Color Vision: A New Understanding

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By all accounts, the mystery of how the eye sees color is solved.

Yet, contradictions, puzzles, and enigmas about human color vision persist.

And how can there be no connection between form and function, cone structure and color perception?

Perhaps it is time to consider another approach to understanding color vision.

With the press of everyday affairs, it's quite natural to take our sense of color vision for granted. And yet, when we do stop and take the time to think about it, like we might when we see a particularly awesome sunset, it’s hard not to marvel at the richness and depth our color sense adds to the visual experience.

Philosophers, scientists, and laymen alike have all long wondered how color vision works. Many of the giants of scientific thinking, including Newton, Goethe, Young, Maxwell, Helmholtz, and many others have explored various aspects of vision and the

question of just how the eye sees colors and all have contributed in important ways to our understanding of the process.

Well, here we are in the Twenty-First Century - the age of supercomputers, molecular genetics, the Internet and space travel so by now we surely know the answer to just exactly how we see colors. Do we not?

What About Our Understanding of Color Vision?

The standard, near universally accepted, Young-Helmholtz trichromatic model explains color vision through the identification of three cone types which explains at a stroke the fundamental fact of trichromacy. Supporting this model, opsins (the protein portion of the photosensitive pigments) that are sensitive to different parts of the visible spectrum have been genetically isolated.

But there are a number of aspects of color vision about which the standard model says nothing, or indeed, says the wrong thing. Consider just ten such items:

1. The identified photopigments in the human eye do not correspond very well to the supposed primary colors, nor are there exactly three of them.

2. Co-expression – Multiple photopigments have been identified within the individual cones of many species with no apparent problem for color discrimination function. There have even been reports of such co-expression in the cones of the human retina.

3. Cones are universally conical in shape. There is an absolute dichotomy in shape between the rod photoreceptors that provide black and white night vision and the cone photoreceptors that provide color vision in day light. This dichotomy in structure has long been a total mystery and has never been tied to any functional difference in the two receptor types. In addition, true monochromats (black/white colorblind) have been found, on autopsy, to universally have abnormally shaped cones.

4. Well-ordered color sensations (subjective colors) are induced by time-modulated purely black and white patterns (e.g., Benham's Top). The correspondence between the color induced and the time coding is universally the same for all color normal observers.

5. Violet -- the shortest visible wavelength -- looks like purple; go past blue on the spectrum and at a certain point it's as if you have suddenly added a red color from the opposite end. The near identical appearance of violet and purple has long been a profound puzzle in terms of any model of color vision yet proposed. Attempts to explain the appearance of the red component at short wavelengths have all presumed the existence of a subsidiary, short wavelength absorption maximum of the "red" pigment sequestered in the "red" cones. In fact, no such

secondary short-wavelength maximum has been demonstrated for any known photopigment of vision.

6. Two varieties of color-blindness -- supposedly the absence of red or green (L and M) cones-- are quite common, but what would correspond to absence of the third type of cone (tritanopia) is incredibly rare. There has long been controversy over whether the common red-green deficit vision is a result of missing red or green cones or else due to the wrong pigment being substituted in a given cone type. Experimental evidence exists contradicting both explanations.

7. Color-blind subjects can (for brighter or larger patches of color) distinguish and correctly name red and green colors, even in cases where they demonstrably lack the genetic machinery for one of the red or green photopigments.

8. As predicted by the standard model, a pure yellow, say, can be matched by a mixture of red and green. Startlingly, the pure yellow and the matched mixture can be distinguished dynamically: a bar of mixed red and green light moved across the retina resolves into red and green leading and trailing edges,while a moving true yellow bar does not.

9. There is a linear relationship between the wavelength of light and its time of perception: red is seen faster than green, which is in turn seen faster than blue.

10. Eye movements are necessary for vision. When vision is fixed (stabilized), visual perception, especially color vision, is promptly lost.

All these facts are mysteries -- or even paradoxes -- under the Young-Helmholtz model. However, they are unproblematic (in some cases, required) for an alternative model of how color vision works, what is here called the Cone Spectrometer Model (CSM).

Consider the fact that the cones are just the right size to serve as effective waveguides (optical fibers) to carry light from any part of the visible spectrum. Optical waveguides transmit light along their length in discrete waveguide modes which essentially correspond to light propagating along the fiber by bouncing at specific angles of reflection with the fiber wall and surround interface. Now, for appropriately "sized" cones, due to the tapering which gives cones their name, successively deeper (narrower) parts of the cone can't carry light of longer wavelengths. Red light only fits into the wide end of the cones, and travels but a short distance before being "squeezed" out by mode cut off; green light gets deeper into the cone, and blue light can shine all the way to the bottom.

The accompanying photograph shows a highly-magnified view of this effect occurring in a small tapered glass fiber immersed in a liquid with a refractive index only slightly smaller than that of the fiber. Long wavelength light is seen to leak out first and progressively shorter wavelengths are excluded at successively smaller portions of the cone. Actually, it is evident that this happens more than once in the fiber. Near the top

where the initially white light is incident, the colors leaking out and visible along both "edges" of the first third of the glass fiber are first white, then rose-colored, then greenish to blue where the second-order mode is cutting off first. There is then a well-order red through blue dispersion of the spectrum along the last two-thirds of the photograph as the lowest-order fundamental waveguide mode cuts off along the smallest part of the taper.

Now light, of course, shines into the cones at the speed of light, but once a detection event happens, the resulting information travels much more slowly as a nerve impulse. The cones are, somewhat perversely, "wired backwards", so that the red-detecting, wide ends are effectively closer to the cone output at their synapse with the bipolar cells. Detection events at the deeper, blue end must propagate back up the length of the cone at this slow speed; as a result, detection of red light is signaled earlier than blue light (and in general, detection time will be proportional to how deep the detection happened). In other words, the taper cutting off different wavelengths at different depths corresponds to differences in timing (of light detection information reaching the brain).

Effectively, the shape of cones sorts wavelength information into a difference in timing; I propose that this is the essential mechanism of color vision.

In this context, what does the CSM model say about the ten problematical items mentioned above?

1. Identified photopigments. The proposed color detection mechanism is inherently indifferent to the details of any photopigments in the cones. Light only needs to be absorbed at a specific location along the cone and the photopigment(s) simply initiate the transduction of light into an electrical signal.

2. Co-expression: Multiple photopigments could actually enhance the operation of the proposed mechanism. While not necessary for its function, it would be more efficient to have long-wavelength absorbing photopigment in the broad entrance end of the cone and shorter wavelength absorbing pigment in the narrower, distal end of the cone.

3. Cones are universally conical in shape: The cone shape itself is the element providing the spread of colors along its length. Structural differences are thus intimately tied to functional differences between cones and rods. Absent the conical shape, the "cones" would not then be able to provide

color discrimination -- just as observed in true monochromats with abnormally shaped cones.

4. Subjective colors: The pattern of achromatic illumination in Benham's Top and the so-called pattern-induced flicker colors (PIFCs) mirrors the temporal order of the proposed mechanism.

5. Similarity of violet and purple: This apparent "closure of the color circle" is directly predicted by the CSM model as a consequence of second-order waveguide mode propagation. Sufficiently short wavelengths of light (violet) can excite both of the two lowest-order modes. The portion of violet light propagating in the higher-order mode will cut off like red light while the portion in the lowest-order mode cuts off more slowly like blue light so that violet will behave like a purple mixture of red and blue light.

6. Two common varieties of red-green color-blindness (protanopia and deuteranopia): the CSM model directly accounts for these in terms of mistuning of the basic mechanism whereby cones that are too small will be "red-blind" corresponding to the protanopic version of color deficit vision and cones that are too large will correspond to the "green-blind" deuteranopic version.

7. Residual color discrimination in "color-blind" subjects: lack of a red or green absorbing photopigment would not disable color function in the CSM model, although mistuned cones would certainly be less effective in color discrimination.

8. Dynamic breakdown of statically established color matches: While this is a critical issue with strong implications for the validity of the traditional Young-Helmholtz model (see below) it is directly in accord with the time-ordered color information of the CSM model.

9. Linear relationship between wavelength and its time of perception: This too is a direct consequence of the basic CSM mechanism.

10. Eye movements are necessary for vision: The microsaccadic eye movements are of just the right amplitude and frequency to provide the necessary synchronization signal to read the time-ordered color information established by the cone shape. On each movement of a color border across a cone, the change in cone output will be temporally correlated with the change in color across the border.

There is actually a good deal more the proposed model says about these and many other aspects of color vision. The following explores many of these aspects of the mysteries of human color vision at a more measured and systematic pace.

The Standard Three-Cone Model of Human Color Vision

Look through any text on vision or any article from the current literature on color vision and you will invariably see a statement very much like the following: Color vision is provided by the existence of three separate classes of cones; a red, a green, and a blue sensitive type.

This explanation, an obvious way to account for the apparent three-dimensional nature of human color vision, is repeated so often and so unequivocally that it is no longer questioned in any serious way. Its experimental support must surely be so solid and unimpeachable that no one should even think of questioning it. So that's it, end of story, right?

Well, perhaps not quite…

To make a bad pun of it, there is more to this than meets the eye. This classic model of color vision, first proposed in its essentially modern form by Thomas Young more than two hundred years ago, is presumed to work in a manner wherein each of three types of cones detects light with a probability determined by the absorption spectrum of the pigment it contains (Young, 1802). Thus, the cone containing the "red" absorbing pigment preferentially signals detection of the longer wavelengths of light. Of course, by itself, a signal from a 'red' cone does not actually say that red light was detected, only that a detection event occurred there and that the probability of that detection was proportional to the value of its pigment absorption spectrum, larger for a longer wavelength, red light.

Similarly, the other cone classes preferentially signal their detection of the other regions of the spectrum. The perception of color is then to be synthesized through the processing of the information from all the cone classes by inter-comparison of the relative responses of each cone type to a given source of light. So, for example, a set of outputs of about equal parts from the red and the green cone classes with little signal from the blue cones would be interpreted as an indication of the presence of yellow light.

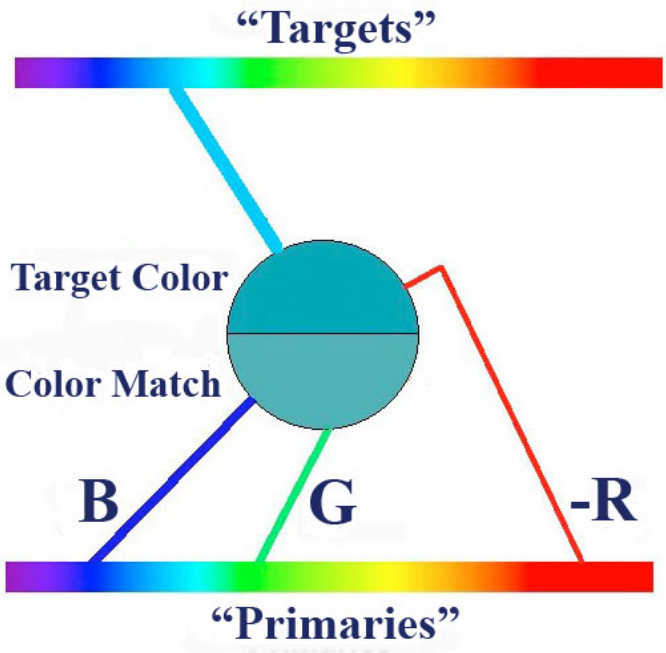
In the classic test for evaluating the appearance of patches of color with different spectral composition (metameric color matches), an observer is set the task of equating the appearance of two separately illuminated halves of a small field. One half is the arbitrarily illuminated target portion to be matched and the other half of the field is a superposition of the variously tuned intensities of the 'primaries' one tweaks to get the match. In practice, it is necessary to add one of the primaries to the target half for this to work. This is equivalent to using a negative value of the primary (adding to the target half is like subtracting from the primaries half).

Early researchers tried valiantly, without much success, to search for the three unique primaries in these matches that would correspond to the presumed three fundamental cone primaries of the eye. However, virtually any three primaries can work so long as

they satisfy a couple of basic conditions (roughly orthogonality and completeness): no combination of any two of them can be matched to the third and some combination of the relative intensities of the three primaries can produce white.

In any case, whether or not such unique primaries can be easily identified, the three dimensional nature of color matching still proves that there are three types of cones anyway. Right?

Well, not exactly…



Setting bipartite metameric matches. Here, a red "primary" is added to the target test patch to produce the match.

The Three-Cone Model is Experimentally Falsifiable

First of all, while color vision exhibits limited dimensionality, that in itself is not proof that the limitation comes about because there are distinct kinds of cones. It is a separate step to prove that one follows from the other. After all, you would have to rule out that the three dimensional nature of color vision is not caused by something else (and there is good evidence for just that, which we will elaborate on subsequently).

Most importantly, however, the premise that the three dimensional nature of color vision is imposed in the first step of the visual process by partitioning detection events among three kinds of cones is directly contradicted by experimental observation.

