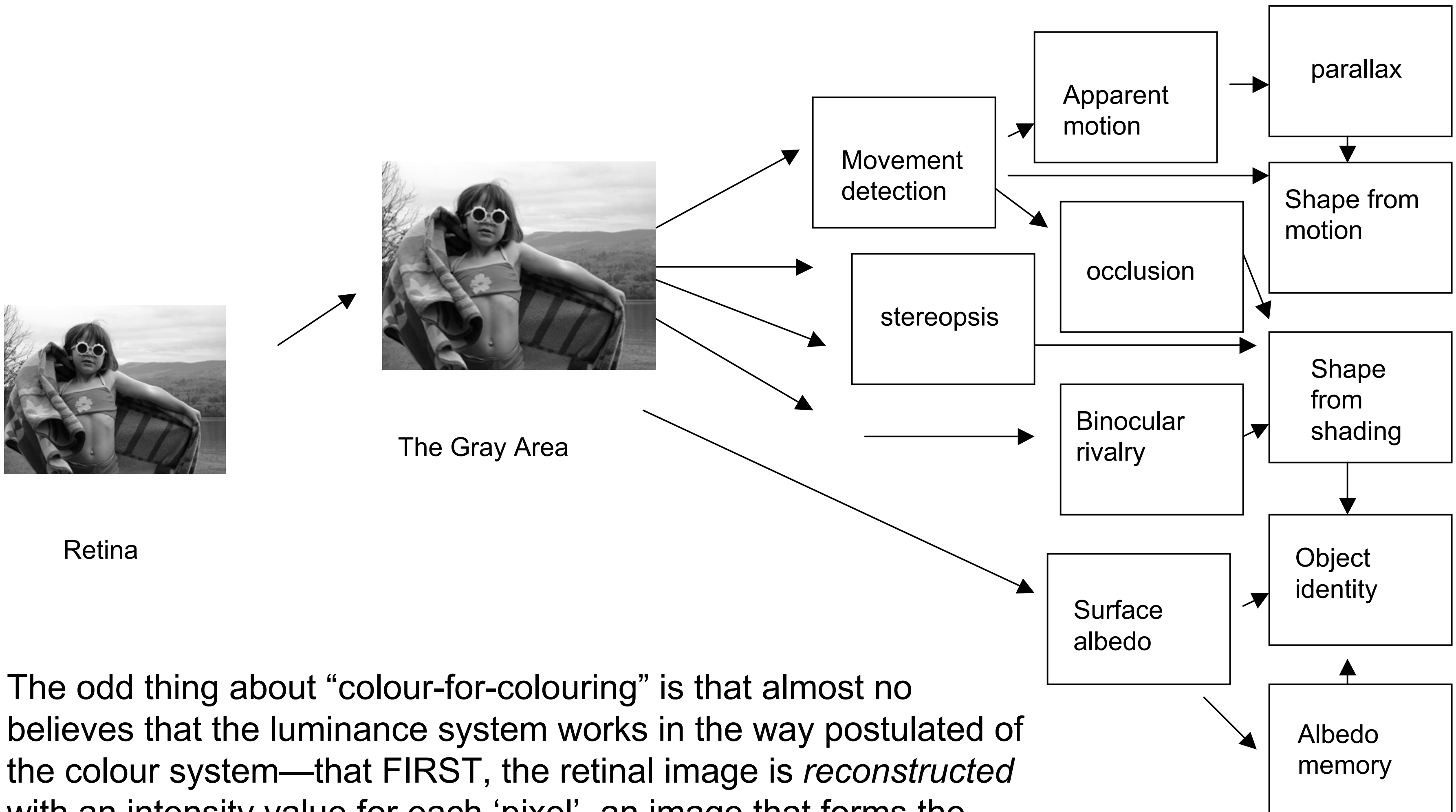


Consciousness and Colour-for-colouring



The odd thing about “colour-for-colouring” is that almost no believes that the luminance system works in the way postulated of the colour system—that FIRST, the retinal image is *reconstructed* with an intensity value for each ‘pixel’, an image that forms the basis of conscious luminance perception.

Where are we and why does it matter?

In our experiments, we mustn't expect colour phenomena to act like UNIFIED phenomena.

Rather, we always need to ask about **spectral contributions** to any visual phenomenon, and there different phenomena will have different kinds of spectral contributions.

When things go wrong—as in cerebral achromatopsia or "colour blindsight" or synaesthesia—the question is not: "Is colour present or is it not?"

There are multiple questions to be asked, about the sources and kinds of spectral information that may or may not be present/available.