It was, in fact, shown to be false by Herbert E. Ives some ninety years ago (Ives, 1918). Despite the straightforward and unequivocal nature of his test, this experimental result has been all but forgotten and its message has been totally ignored by the experts in the field.

Consider, again, the basic premise of the three-cone model and how it works. The view is that each cone simply reports how much light it detects, its so-called 'quantum catch'. This (presumed) univariant response of the cone itself has no intrinsic information about the color of the light it caught. In this view, that spectral information is discarded in the

very first step of visual perception and is not retrievable by any subsequent manipulation of the cone output signals. It is only by comparing the relative output of each of the three cone classes that the color of the incident light is synthesized.

Look at a simple case of how this operates, in the perception of yellow, for example. We know that there is more than one way to make a yellow light. One could simply use a monochromatic yellow sliced from the visible spectrum at a wavelength of about 580 nm. One could also use a mixture of red and green light. By adjusting the ratio of red and green (essentially an equal amount of each for color normal observers), one can make a compound yellow that essentially matches the pure monochromatic yellow. This is simply a direct consequence of the limited dimensionality of color vision. These two yellows (a pure monochromatic yellow and an appropriate mixture of red and green) are simply a metameric match. In the three-cone model, any information that they were created in different ways is lost and is irretrievable. That information was discarded in the very first stage of the visual process and the two yellows look the same because they excite the 'red' and 'green' cones identically.

However, Ives' experiment shows that this is not true and the three-cone model is wrong. He did this by first superimposing a red and green bar of light so that it looked yellow. He then scanned this compound yellow light across the field of view of the observer. What he found was that as the compound yellow moved across the retina, color separation occurred so that the bar had a leading red edge, a yellow middle, and a green trailing edge.

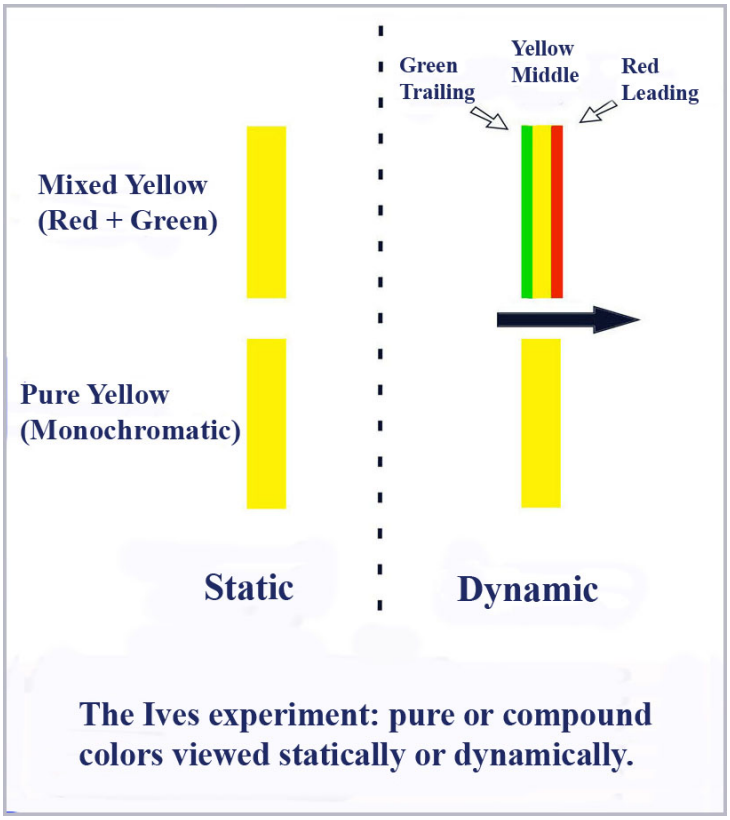
Well, ok, one might say, that simply means that the 'red' cones must have a faster response time than the 'green' cones and turn on first as the bar moves across the retina and stimulates the receptors while the slower 'green' cones turn off later than the 'red' cones as the bar passes by, leaving the yellow sensation in the middle. So far so good, although there is no obvious explanation about why 'red' cones and 'green' cones, which for all intents and purposes are otherwise identical except for the slight difference in the photopigments they contain, should have a different response time in any case. But, for the sake of argument, say that they do and the separation of the compound yellow is thus explained.

Now what happens if you try this with a pure, monochromatic yellow? In the standard three-cone model we have been discussing, the same thing must happen. Since it appears yellow because of the equal excitation of the red and green cones the way a mixed yellow does, it cannot be different. Right?

Wrong!

When a bar of pure yellow is moved across the retina, it does not separate into a red leading edge and a green trailing edge. Rather it retains the same yellow color throughout. In Ives' own words:

"*The next point taken up was the behavior of the pure yellow, adjusted to be a subjective match with the compound yellow, and arranged to exactly take its place between the red and green. It was at once apparent that pure yellow does not separate into red and green. This fact is strikingly shown by arranging the slit so as to be all compound yellow, except a small portion of pure yellow. When stationary the slit appears alike throughout its whole length in brightness, hue and definition. But upon moving the image sideways, or oscillating it, the compound yellow immediately broadens out and becomes ill-defined, the pure yellow remaining narrow and sharp*" (original emphasis).



The Ives experiment: pure or compound colors viewed statically or dynamically.

So this flat out says the standard three-cone model must be wrong. End of story? Well surely not you might say. After all this is only one experiment and it was done almost a hundred years ago. None of the experts have paid any attention to this result, so, did Ives get it wrong? Is it repeatable?

Verifying Ives' Result

I wondered that too. This result is so important and so unequivocal that it should be repeated and verified (or invalidated). Many times. My colleagues and I have repeated the experiment and we did indeed get the same result (and a good bit more actually).

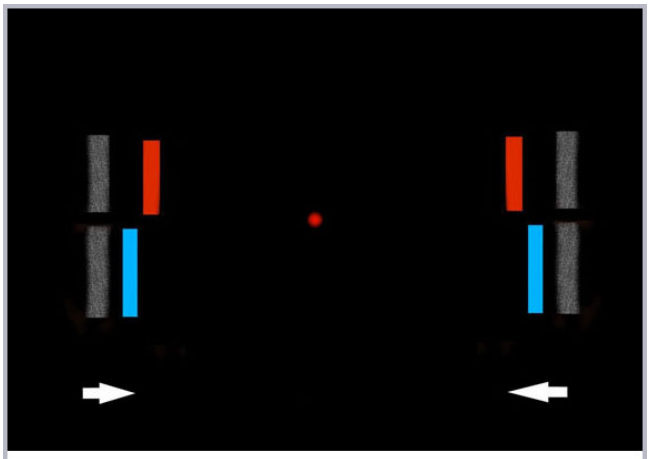
Several years ago, I assembled an apparatus consisting of multiple monochromators to provide bars of light of tunable color that could be optically combined through beam splitters and adjustable in position so that the bars could be separated or superimposed. This output was then directed into the eye after reflection from a scanning mirror. A critical condition that has to be provided for this to work is a fixation light. That is, it is necessary for an observer to be looking in one fixed direction so that the moving bar(s) of light will scan across the retina of the eye. It is also important to do this in a darkened room to make the phenomenon easier to see.

If one superimposes a red and a green light tuned to look uniformly yellow when stationary, then as the bar is moved and one looks straight ahead as the bar scans across the retina, you will indeed see – as we did- the compound yellow light to broaden out with a leading red fringe and a trailing green fringe. If you tune both outputs to be monochromatic yellow and repeat the scanning, you will find - again as we did – that it has no such color separation, verifying the Ives' result and falsifying the three-cone model of color vision.

When my colleagues and I did this experiment, we did find a good bit more than just the verification of Ives' result (Medeiros, Caudle, and Schildt 1982). Under carefully controlled conditions, we also observed a whitish, shimmering afterimage trailing behind the colored bar by an amount that depended on the speed of movement of the bar (and its color and intensity). Now afterimages are not a new thing and are, after all a common part of everyday experience. Indeed, an afterimage similar to the one we are talking about here has been known and studied for over a century. That afterimage effect goes by various names, including Bidwell's Ghost, Hamaker's Satellite, and the Pursuant Image. However, what we are discussing here is not this afterimage effect (with a time delay on the order of a few hundred milliseconds) but something entirely different with an order of magnitude shorter time constant, on the order of a few tens of milliseconds.

While the details can be found elsewhere (in the book, **Cone Shape and Color Vision: Unification of Structure and Perception**- Medeiros, 2006) we mention here that we conducted a series of experiments to demonstrate that this whitish shimmer was, in fact, the direct perception by the rods and not an afterimage as such.

We were thus able to separately and simultaneously observe the direct and separate perception by the cones (the colored bar) and the rods (the following shimmer). Since we were able to experimentally demonstrate that the delay of the rod perception itself was totally independent of the wavelength of the inducing light, we could use it as a reference to time how much shorter the latency of perception was for each color by the cones. What we found was a monotonically increasing delay in the perception of color as wavelength is decreased. This, in fact, is what accounts for the separation of red and green perception.



Appearance of moving bars of light. Red or blue bars moving right or left. Rod shimmer trails cone color response.

Now, the effort to measure the chromatic latency of human color perception has enjoyed a long, tortured and controversial history. For example, Uttal (1973) tabulates a list of eighteen separate

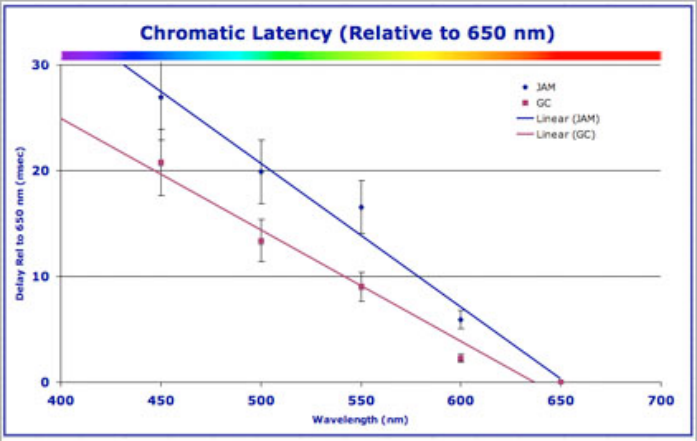
reports on attempts to measure chromatic latency by a number of different techniques. In that list, eight studies reported no variation in chromatic latency as a function of wavelength, four reported a longer time constant for longer wavelengths, and six reported a shorter time constant for longer wavelengths. This muddled result is a reflection of the difficulty in measuring the small time differences involved (only a few tens of milliseconds) by various reaction time techniques or of separating the effects of phase differences and true time constant differences in the various approaches employing flicker minimization by alternating colors. Moreover, given that the intensity of a given color can also affect its apparent delay time, it can be difficult to separate intensity effects from purely chromatic effects in these measurements.

In our studies using the wavelength-independent rod response as a reference, we were able to conduct latency measurements of each color with a resolution on the order of two milliseconds. We also conducted the latency measurements at near threshold intensities for each color to minimize the intensity dependence of the effect. Our measurements were repeated numerous times, on a number of different days for two color normal male observers.

We did not find three separate groups of delay times, but rather that the latency was a direct linear function of decreasing wavelength. While it was not possible to measure the absolute time delay of the color perception, we were able to measure the time delay of a given color perception relative to that of another color percept. Our experimental results for the time delay (in milliseconds) can be expressed for any wavelength, λ (in nanometers) relative to the perceptual delay of a 650 nm red light to be approximately:

Delay (msec) = 97.5 - 0.15 λ (nm).

This gives a delay of 0 msec for red light of 650 nm (relative to itself) as it should and a delay of 30 msec for the shortest wavelength of light we tested, 450 nm in the blue.



Chromatic latency measurments for two observers. Error bars (± 1 std. dev) are essentially a measure of repeatability of the trials. Each data point represents multiple measurements on a given day over a number of different days.

Our data for two color-normal male observers is shown in the accompanying plot. While the two observers had latency values that were slightly different, both exhibited essentially monotonically increasing delay for shorter wavelength.

So all this begs the question, just how does human color vision work? What might this time delay have to do with it and how could it even come about? But wait, surely we can't be done with the three-cone model, after all there is direct evidence that different photopigments are present and this must mean that the three cone classes have been proven to exist, right?

Well, again, not exactly…

Multiple Pigments

What has been proven is that there are multiple cone pigments. In fact, more than three. However, the existence of multiple pigments is a separate issue from multiple cone types. In the currently accepted model of color vision there must be exactly three cone classes, each containing its own unique photopigment. The fact is, this has not been proven. The literature generally focuses on three of these pigments as if they are uniquely sequestered in the three cone types. These three pigments are maximally absorbing at around 560, 530, and 450 nm and are usually referred to as the L (long), M (middle), and S (short) wavelength pigments (see the figure below). They are so-named since what should be the red pigment is in fact in the greenish-yellow part of the spectrum. Moreover, their maximum sensitivities are rather poorly distributed for three-dimensional color vision spanning the spectrum to which the eye is sensitive.

While it has been relatively easy to extract and characterize the rhodopsin photopigment of the rods, it has proven to be very difficult (i.e., impossible) to directly find the cone pigments in ***the primate retina by actual extraction***. Their best identification has been through the use of a number of indirect techniques including molecular genetics, microspectrophotometry, and reflection densitometry. We examine here what has been determined by each of these methods.

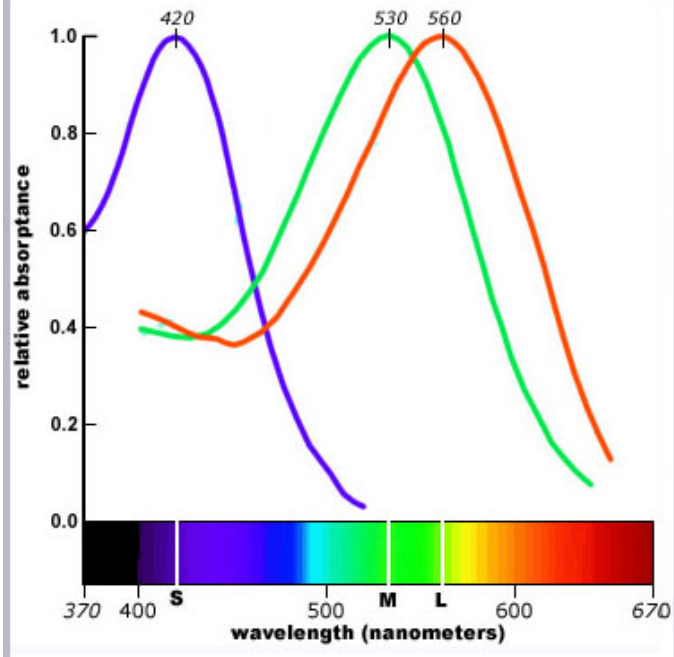
Perhaps the best approach to identify the cone photopigments is by identification of the DNA machinery that codes for the protein opsin portion of the pigments (Nathans, et al, 1986). This has worked well, but perhaps too well since this line of research has found an entire array of pigments with absorption spectra that have peaks spanning the red-green range (c.f. Neitz & Neitz, 1995). In any event, the results from the molecular genetics work only shows that the machinery exists to make multiple pigments. It does not prove there are multiple cone types. Multiple pigments could, after all, be used to augment some entirely different way to provide color discrimination in the human eye.

So, if molecular genetics can't exactly tell us about cone classes, what about the results from microspectrophotometry (MSP) on the retina (Marks, et al, 1964; Brown & Wald, 1964; Bowmaker, et al, 1980)? In MSP, one shines a small spot of light on an excised (dead) piece of retinal tissue, ideally a single cone, and measures the light transmitted as a function of the illuminating wavelength. The retinal tissue is then bleached by a high-intensity light and the spectral scan is then repeated on the bleached receptors.

The difference in transmitted light before and after the bleach is interpreted as the absorption spectrum of the photopigment in the cone.

There were suggestions in the early MSP measurements that both red and green absorbing pigments are present within the same cone (c.f., Marks, Dobelle, and MacNichol, 1964). Many other lines of evidence also suggest this pigment co-expression (Jacobs, et al, 2004; Lukáts, et al, 2002; Lukáts, et al, 2005; Parry & Bowmaker, 2002; Röhlich, et al, 1994; Williams, et al; 2005). If there is more than one pigment within the cone, the light transmitted depends critically on illumination conditions, pigment densities and distributions. It also depends importantly on the waveguide characteristics of the cones and how light is coupled into the cone structure.

It is well known that these MSP measurement are notoriously difficult to do. In the earliest attempts to measure cone photopigments through MSP where success was reported (Marks, et al, 1964; Brown & Wald, 1964) the probe beam was directed axially through the photoreceptors in order to maximize the path length through the pigment. These measurement efforts suffered some severe problems. One critical difficulty was the high levels of light scattering through the retinal tissue as a result of postmortem changes. An additional problem was the mismatch between the numerical aperture of the microscope optics employed and the acceptance angle of the cone waveguide structures they were probing. Liebman (1972) reviewed these measurements and commented: "***Unfortunately, almost none of the original data has ever been shown in reports on primate pigments, and no mention has been made of the unacceptable experimental conditions that have been tolerated***." Further, in regard to the peak spectral sensitivities and optical densities reported he concluded: "***... the MSP data alone can not be regarded as accurate to better than 20 to 30 nm, and published densities can not be regarded as indicative in the least of what exists in the living eye.***"



Absorption curves for the three accepted cone pigments. Note that the "red" pigment absorption maximum is in the greenish yellow.

In order to circumvent the limitations inherent in probing the cones longitudinally, MSP measurements have also been conducted by transverse probe beams on cones teased from excised retina (Bowmaker, et al, 1978: Bowmaker, et al, 1980). While this technique avoids some of the difficulties inherent in longitudinal probing, it does suffer the problems of both

very short path length through the cones and that only one measurement per cone is possible. That is, the technique must necessarily measure the transmission of a light beam before and after a strong bleaching light clears out all the photopigment in a (dead) cone. There is no chance to get repeat measurements and determine if there are perhaps more pigments present in any one cone. If there is more than one photopigment in a cone, there will then be no opportunity to determine how they might be distributed.

Despite these difficulties, there is a general concurrence in the field that the results from MSP measurements and the molecular pigment genetics point to the existence of the three cone photopigments as displayed in the plot above. Recall, however, there remains substantial uncertainty about exclusive occupancy in a given cone with a given photopigment. In addition, evidence from both MSP and pigment genetics point to the existence of a range of photopigments in the 520 to 565 nm range (not just the two usually plotted).

If both pigment genetics and MSP leave uncertainty about the cone photopigments and their distribution, what about approaches using retinal reflection densitometry? Retinal reflection densitometry has the great advantage of being conducted on the living eye under normal physiological conditions. Light is sent through ophthalmic optics and is incident on the cones in the retina from their wider entrance end. Any reflections that return the signal back from the cones to the experimenter are due to coupling to the backwards modes of the cone waveguide structure. The test light probes the cones along a linear axis from the wide end in. Most of the reflection will doubtless occur from this wider, proximal portion of the cones. None-the-less, to some extent the entire length of the cone photosensitive portion can be sampled. But again, is there only one pigment in the cone and if multiple pigments are present, how are they distributed?

Early attempts to characterize cone photopigments by this technique (Ripps and Weale, 1964; Rushton, 1964) suffered from serious signal-to-noise limitations and necessarily had to probe rather large areas of the retina involving many photoreceptors at a time. The technique did provide data on photopigment kinetics (pigment regeneration rates) but were ill-suited to probe individual cones.

The limitation of probe-beam size on the retina was dramatically circumvented in recent years by the techniques developed by the Center for Visual Science group at the University of Rochester. They employed wavefront correction in an adaptive optics technique to illuminate a spot smaller than a single cone in the living eye (Roorda & Williams, 1999). While this approach substantially improves the signal-to-noise problem and also assures the experimenter of probing but a single cone, it still suffers the same limitations mentioned above for any axial probe of the retinal cones. That is, such probing of resident photopigments can not be divorced from waveguide coupling effects and are likely to preferentially probe the proximal regions of the cones. What has been found by this technique is a high preponderance of what appears to be red cone types, fewer green and very few blue. This is perhaps, just what might be expected for

probing into a tapered cone waveguide from its wide end where there might (or might not) be a differential distribution of pigment.

Not so incidentally, using a version of this technique, the University of Rochester group also probed the *actual sensation* elicited from single cones as reported by their subjects. Now, in any three-cone model, illuminating any one cone must produce the sensation of red or green or blue (depending on which cone "type" was stimulated) regardless of the color of the illuminating light. Instead, they (Hofer, Singer, and Williams, 2005) found that **the stimulation of any one cone could elicit any color sensation, even that of white!** These kind of observations make no sense whatsoever in terms of the standard three-cone model of human color vision.

Ok, so even if the 'evidence' for three cone classes is equivocal and operation on that basis is directly contradicted by dynamic measurements such as the Ives' result, the model must be a good one since it explains how color vision works anyway, right?

Well, not exactly.

What Does a Color Vision Model Have to Explain?

Actually the three-cone model explains well almost nothing about how color vision works. Explanations of color vision phenomena in terms of the three-cone model tend to be rather contrived and involve assumptions about the existence of improbably large pigment densities, or non-linear processes occurring in the cones or their subsequent processing circuitry in the retina or the brain. A short list of what it does it not explain very well would include the following:

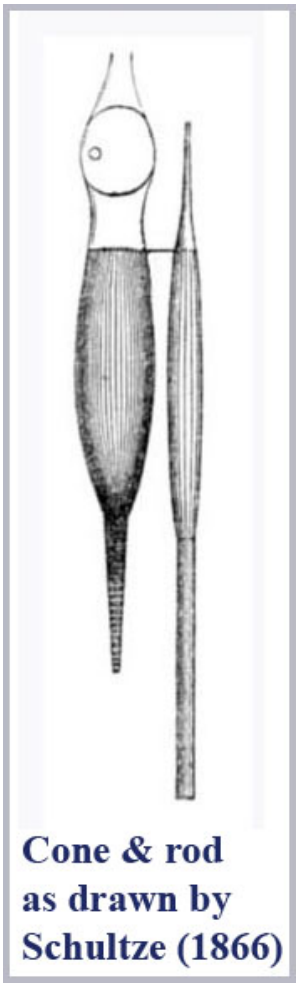
- The exact shape and details of the color (hue) discrimination curve
- The colorimetric purity (saturation) function
- Color defective vision in which the common forms of (red-green) color blindness are poorly explained by either the missing-cone type explanation or the substituted wrong pigment approach and where, even in dichromats with only one X-chromosome opsin, consistent color-names are used for the correct colors in otherwise "color-blind" subjects. Underscoring this problem (for the three-cone models of vision) is the careful work of Crognale, et. al. (1998) who examined dichromatic subjects that had only a single X-linked pigment gene but who could none-the-less make chromatic discriminations by Rayleigh matching (a standard technique to test red-green vision). After ruling out involvement by other possible receptors (rods or other types of cones) they concluded: "***The mechanism of chromatic discrimination in the presence of a single photopigment therefore remains unknown***."
- Subjective colors, where colors are seen by all observers in a consistent and universal way with intermittent black and white illumination, as in the Benham's Top phenomenon
- The Stiles-Crawford Effect of the second kind (SC-II), the change in the apparent color of a light with its direction of incidence on the retina (Stiles, 1937; Enoch and

Stiles 1963). The change is predominantly a red shift. Within the context of the three-cone model, attempts have been made to explain the effect in terms of "pigment self-screening" (Walraven & Bouman, 1960) without notable success (Fuld, Wooten & Katz 1979; Alpern, 1986).

- The similar appearance of short-wavelength violet light and of purple, a mixture of red and blue
- That color vision function is only three dimensional to a first-order approximation. There is ample evidence that human color vision is substantially better than an absolute partitioning into only three dimensions at the first stage of detection would suggest. For example, Nascimento, Foster, and Amano (2005) conducted a principal component analysis of the psychophysical perception of natural scenes and stated as a result that: "***The combination of the spectral diversity of the natural world and the observed levels of color discrimination suggest that estimates of the minimum number of basis functions necessary to reproduce natural scenes may need to be revised upward.***" They concluded, in fact, that the "... ***original images were visually indistinguishable from their approximations only if there were at least eight basis functions***."
- That any one cone can report any color, including white (see above)
- And most importantly – the cone shape!

So, is that it? Are we left with nothing, with no idea about how human color vision works?

Well, no. The key is the cone shape.


Cone & rod as drawn by Schultze (1866)

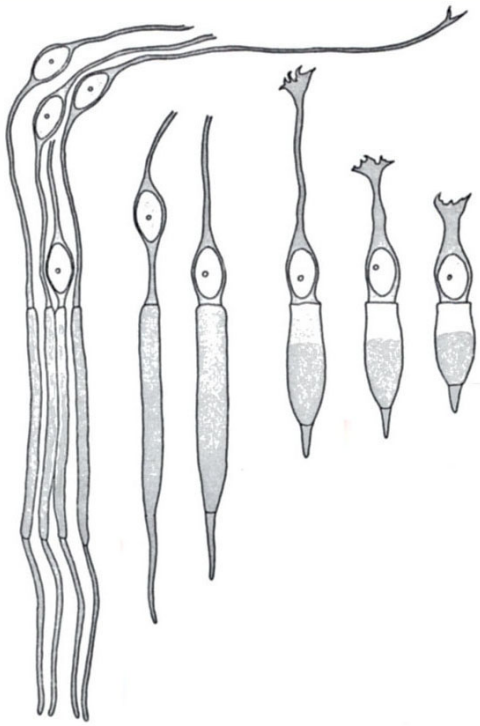
What About the Cone Shape?

The achromatic receptors of night vision (scotopic vision) are the rods, so-named because of their shape. The color vision receptors of daylight vision (photopic vision) are the cones, also so-named because of their shape. The duplicity theory of the eye in terms of the operation of these two receptor types has been known for a long time, but there has never been any explanation for the universal dichotomy of receptor structure. That dichotomy is apparent in the classic rod and cone drawing by Schultze (1866) who first clearly articulated the duplicity theory of retinal receptors.

Surely nature didn't build the two receptor types with different shapes just so researchers could tell them apart!

It is also notable that the cone shape is not identical throughout the human retina. The photosensitive outer segment portion of the cones varies systematically from being long and gently

tapering in the central (foveal) part of the retina to being shorter and squatter (more obviously tapering) in the peripheral portions of the retina (von Greef's drawings of the cone morphology over various regions of the retina are shown at the right).

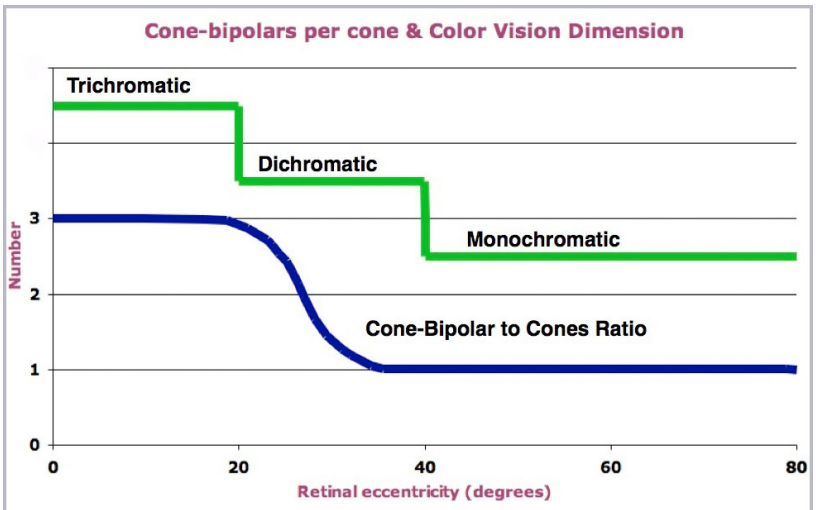


Cone shapes across the retina as drawn by von Greef (1900). Central (foveal) cones on the left, more peripheral cones towards the right.

Coincidently, the color vision function provided by the cones also varies systematically from the center to the peripheral portions of the retina. Color vision has the best resolution (three-dimensional or trichromatic) where the cones are long and gently tapering, decreases in resolution (to be essentially two-dimensional or dichromatic) in intermediate areas of the retina, and decreases further to its lowest resolution (essentially one-dimensional or monochromatic) in the far periphery of the retina (although color vision function is not totally lost for sufficiently bright or large patches of color).

So, why is there a systematic shape change of the cones across the retina and why is it apparently correlated with color vision function? Is this just coincidental?

The signals generated by the retinal cones are relayed through the bipolar cells with which they make synaptic contact. (The bipolars in turn contact the ganglion cells which relay the visual information on to the brain.) Cell counting studies (Missotten, 1974; Vilter, 1949; c.f. Sheppard, 1968) have shown that the number of bipolars per cone is correlated with the dimensionality of the color vision provided in each area of the retina. That is, there are three bipolars for each cone where color vision is trichromatic in the center of the retina, two bipolars per

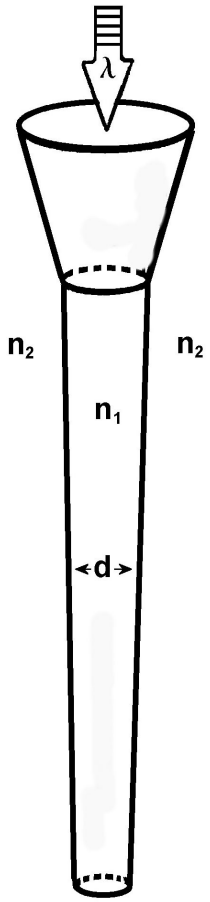


Plot of cone-bipolar to cones ratio as a function of retinal eccentricity (fovea is zero degrees eccentricity). Plotted in green is the approximate dimensionality of color vision across the retina as derived from typical perimeter plots.

cone in the intermediate areas where color vision is dichromatic and but one bipolar per cone where color vision is monochromatic in the retinal periphery (see the figure above). Is this too a coincidence?

In any case, besides having a conical shape, the color receptors are small, with the diameter of their photosensitive outer segments barely larger than the wavelength of light itself. That the photosensitive portion of the cones are so much smaller than the minimum resolvable spot of light focused on the retina by the eye's optics and that they are tapered make no sense in the standard three-cone model of color vision. However, these two bits of information are critical jumping off points to describe the physics of what is happening to light in these receptors and perhaps a new understanding of human color vision.

If one tries to model how light propagates within the cones, one finds that you have to employ waveguide mode physics computations. The details of this computation may be complicated, but the physical processes that are going on are not.



Cone waveguide geometry: light is incident from the wide end and the refractive indices inside and outside the cone of variable diameter , d, are indicated.

The Cone Spectrometer Model (CSM)

Just as in an investigation of a crime scene where one tries to determine who has the means, the motive, and the opportunity to commit a crime, we could apply this approach to the investigation a new model of color vision and see if it is a plausible or provable candidate. Starting with opportunity – can the model work, is it physically possible? Turning next to means, how could it be implemented in a workable model of the process in terms of the physical, chemical, and biological components present in the eye? Finally, examine the motive, what is such a model good for and does it explain the facts of color vision better than some other theory?

While fitting this examination of a proposed color vision model within the context of crime scene investigation is a bit of a stretch, it can still be rather useful approach to putting the pieces together to try to better understand human color vision.

First the opportunity; what is the model and is it physically possible?

The Opportunity

To begin with, we should take note of the fact that the understanding that the photoreceptors are optical waveguides is well established. The receptors have a higher index of refraction than the medium in which they are immersed so that the conditions for light guiding within the rods and cones exist. The particular values of the refractive indices of the receptors and their surrounding medium, the exact dimensions of the receptors, and the launch conditions for light entering the receptors will all influence just what waveguide modes are propagating within them.

Low-order waveguide modes propagating in the receptors have been directly observed in microscopic examination of excised retina (Enoch, 1960, 1961, 1963). It is widely accepted that the explanation for the Stiles-Crawford Effect of the First Kind (SC-I) whereby light incident off-axis on the receptors excites them less efficiently than on-axis light, is a consequence of waveguide behavior (Snyder & Pask, 1973). However, despite the evident existence of waveguide mode propagation within the retinal receptors, there has been widespread resistance among vision scientists to the consideration of any possible role for waveguide effects in basic receptor function.

Part of this resistance is because of the mathematical complexity of computing the details of waveguide mode propagation. However, the physical explanation of what happens in a small, tapered fiber (a cone) is relatively straightforward.

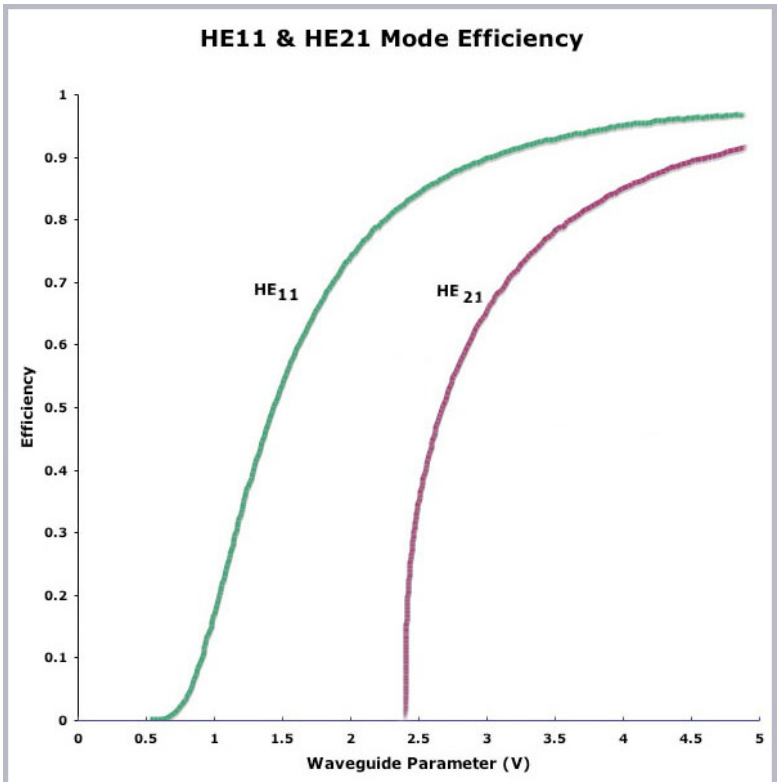
First, what are these waveguide modes? Essentially, each waveguide mode is light propagating within a fiber at a specific angle to the fiber axis. When the fiber is large (as scaled by the wavelength of the light being propagated) many modes (propagation angles) are allowed and the fiber acts as a simple conduit piping light along its length through total internal reflection at the fiber-surround interface.

However, as the fiber decreases in size, the number of modes or propagation angles that “fit” within the fiber decreases due to the wave nature of light itself (essentially wave interference effects). As conditions become more restrictive, the various modes are said to be cutoff. Computed mode cutoff curves are shown below for the two lowest-order modes (the so-called HE_{21} and HE_{11} modes). These curves plot the efficiency of an optical fiber, defined as the ratio of light propagated within the fiber to that propagating outside the fiber in its so-called evanescent wave, as a function of waveguide “size”. As the efficiency drops to zero, light is no longer confined to the fiber and it then radiates away. The measure of waveguide “size” against which this efficiency is plotted is the dimensionless waveguide parameter, V. This parameter is defined to be

$$V = (\pi d/\lambda)(n_1^2 - n_2^2)^{1/2}$$

where d is the diameter of the waveguide, λ is the wavelength of light (in the same units as d) and n_1 and n_2 are the refractive indices of the material inside and outside the guide, respectively (π is just the usual constant circumference to diameter ratio of the circle).

So this measure of waveguide "size" becomes smaller as either the physical diameter of the guide becomes smaller or the wavelength of the light is larger. The waveguide size also decreases for smaller differences in refractive index between inside and outside the guide. Referring then to the cutoff curve of the HE_{21} mode in the figure, we see that the mode is abruptly cutoff (its efficiency drops to zero) for a value of the waveguide parameter of about two and a half (actually at V = 2.405…, a value related to the zeros of a Bessel function which is mathematically used to describe the waveguide propagation conditions). This relatively abrupt cut off of the HE_{21} mode is typical of all the higher-order modes of the waveguide (not shown in the figure).



Plot of the two lowest order modes of the dielectric waveguide. For a cone with waveguide parameter values in the range of this plot, successively more severe mode cutoff is encountered with decreasing diameter.

Now, at even smaller values of V, below this value of 2.405, only one mode can propagate, the lowest order, so-called fundamental or HE_{11} mode. This mode too drops in efficiency for even smaller values of V although not quite so abruptly as all the other, higher order modes. Note, though, that the efficiency of this mode is essentially zero by a value of V of about 0.6 so that below this value virtually no light is propagated within the fiber (it is all outside of the fiber in its evanescent surface wave).

So what would all this mean in terms of discriminating color? Consider that cutoff, the shunting of light from the inside to the outside of the fiber, becomes more pronounced as the fiber diameter decreases. So, for the right conditions, as light enters a cone from its broad (base or proximal) end and propagates down the cone towards its narrower (tip or distal) end, as it does in the retinal cones, light will be progressively shunted out of the interior of the cone. This effect will be differential with wavelength since the cone

is effectively “smaller” for larger wavelengths. Thus, for a full spectrum of white light entering the base end of a properly sized cone, long wavelength red light will be shunted out first, with progressively shorter wavelengths being shunted out as the cone diameter decreases along the propagation direction. That is, the cone shape itself will produce a spectral dispersion of the incoming light along the length of the cone. Such a cone is essentially a miniature spectrometer. Detect the length-dependent distribution of light along the cone and you can discriminate colors.

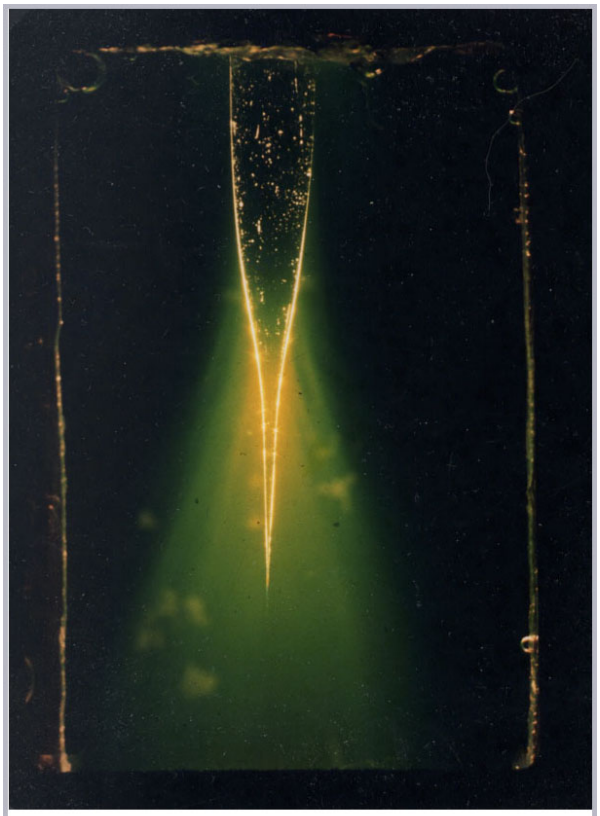
Now there are separate questions about whether it is possible to detect this spectral information in a way that is consistent with the physics and physiology of the retina and if the quantity and quality of the color information you could get this way is consistent with what is known about color vision. We will show that the short answers to these questions are “yes” and “yes”, however we would be getting ahead of ourselves since we are still discussing the “opportunity” of this model, is it a possible one?

Here, I have simply made a physical argument about how this spectroscopic effect would work. More details about the mathematical description and the theoretical underpinnings of this effect can be found in the book, **Cone Shape and Color Vision: Unification of Structure and Perception**.

We would like to confine ourselves here to the big picture and how it fits in within the lines of evidence. So, given this general description of the process, is it a physically realizable one and if it is, could it be present in the cones of the human retina?

While the prediction of the effect follows directly from the basic physical and mathematical description of waveguide propagation (although, astonishingly, this spectroscopic effect has not been mentioned, discussed or predicted anywhere else that I am aware of) what about a physical demonstration of the effect? If you send light down a fiber of decreasing diameter can this effect be seen?

To explore this effect, I heated a quartz rod near its middle with an acetylene torch and allowed gravity to pull down on the lower half to produce gently tapering ends on two rod halves as it was stretched apart. I then immersed one of these tapered fibers halves in a liquid with the refractive index adjusted to be only very slightly less than



Tapered quartz rod in viewing cell showing overall geometry.

that of the tapered rod. Then, illuminating the rod top (entrance end) with a focused beam of white light, I took microphotographs of the light leaking out of the rod near the very small tapered tip.

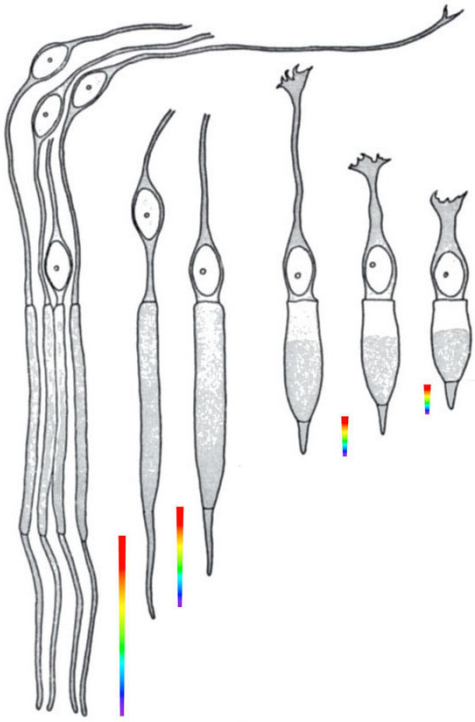
The figures show the result. As predicted, light is spectrally dispersed by mode cutoff at the tapered end of the fiber. Two photographs are shown. The first is an overall perspective view showing the setup with a tapered rod in the cell containing the index matching liquid. White light is focused into the top of this rod and large light losses are evident through the tapered portion of the rod. The yellow-greenish cast of these light losses are due to the fluorescence of the disodium fluorescein dye dissolved in the medium surrounding the rod which was used to help visualize the radiative losses from the tapered rod. Near the very tip of this tapered rod, one can barely make out some color differentiation along the rod wall.

Close-up of tapered fiber tip showing light excluded by mode cutoff.

The second photograph is a highly magnified view taken with close-up optics of the very end tip of this tapered rod. Evident here is the spectral dispersion due to mode cutoff along the outside of the fiber with the longer wavelengths being excluded first. The shortest wavelength light is the last to be seen along the wall of the tapered fiber until there is nothing left within the cone structure. If one looks carefully, it is also evident that there are two mode cutoffs occurring. In the taper near the top in this micrograph, the evanescent wave is first reddish, then passing through to a pale blue before the last mode cutoff occurs showing the entire progression of spectral colors. Notice that the first mode sequence to cutoff here (presumably due to HE_{21}) occurs over a shorter distance than the final sequence due to HE_{11} cutoff. This is in accord with the expected more abrupt cutoff of the second-order mode as compared to the lowest-order fundamental mode.

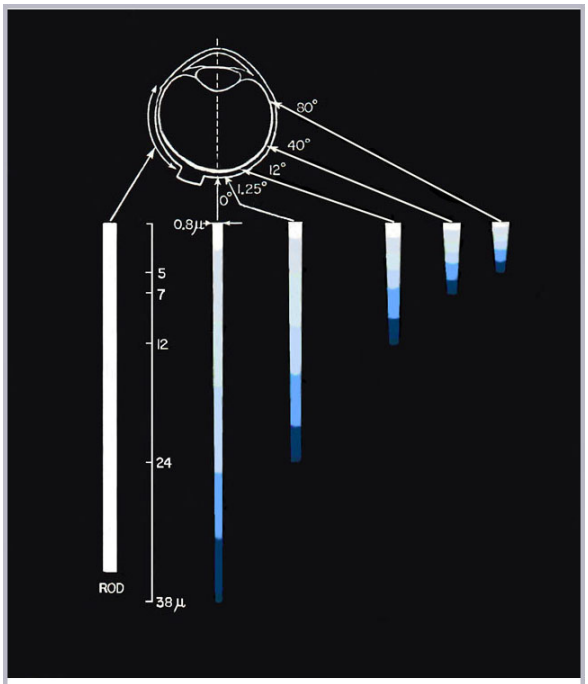
So, the effect is possible in principle and is physically realizable. Is it present in the human cones? Absent direct observation (which would be exceedingly difficult to do for the very fragile and delicate living retinal tissue where high magnification is required) one needs to know the actual values of the cone diameters (relatively easy) and the values of the refractive indices inside and outside the cones (very difficult).

The dimensions of the cone outer segments can only be determined on dead tissue where one has to fix and preserve the delicate retinal material with necessarily somewhat uncertain consequences on its exact form and dimensions. This has been done by many observers under various protocols for both human retinal samples as well as that of various, closely related primate species. There is some variability from observer to observer on the cone dimensions reported although there is a general concurrence that the photosensitive outer segment portion of the central (foveal) cones of the retina has a maximum diameter of about 1 μm (about two times the diameter of the wavelength of visible light). Significantly, there is, as well, a pronounced systematic progression of retinal cone shape from the central (foveal) region to the peripheral portion of the retina.



Cone shapes across the retina again with spectral dispersion of light excluded from outer segments indicated.

The best "big picture" of these dimensions is probably provided by the drawings of von Greef reproduced above and again here with the spectral dispersion of light excluded from the cones outer segments indicated. A schematic based on those and similar measurements is also shown below indicating the appropriate location in the retina of the progression of cone shape (note that the rods have the same shape throughout the retina). There is an evident systematic change in the cones from being long and gently tapering in the fovea to being shorter and more abruptly tapering in the periphery. In this schematic, I have colored the cones with a representation of the light remaining in the cone along its length for white light initially incident. Since longer wavelengths are excluded from the cone outer segments first, the light remaining in the cones is progressively bluer towards its distal tip until only the shortest wavelengths remain at the furthest end.



Schematic of rod and cone o.s. shapes across the retina (based on von Greef's drawing) with light remaining inside after mode cutoff indicated.

Not so incidentally, the foveal cones, because of their very slight tapering, have often been called rod-like in the literature. Because they

also provide the highest resolution color vision, this has led to the tendency by researchers in the field to discount the cone shape in any aspect of its functioning. However, these foveal cones are tapered and the spread of the taper over their long length results in the spread of color dispersion over a greater length. This has the result that these foveal cones will have the potential to be read with the greatest accuracy (for the same resolution of any read-out mechanism).

To explicitly evaluate the tapering of the foveal cones, my colleagues and I conducted anatomical measurements on (monkey) foveal cones where the retina was sectioned transverse to the axis of the photoreceptors (Borwein, Borwein, Medeiros, and McGowan, 1980). Diameters of successive slices along the cone outer segment length were measured at their smallest dimension (non-perpendicular slices would give an elliptical shape with the ellipse minor axis being the cone's true diameter at the sectioned position). While this anatomical study (and others, of course) revealed a wealth of structural detail present in the photoreceptors, the net result of these measurements is that foveal cones are somewhat less than 1.0 μm (1000 nm) in diameter at the beginning of the photosensitive outer segment and taper to about 0.6 μm near their tip. Over the roughly 40 μm lengths of the outer segments, this gives a full cone taper angle of just over half a degree. This indeed is barely different in appearance from a true rod, but the 40% diameter change over the length of the cone can produce substantial dispersion of the spectrum if the refractive indices are properly tuned (note that the difference in wavelength between 650 nm red light and 450 nm blue light is just over 30%).

There are very few measurements of receptor refractive index. Perhaps the best are still that of Sidman (1957) who used a fluid index matching technique to get a value of 1.387 for the cone outer segments. The refractive index of the medium surrounding the living receptors has not been directly measured although it has been estimated by Barer (1957). The index of this medium cannot be less than that of saline (1.334) and must be somewhat larger because of the inclusion of suspended solids in the medium. Barer suggested a value close to that of serum, 1.347.

So, using these values of refractive index for the cones gives their dimensionless waveguide parameter, V, to be:

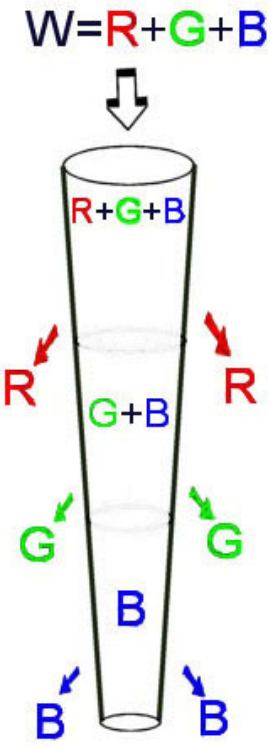
$$V= (\pi d/\lambda)\ (n_1^2 - n_2^2)^{1/2} = 3.14\ (d/\lambda)(1.387^2 - 1.347^2)^{1/2} = 1.04\ (d/\lambda),$$

or to a good approximation, just the cone diameter divided by the wavelength of light (d//λ). Thus the range (maximum to minimum) of V values in the foveal cones for the spectral range (450-650 nm) will span that of the largest diameter divided by the shortest wavelength (~ 1000 nm/450 nm = 2.22) to that of the smallest diameter divided by the longest wavelength (~ 600 nm/ 650 nm = 0.92). Notice that this places the operating range of the foveal cones right in the middle of the cutoff region of the HE_{11} efficiency curve (2.4 to 0.6), ideal for spreading the spectrum along the length of the cone.

So it all fits and the opportunity is there. Now what about the means? How could this Cone Spectrometer Model be implemented in a workable way to provide the color information in terms of the physical, chemical, and biological components present in the eye? For that we turn to the means.

The Means

So far, we have seen that this cone spectrometer effect is theoretically possible, it can be physically demonstrated in appropriately dimensioned tapered fibers, low-order waveguide modes have been directly observed in retinal tissue, and the retinal cones are ideally dimensioned to exhibit the effect. So the spectral dispersion described here is surely present in the retinal cones. The overall scheme for how incident white light will be dispersed in an appropriately tuned cone is shown in the cartoon illustration below.



Schematic illustration of spectral dispersion in a "properly sized" cone. For initially white light incident at the broad entrance end, the longest wavelengths are shunted out of the cone first, leaving it filled with progressively shorter wavelengths.

Continuing to push the crime scene evidence analogy, the trick is now to determine the means or method by which the length encoded color information is deciphered. Absent any direct connection to (say) three different portions of the cone along its length (for which there is no evidence) a good alternative is to convert the length code into a time dispersion encoding. We already know that there is temporal dispersion in color information, with, for example, blue (450 nm) light perception delayed by about 30 msec from that of red (650 nm) light. This value came from our measurements on moving bars of colored lights discussed previously, so converting to a time-correlated color code seems like a promising approach.

Now, light itself propagates at the enormous speed of 300,000 km/sec so we are not, of course, suggesting that there are any significant delays or associated conversion to a time code due to optical propagation. However, conduction of electrical signals along nerve fibers are much slower than light speed, typically meters per second. Moreover, the complex ion channel and membrane structure of the cone outer segments are more properly modeled as RC-circuits with (potentially) significant delay

times. Thus, time delays of millisecond duration in signals from the distal end of the cone compared to the near end would seem realistic.

Two critical items are needed for the length signal to be sensibly converted into a time signal. First the source of the electrical transduction signal of light detection along the cone length must be uniquely associated with a location along the cone. That is, each detection event must be localizable and the cone not act simply as a diffuse bag of photo-absorbing pigment with no ability to differentiate where along the cone length a detection event occurs. Secondly, we need a synchronization signal to determine what signals are delayed relative to what. The evidence is that the conditions necessary to satisfy both of these requirements are indeed present.

First, consider signal localization. The diffusion of an electrical signal following a photoabsorption event in the cone has been both theoretically calculated and directly measured (Holcman and Korenbrot, 2004) to be localized to within 1 μm or less of the location of absorption. Thus, a given single foveal cone could have its spectral dispersion over its length potentially readable to within one part in 40 (for a 40 μm long cone). Note that the color discrimination potential for such a single cone is thus 1/40th of the spectrum dispersed over its length. For a span of colors of 200 nm (650 to 450 nm) this can provide the potential to discriminate lights differing in wavelength by as little as 5 nm. With more cones participating, we can expect the available hue discrimination resolution to be even better.

For the second requirement of a synchronization signal to read out the time code, we find that there exists a ready-made on-going synch signal each time the eye undergoes a microsaccadic movement. The existence of these microsaccadic eye movements has been known for a long time. At first glance, it would be natural to assume that these motions are simply the result of residual instabilities in the control movements of the eye muscles directing the pointing of the eyeball. So one would naturally have assumed that if these residual jerky motions could be removed by somehow stabilizing the image on the retina, that vision would improve.

Now image stabilization has in fact been done by various experimenters through a number of different techniques with varying degrees of success in the complete stabilization of the retinal image. What all these researchers have found is that vision, in fact, does not improve under these conditions. Instead it gets much worse and within a very short time of the imposition of (complete) image stabilization visual function disappears altogether (Ditchburn & Ginsborg, 1953; Riggs, et al, 1953).

Now these microsaccadic movements are involuntary (occurring all the time), they are small (corresponding, on average, to the displacement of the retinal image by something like ten to twenty cone diameters) and frequent (occurring on average roughly ten times per second or so). These motions thus provide a perfect synchronization signal for reading the cone's color information. Each time the light illuminating a cone changes (as a color border in the retinal image passes over it due to a microsaccade, for example) then a new read-out of the time delays of the signal

coming from the length of the cone is possible. Note that this synchronization happens globally for all receptors over the entire retina. If there is no change in the illumination of the cone as a result of the saccade, there will be no change in the cone output. However, all cones that experience a change in their input as a result of the passage of a color border over the cone entrance (for example) will synchronously begin putting out a changed signal; the details of that change will depend on the color differences in the input illumination altered by the saccadic eye movement.

What would this signal look like and what information would it contain? Changes in the early part of the cone output signal will result from differences in illumination in the part of the cone nearest to its output connecting synapse with the bipolars, its broad entrance end of the cone outer segment. Here a signal can be generated by light of any color (including red, of course) since all light entering the cone passes through this part of the cone and can thus cause a photo-absorption (in proportion to the absorption spectrum of the photopigment there). Signals coming slightly later, from the middle portion of the cone can be generated by changes in any color except red, since it has been shunted out of the cone by this point. Signals coming latest, from the distal, small end of the cone uniquely signal changes in blue light since all the longer wavelengths have been shunted out by that part of the cone. Note that there is a degree of asymmetry in how signal changes are correlated with optical wavelength. Changes to the latter part of the cone signal can only be a result of changes in the short wavelength content of the illumination while changes in the early part of the cone signal can be caused by changes in the amount of any wavelength. This ambiguity is, however, removed on examining the entire signal change from the cone; if there is a change in the early part of the cone signal without a change in latter parts of the signal, then the change can be confidently assigned to differences in long wavelength illumination only.

Now this time code sounds like a convenient method for reading the color information, but is there any evidence that the eye actually uses a time-color code like this? Actually, there is indeed direct evidence that the eye does use such a time-color code. The existence of so-called subjective colors induced by appropriately modulated black and white illumination directly points to such a code. Some 170 years ago Gustav Fechner (1838) noted that a complex series of colors could be induced with intermittent illumination. Perhaps the best-known example of this color induction effect is Benham's Top, a half-black and half-white disk with circumferential black arc

Typical configuration of Benham's Top. CW rotation gives arc colors of red, green, and blue from inner to outer set. CCW rotation reverses the order of colors.

segments arraigned on the white semi-segment. (These subjective color effects are also referred to as Fechner-Benham colors and also as Pattern-Induced Flicker Colors, PIFCs.)

A typical configuration of Benham's Top is shown in the figure. When the disk is spun at speeds around 8 to 12 times per second, one sees the arcs blur out to be continuous circles and to take on more or less desaturated colors. For a disk configured as shown in the figure, upon counter-clockwise rotation, the outermost arcs take on a reddish color (often very bright red), the middle arcs a vague greenish-grey color, and the innermost arcs a dark blue or blue-black color. If the direction of rotation is then reversed, the colors of the arcs are also reversed with the outermost being blue, the middle remaining green, and the innermost being red.

This subjective color phenomenon makes little sense in the standard model of color vision (and has not hitherto been plausibly explained by any model of color vision). Benham's Top was an invention of British toy maker CE Benham (Benham, 1894) and was a popular toy in Victorian times. The phenomenon has been extensively investigated for more than a hundred years and it has long been clear that it has something to do with the differential latency of different colors but there has hitherto been no coherent way to put these observations together in terms of any model of how the eye sees color (Roelofs & Zeeman, 1958; Campenhausen & Schramme, 1995). The point here, of course, is that the time code of the Benham's Top is a direct consequence of how the proposed CSM model reads color information from the cones.

Since all observers see the same color ordering and the effect appears to be universally present (except that the effect has been inadequately explored for color blind observers, although at least one report states that colors are observed the same way, but less saturated - Stewart, 1924) then only a color vision model tied to the ordered timing of color perception would seem to make sense, i.e., a dynamic, rather than static, model of color vision.

Note that on rotation, the back edge of the black half of the disk provides a time reference for the arcs on the white half. The arcs that appear first (regardless of rotation direction) appear to be red and the arcs appearing last appear to be blue. There are a number of good examples of Benham's Top on the Web with a simple search where one can vary the dynamic parameters to see the induced subjective colors. I should point out, by the way, that the induced colors are not actually produced on the black part of the arcs themselves. Rather, they are induced at the border between the black arcs and the white surround. For arcs of sufficiently small width, the color "bleeds" over so that the entire arc does look colored. If the arcs are made too thick, the colors will be less evident.

So, what about the time scale for the phenomenon – does it make sense in terms of the time delays we have been talking about for the retinal cones? For a typical rotation rate of 10 Hz and the arc distance of 120^{o} between the start of the red and blue sensations on the rotating arcs, the time delay is 1/3 of 1/10 of a second or 33 milliseconds. This

time difference is in very good agreement with the measured time delay between the perception of red (650 nm) and blue (450 nm) light we discussed before, namely 30 milliseconds.

So the means are there – the cone spectrometer model could indeed work by conversion of the length-dispersed color information into a time code. Photo-absorption events along the cone length can be localized to one micrometer or less and the microsaccadic eye movements provide a natural, global synchronization signal to coherently encode the color information.

What then about the motivation? Why would we want such a model, what is it good for and does it explain the facts of color vision better than any other theory?

The Motive

So the question is: is the motivation there and does the Cone Spectrometer Model (CSM) as described here have any utility? Does it explain color vision in a sensible way and can it explain the myriad aspects and phenomenology of human color vision?

Again, we would suggest that the short answer is yes; it does address and directly explain many aspects of how human color vision seems to work. To this point we have shown how the CSM model is in accord with the anatomical structure of the cones and how its dynamical aspect explains the existence of subjective colors. Both of these aspects are notable failures of the standard, three-cone model of color vision.

There exists a vast body of scientific research and published literature on human color vision. In part, this is a reflection of the natural interest in the functioning of one of our most profound and treasured human senses. It is also a reflection of the confounding complexity of the perception (involving psychology, physics, neurophysiology, biochemistry, and psychophysics) and the lack of a widely accepted and truly comprehensive model to explain the myriad aspects of the phenomenology of color vision. Given the vast array of phenomenology involved, we will not be able to address all of it here at the present time (although a lot more is covered in the book, **Cone Shape and Color Vision: The Unification of Structure and Perception**.)

Consider for a start what any such model of human color vision must encompass and explain. We present here a laundry list of such properties and characteristics, a list that is extensive but by no means totally comprehensive.

The list is divided into three categories:

I. Anatomical and structural features of the cones and their organization,
II. Physical properties of the operation of color vision, and
III. Effects or observed phenomenology of the perception.

I. Anatomical and Structural Features

1. **Cone shape**: The photosensitive outer segment of the photoreceptors of color vision is uniformly conical in shape as contrasted with the outer segment of the rod photoreceptors of achromatic night vision which is uniformly cylindrical.

2. **Local uniformity of cones**: All the cones within a given region of the retina are histologically similar (or identical) with no physically identifiable cone classes (with the possible exception of so-called blue cones).

3. **Systematic variation of cone size and shape across retina**: The longest and most gently tapering cones are in the central retina (fovea) where color vision is best and they gradually decrease in length and become more obviously tapered as one progresses further out in the retina in accord with the decrease in color vision function in the peripheral retina.

4. **Equivalence of bipolar/cone ratio to dimensionality of color vision:** There are three bipolar cells (outputs) per cone in the central retina where vision is three dimensional, decreasing to 2:1 where color vision becomes dichromatic, and 1:1 in the peripheral retina as color vision function becomes monochromatic (Missotten, 1974; Sheppard, 1968; Vilter, 1949).

5. **Small diameter of the photosensitive portion of the cones**: The cone's photosensitive outer segment is much smaller than required for spatial resolution alone and is substantially smaller than the inner segment diameter. The outer segment dimensions do appear to be ideal for low-order mode cutoff.

6. **Correlation between cone length and the color resolution provided**: This is part of the systematic variation described in (I.3) above.

7. **Localization of photoabsorption events along the cone length**: Absorption of light triggers a cascade of biochemical events that results in the closure of ion channels within a region one micrometer or smaller in extent along the length of the cone so that it is a local event (Holcman & Korenbrot, 2004).

8. **Numerous photopigments**: Molecular genetics have revealed the existence of a host of variants of the "red" and "green" photopigments. These photopigments have values of their absorption peak deviating by 5 nm or so from that of the "standard" versions.

9, **Multiple photopigments within single cones**: Evidence indicates that cones may have more than one photopigment within individual cones (pigment co-expression, c.f., Glösmann & Ahnelt, 2002; Jacobs, Williams, & Fenwick, 2004; Marks, Dobelle, & MacNichol, 1964; Parry and Bowmaker, 2002; Röhlich, Veen &. Szél, 1994; and Xiao &

Hendrickson, 2000). For example , Jacobs, Williams, & Fenwick (2004) in demonstrating the existence of color vision in the mouse despite extensive and complete co-expression of both of the rodent's visual pigments in all cones had to conclude: “Since mice can make dichromatic color discriminations, their visual systems must be able to exploit differences in the spectral absorption properties among the cones. *Complete selective segregation of opsins into individual photoreceptors is apparently not a prerequisite for color vision*.” (Emphasis added.)

10. **Uniform color vision function despite wide variation in apparent “red” and “green” cone reflectances**: In MSP measurements on living retina, researchers have found enormous variation in the relative number of apparent “red” and “green” cones among different subjects (40:1 variation among subjects) with no apparent difference the subject’s color vision function (Carroll, Neitz & Neitz, 2002; McMahon, Neitz, & Neitz, 2004; Hofer, Carroll, Neitz, Neitz, & Williams, 2005). Recall that while there are good arguments suggesting that these retinal densitometry measurements don’t necessarily indicate a unique pigment in each cone, none-the-less, the remarkable constancy of color vision function seems to be independent of variations in measured apparent photopigments.

11. **Color vision function is independent of the blotchiness of red/green cone distribution**: Observations by Roorda and Williams (1999) has shown not only large inter-individual variations in ratios of apparent cone types, but also that the mosaic of these cones is not all regular, being essentially random and very "clumpy". None-the-less, this patchiness seems to have no effect on the individual's color vision function.

12. **Peripheral cones have scotopic spectral sensitivity**: While the overall spectral sensitivity of the cones in the central retina peaks at about 555 nm in the green (photopic spectral sensitivity) in the periphery, cones have a spectral sensitivity peak at about 500 nm and their spectral sensitivity is essentially indistinguishable from the scotopic spectral sensitivity of rods (Abramov and Gordon, 1977; Weale, 1953; Wooten and Wald 1973). Thus, compared to more central cones, the peripheral cones have a more conical shape, simpler neural connectivity, poorer color discrimination function, and the spectral sensitivity of rods.

II. Color Vision Functions

1. **Color discrimination characteristics**: Data on the characteristic curve of hue discrimination show broad minimum at around 580 nm and 500 nm and a more abrupt local minimum around 440 nm while going to unbound maxima (worse discrimination) at either end of the spectrum.

2. **Spectral purity characteristics**: The plot of spectral purity (difference from white, a measure of saturation) has one broad minimum around 580 nm. That is, yellow is the least saturated color and is the color that is least different from white (lowest “purity”).

3. **Unique yellow**: Virtually all human observers identify a reproducibly stable monochromatic wavelength around 580 nm or so as being a pure yellow, balancing between the red and green sensations

4. **Color constancy**: Human color vision has the remarkable property of the stability of perceived hue in a scene regardless of variation in the colorcast of the general illuminant used (and consequent wide variation in actual spectral content of light entering the eye, that is, the eye has a powerful ability to discount the overall color tint of the general illumination).

5. **Ordered chromatic latency of color perception**: Experimental data shows that the delay in perception of monochromatic light varies systematically and monotonically with wavelength (Medeiros, 2006). In particular red light is perceived fastest and as the wavelength is decreased, the perception is delayed linearly so that blue light is perceived about 30 msec later than red light.

6. **Similarity of violet and purple**: The color violet (wavelengths shorter than about 460 nm) looks very similar to a mixture of blue and red, the color purple. Indeed, if one looks at the output of a monochrometer as one tunes to progressively shorter wavelengths, around 460 nm it looks exactly like a component of red light is being added to the blue. Attempts to explain this perceptual similarity have postulated the existence of a subsidiary maximum at short wavelengths in the absorption spectrum of the "red" pigment. However, there is no compelling evidence for such a sub-maximum and in any case, even if it were present, it could not have the abrupt rise required to provide the similarly abrupt turn-on of the red part of the violet perception.

7. **Invariance of color perception with reversed direction of incidence**: In a famous experiment Brindley and Rushton (1959) found that the perceived color of light is the same whether that light is incident on the cones in its usual (forward direction) or reversed (having passed into the retina from the back of the eye). This result clearly rules out color vision being based on any sort of filter in front of the cones and was also originally interpreted as ruling out models based on any waveguide effects. However, the fundamental Reversibility Theorem of optics states the path of light through any optical system is physically the same on reversal and thus the Brindley and Rushton observation does not rule out any color selection process based on the physical transmission of light.

8. **Color defective vision**: There are a number of ways in which color vision fails, but by far the most common forms of “color blindness” are the two forms (protan and deutan) of red-green defective vision. In addition to the similar (but not identical) red-green confusions for these two forms of dichromatic vision, there is a marked reduction in the sensitivity to red light in protanopes but no similar reduced sensitivity to green in deuteranopes. It has been directly demonstrated that despite the absence of the genetic machinery for one of the "red" or "green" photopigments, such dichromats can still distinguish red and green in color-naming experiments. Particularly telling in this regard

are the results of Watcher, Dohrmann, and Hertel (1974). Quoting from their paper: "***Protanopes and deuteranopes, despite lacking a chromatic dimension at the receptor level, use the color terms ‘‘red’’ and ‘‘green’’, together with ‘‘blue’’ and ‘‘yellow’’, to describe their color percepts. Color vision models proposed so far fail to account for these findings in dichromats. We confirmed, by the method of hue scaling, the consistent use of these color terms, as well as their dependence on intensity, in subjects shown to have only a single X-chromosomal opsin gene each.***"

9. **Color anomalous vision**: In addition to the extreme forms of red-green color blindness, there also exist anomalous forms of defective color vision (protanomalous and deuteranomalous) spanning a gradation in function from the extreme forms with (near) total inability to discriminate reds and greens to virtually normal color vision. Protanomalous (“red-blind”) subjects, for example, were found with “red” and “green” pigments that had identical peak sensitivities, but yet had (limited) red-green color discrimination (Neitz, Neitz, He, and Shevell 1999).

10. **Individual cones elicit any color sensation, including white**: In a recent, very fascinating, experiment (Hofer, Singer, and Williams, 2005) used an adaptive optics technique to illuminate single cones in the living eye. They found that, regardless of the color of illuminant they used, the color perceived by any one cone could be any color, including the sensation of white.

11. **Photochromatic Interval**: Better termed the achromatic interval where, as the brightness of a monochromatic light is decreased it changes from being colored to being gray (or white) near threshold for all wavelengths except red. This interval is largest for the shortest wavelengths and smallest for the longer wavelengths.

12. **Blue component of violet perceived before red component at threshold**: At low intensities of short-wavelength light, as the intensity is brought up from subthreshold values, the blue sensation is perceived first and the ‘added’ red component of violet is seen only later at higher intensities (Gothlin, 1944).

13. **Electrophysiological response of the eye to alternating colored lights:** Shown to be directly proportional to the difference in wavelength of the lights (Riggs, Johnson, and Schick 1966).

14. **Pupil dilation response of the eye to alternating colored lights**: Shown to be directly proportional to the difference in wavelength of the lights (Young and Alpern, 1980)

III. Color Vision Effects

1. **Breakdown of statically established metameric matches under dynamic conditions**: Ives (1918) demonstrated in his paper, “Resolution of mixed colors” that a mixture of red and green that looked yellow, resolved into a red leading edge and a green trailing edge as a bar of the mixed light was moved across the retina while a pure monochromatic yellow that matched the mixture under static presentation did not similarly resolve when moved. My colleagues and I have repeated this experiment with the same result. ***This experimental result flatly contradicts the standard three cone model of color vision.***

2. **Subjective colors (Fechner-Benham colors)**: This is the invocation of ordered color perception with intermittent achromatic illumination and the correlation of the order of the induced colors with a systematic temporal code with time constants the same as measured for differential chromatic latency. While the perceived subjective colors are somewhat desaturated, they are universally seen in the same spectral ordering by all observers with normal color vision.

3. **Loss of color vision under image stabilization**: It is found that there is a rapid and complete loss of vision, particularly color vision, when the image on the retina is static (stabilized).

4. **Fluttering Heart Effect**: This is a perceived lagging of a colored target on a background of a different color when the two are oscillated together. For example, the effect is easily invoked with a blue target on a red background where the blue target is seen to "lag" behind the red background. Helmholtz (1867) was the first to clearly suggest that the effect is caused by a difference in the perceptual latencies of different colors. Clearly this is in accord with the measurements we have discussed on the differential chromatic latency, an effect necessary for the proposed CSM model but rather mysterious in the context of the three-cone model.

5. **Stiles-Crawford color change:** Also known as the Stiles Crawford effect of the Second Kind or SC II, where the perceived color of a monochromatic light changes as the angle of incidence of the light at the retina is changed (Stiles, 1937; Alpern, 1986). The better-known SC I effect is the reduction in intensity of a light as its angle of incidence at the retina is increased. The SC II effect is predominantly a red shift with increasing angle of incidence, uniformly so for small angles, and mostly so for all angles and colors. Explanations of this effect within the context of the trichromatic model have been proposed previously in terms of pigment self-screening effects (e.g., Walraven & Bouman, 1960). Experimental measurements contradict such explanations. For example, Wooten, et al (1978) examined the effect for conditions where much of the visual pigment had been bleached but the effect was still present, ruling out self-screening explanations. In the end, they stated "*... we must conclude that the only framework that is capable of accounting for our high bleach measurements is*

waveguide theory." In fact, the shift is well modeled by a wavelength change proportional to [1/cos(ø)] where ø is the angle of incidence (Medeiros, 1979, 2006). We compare this function, a direct consequence of the CSM model, with the experimental data on the SC II effect in the book, **Cone Shape & Color Vision** where an excellent fit is demonstrated.

6. **Bezold-Brüke Effec**t: This is the change in perceived color of a monochromatic light as its intensity is varied. While the exact details are somewhat complex, the primary effect is a shift to shorter wavelengths for light with a wavelength longer than 580 nm and a shift to longer wavelengths for light with a wavelength shorter than about 580 nm.

7. **Abney Effect**: This effect involves a change in the apparent hue of a monochromatic light with the addition of white light (Abney, 1909; Kurtenbach, et al, 1984). For example, addition of white light to red changes the apparent hue towards yellow.

8. **Tyndall's Paradox**: The paradoxical improvement in hue discrimination with the addition of white light to a monochromatic light (especially in the blue region of the spectrum). First noted by Tyndall (1933) and subsequently explored in more depth by Mollon and Estevez (1988).

9. **Constancy of white perception across the retina**: While colored lights are perceived differently in different parts of the retina, white is perceived the same even though the eye has a remarkable sensitivity to differences in the appearance of a white illuminant (Hartridge, 1948).

10. **Blue Arcs of the Retina**: When an area near the fovea is stimulated by (virtually) any color of light, blue colored arcs (or spikes if the illumination is between the fovea and optic disc) are seen following the pathway of the ganglion cells sending signals from the illuminated area to the optic disc. The phenomenon is clearly due to induced signals from parallel fibers (Alpern and Dudley, 1966), but why is the induced color always blue (c.f., Ingling & Drum, 1977)?

11. **Land Effect**: As demonstrated by Edwin Land in the 1950's and 1960's, it is found that only a wavelength difference in two superimposed projections is needed to reproduce the full range (albeit desaturated) of perceived colors (Land, 1959). For example, if two recordings of a natural scene are made, one through a filter with a long wavelength passband and one through a filter with a short wavelength passband, then if the recorded long-wavelength scene picture is projected through a red filter and the short-wavelength record is projected with no filter (black and white only) and the two projections are superimposed, then the projected scene will have natural and correct coloration exhibiting virtually the full range of spectral colors. This is an astonishing departure from what might superficially be expected from such a two-color projection, namely a scene with a general pink (desaturated red) cast with no properly ordered colors. Evidently the human color vision system can interpolate the full range of correct colors from just the ordered projection of the record of the long-wavelength and short-wavelength portions of a scene.

12. **Chromatic adaptation**: when a colored background illuminant is used, the spectral sensitivity of the eye changes in very particular ways (c.f. Boynton,et al 1959; Boynton, 1956; MacAdam, 1956; Speelman and Krauskopf, 1963; Delahunt and Brainard, 2000) . To a rough approximation, red sensitivity is most strongly affected (reduced) by adaptation to any background color.

13. **Violation of Univariance**: Brown (1983) reported measurements of the time course of dark adaptation after exposure to different colors (supposedly equated for "red" or long wavelength sensitive cones) that showed clear violations of the so-called Principle of Univariance (Naka and Rushton, 1966). That principle was formulated as the underpinning of the three-cone model to state that the output of a receptor was to be only dependent on its total quantal catch of light and to be independent of wavelength. Similar violations of the "Principle of Univariance" were also noted by Augenstein and Pugh (1977), Pugh and Mollon (1979), Fuortes, Schwartz, and Simon (1973), and others. Note that in the CSM model we have proposed here, that the output of the cones is not fundamentally different for different wavelengths. Different colors of inputs to the cones simply give different rise (and fall) times of their output signal as the input is modulated.

14. **Breakdown of color matches with high intensities of adaptation**: Wright (1936) observed that for a yellow initially matched by a red and green mixture, after adaptation to very bright light, the match was no longer satisfactory, generally requiring more red in the mixture for a match (further explored and verified by Brindley, 1953). Such an effect violates the standard laws of additivity (Grassman's Laws) as it is generally understood to be required by the three-cone model.

15. **Special significance of yellow**: Observers can readily and consistently identify a unique yellow (with either no reddish or greenish tint) and this unique yellow remains invariant for each observer across a wide range of observing and viewing conditions (Abramov and Gordon, 2005). Moreover, the wavelength of this unique yellow (usually in the range of 575-585 nm) corresponds to the position of both the least saturated color and the location of best color discrimination.

16. **Special properties of blue light**: The color blue has long been known to exhibit some unique features, including a very high chromaticity value (Mollon, 1977). That is, blue light contributes to chromatic value of a patch of light more strongly than any other color. Moreover, under conditions of rigid fixation, blue perception is preferentially lost before other chromatic perceptions in an effect known as small-field tritanopia (McCree, 1960, Wright, 1977). In the CSM model, blue light is uniquely present in the most distal portion of the cones so that the last-to-arrive signal from a cone uniquely signals the presence of a blue component of incident light.

This is quite a list (42 items in three categories). I would not even suggest that the list is exhaustive. The fact is that the standard, widely accepted, three-cone model of human color vision explains almost none of the items on this list in a straightforward and non-

contrived fashion. Indeed that model is flatly contradicted by much of what is on the list. Given this state of affairs, it is somewhat incredible that the standard model is so widely and dogmatically held and that so little credence has been given to efforts to find some better way to explain color vision. To make the inadequacy of the standard three-cone model of color vision more apparent, I have included a chart of these 42 properties and effects and the way the proposed CSM model compares with the standard model in terms of explaining these characteristics. While the exact assignment of how well each model might or might not explain or be consistent with each of the listed properties may be somewhat up for interpretation depending, on your point of view, I have tried to be

Aspect of Structure or function in Color Vision (CV)	CSM	3-cone
I.1 Cone Shape	Yes	No
I.2 Local uniformity of cones	Yes	No
I.3 Systematic variation of cone shape	Yes	No
I.4 Equivalence of bipolar/cone ratio & CV dimensionality	Yes	No
I.5 Small diameter of cone outer segments	Yes	Indifferent
I.6 Correlation cone length & CV resolution	Yes	No
I.7 Localization of photoabsorption along cone length	Yes	Indifferent
I.8 Numerous photopigments	Indifferent	Indifferent
I.9 Pigment co-expression	Yes	No
I.10 Uniform CV despite wide variation of cone "types"	Yes	No
I.11 CV function independent of cone mosaic blotches	Yes	No
I.12 Peripheral cones have scotopic sensitivity	Yes	No
II.1 Color discrimination curve	Yes	Maybe
II.2 Spectral purity characteristics	Yes	Maybe
II.3 Unique Yellow	Yes	No
II.4 Color constancy	Yes	Maybe
II.5 Ordered chromatic latency	Yes	No
II.6 Similarity of violet and purple	Yes	No
II.7 Invariance of CV with reversed light direction	Yes	Yes
II.8 Color defective vision	Probably	No
II.9 Color anomalous vision	Probably	No
II.10 Individual Cones can report any color, including white	Yes	No
II.11 Photochromatic Interval	Indifferent	Indifferent
II.12 Blue part of violet perceived before red at threshold	Yes	No
II.13 ERG signal proportional to wavelength difference	Yes	No
II.14 Pupil dilation proportional to wavelength difference	Yes	No
III.1 Dynamic breakdown of metameric color matches	Yes	No
III.2 Subjective colors	Yes	No
III.3 Loss of CV under image stabilization	Yes	Maybe
III.4 Stiles-Crawford color change (SC-II effect)	Yes	No
III.5 Bezold-Bruke effect	Maybe	Unknown
III.6 Abney effect	Maybe	Unknown
III.7 Tyndall's Paradox	Probably	No
III.8 Broca-Sulzer phenomenon	Indifferent	Indifferent
III.9 Constancy of white perception across retina	Yes	No
III.10 Blue arcs of the retina	Yes	Unknown
III.11 Land effect	Yes	No
III.12 Chromatic adaptation	Yes	Maybe
III.13 Adaptation effects	Yes	No
III.14 Breakdown of color matches at high intensity	Yes	No
III.15 Special significance of yellow	Yes	Unknown
III.16 Special properties of blue	Yes	Maybe

conservative in my assignment of success (green), indifference (yellow), or failure (red) of each model. Even, allowing that I might have a somewhat biased view of these issues, the dichotomy between the two approaches to explaining human color perception is still rather stark.

Many of the 42 items on the list are directly addressed in the current document (including further discussion below) and most of the rest are covered in the book, **Cone Shape & Color Vision**. A few of the items on the list are not directly addressed either here or in the book (about four or five such items). I do plan to cover these, as well as other items not mentioned in this list, in future publications.

Despite the evident failures of the trichromatic theory , part of the resistance to abandoning the model is that color vision clearly is (at least to a first approximation) three-dimensional (as in three primaries required for metameric matches) and that three cone classes are an easy way to explain this. However, the widely ignored evidence is that, as noted above (I. 4.) the dimensionality of color vision is more closely associated with the number of bipolar outputs per cone. Moreover, the Ives (1918) experimental result flatly contradicts the three-cone model and proves it cannot be right. None-the-less this and other evidence from the list above has long been ignored as many in the field have insisted on fitting the phenomenology to the three-cone model.

In contrast, the cone spectrometer model (CSM) I have proposed has none of these contradictions; it is consistent with all of the experimental evidence, and goes a long way towards explaining every one of the features mentioned in the above three-part list of structure, function, and phenomenology. The CSM theory directly makes use of the small size and conical taper of the retinal cones to sort the visible spectrum along the length of the cone through low-order waveguide mode cutoff. The ordered spectral information along the cone length is then read out in a time-ordered code that uses microsaccadic eye movements for a temporal reference. The resulting time-ordered color information then directly explains the Ives (1918) result, our measurements of chromatic latency, and the details of subjective (Fechner-Benham) colors.

Virtually all the items on the above list are addressed in terms of CSM in the book, **Cone Shape & Color Vision: The Unification of Structure and Perception**. The book is available as a soft cover volume (figures in black and white only) or as a downloadable PDF file (with figures in color) from all the standard on-line booksellers such as Amazon.com, Barnes & Noble, etc.

Some of the items addressed in greater detail in the book include:

- the direct explanation and modeling (in terms of the basic waveguide cutoff mechanism) of the spectral purity function (saturation of colors),
- a model of color deficit vision (color blindness) in terms of mistuning of the cone spectrometer function,
- the SC-II color change effect as a direct consequence of waveguide propagation,
- the similarity of violet and purple as a consequence of second-order mode excitation, and

- subjective colors and Benham's Top.

The book also has more in-depth coverage of the experiments on the separation of rod and cone perception. A good idea of what is covered in the book can be gleaned from the table of contents found at the end of this monograph.

Hue Discrimination and the Similarity of Violet and Purple

Before closing the current discussion, it is perhaps worthwhile exploring the power and utility of the CSM model with a specific example or two. Perhaps one of the most important things a model of human color vision should be able to do is to explain the basic hue discrimination function. Now in order to do a complete job of this in the context of the CSM model, we would need a lot of detail about quite a few things, including:

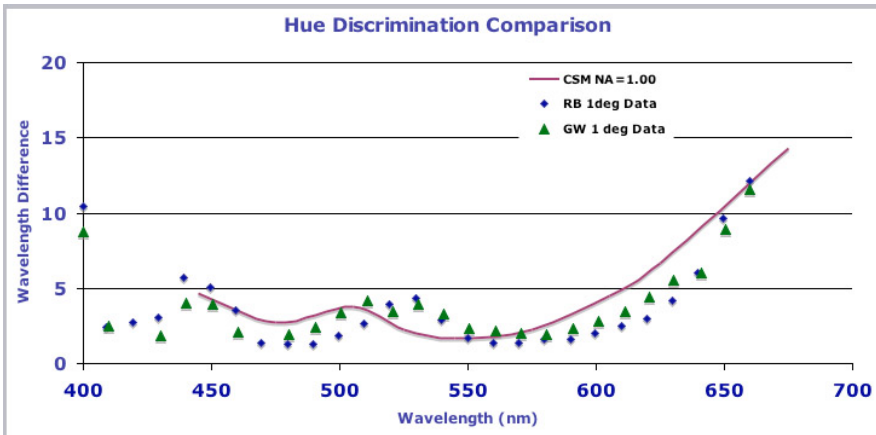
- the exact dimensions and refractive indices of the cones and their surround,
- the details of spectral absorption curves, optical densities, and distribution of the photopigment or photopigments in a cone,
- details of how the temporal conversion code is executed within a cone and the how the subsequent neural circuitry encodes and uses the information,
- details of how the cones in adjacent regions cooperate to enhance or inhibit each other's signals, and
- details of how the overall "white" that is illuminating a region is interpreted by the ones and used in neural processing to help set the color constancy of human color vision.

This list of necessary information is probably not even complete. But even so, absent these details, we could ask the question: is there anything useful we can do to see if the CSM model could plausibly explain the hue discrimination function?

In fact, there is. Assuming nothing about any photopigments, indeed using a very simplistic model where all wavelengths are equally likely to be absorbed in a cone and using only the waveguide dispersive property of mode cutoff, we get a very plausible hue discrimination function. Using a very simple model with the cone waveguide parameter given by $V = d/\lambda$ and a largest (entrance) cone diameter of 1 μm and smallest (distal) diameter of 0.6 μm, I calculated the amount of light present along the cone for pairs of input monochromatic light with wavelengths separated by 10 nm. I did this for a number of wavelength pairs in the range from 680 to 440 nm. For each pair I integrated the difference in the distribution along the cone length to get a single number that would be proportional to how different the two distributions would be. This I took as a simple measure of how well colors at a wavelength intermediate between the pairs could be discriminated (a larger value means they are more easily discriminated).

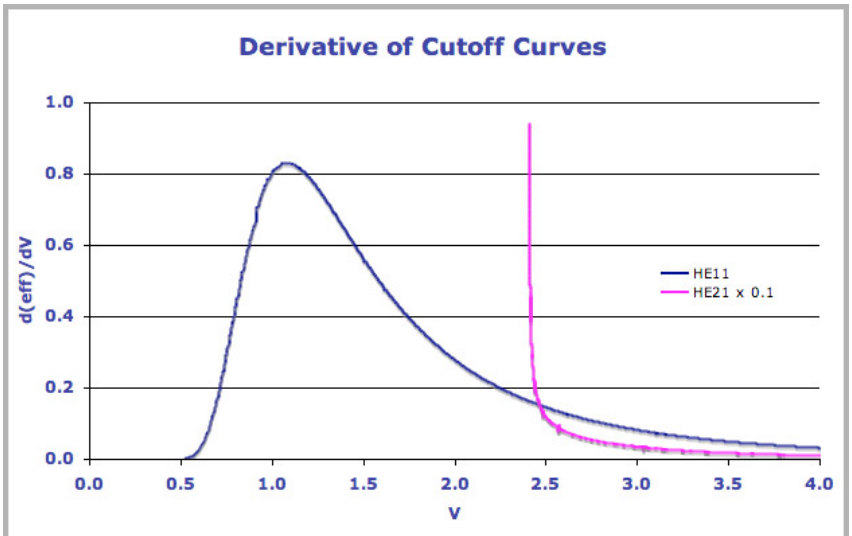
To display this in a fashion that can be compared to the usual hue discrimination curves, I took a difference of this integrated number for each wavelength pair from a constant

and then (absent any direct information about how the cone signals are scaled) uniformly scaled the result (i.e., multiplied by a constant). The chart below shows the result compared with the one degree hue discrimination data of Bedford and Wyszeki (1958). As can be seen, this very simple model - with no assumptions about the cone photopigments (indeed, a very simple assumption of uniform absorption) does rather well in giving the overall hue discrimination function.



Comparison of hue discrimination data of Bedford and Wyszecki, 1958 (data points) and a theoretical estimate based on the Cone Spectrometer Model by a method described in the text (solid line). This computation makes no assumption about what photopigments might be present or how they are distributed. It uses a simplistic model where all wavelengths have the same probability of being absorbed. Here, hue discrimination results entirely from differential mode cutoff.

As I stated, the basis of this discrimination curve is purely due to mode cutoff in a tapered fiber for different wavelengths (no photopigment effect incorporated into the analysis). A good idea of what is happening here and how the mode cutoff curves contribute can be garnered from a perusal of the derivative of the cutoff curves. We plot below, the derivative, d(eff)/dV, of the cutoff curves shown previously for the HE_{11} and HE_{21} curves. A couple of features of this plot are worth pointing out. First, the derivative of the HE_{11} cutoff displays a maximum value corresponding to the inflection point in the mode cutoff curve and it represents the position of best color dispersion. If one is building a cone spectrometer based on

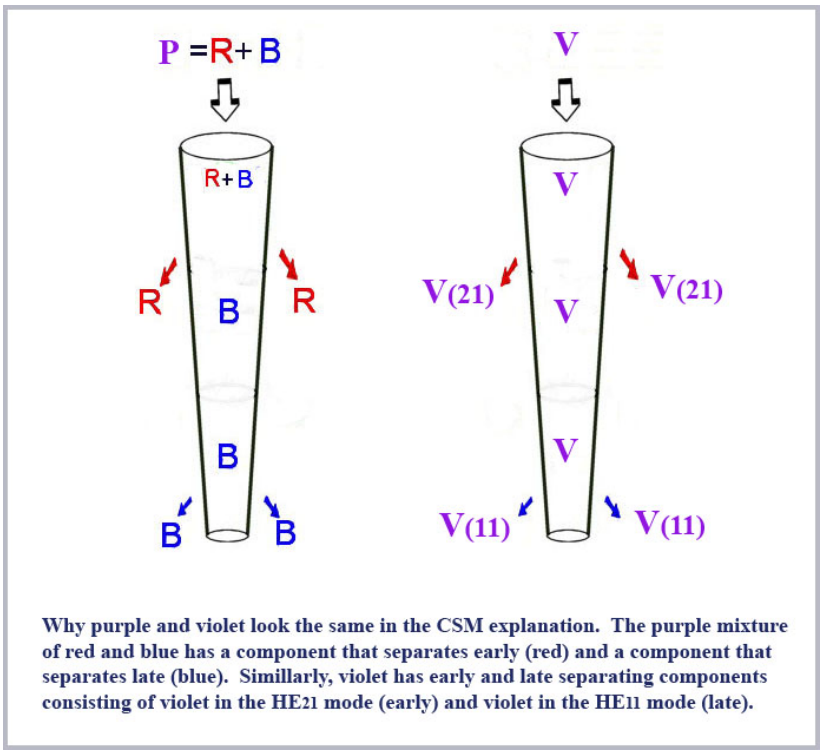


Derivative of the cutoff curves for the two lowst order waveguide modes. The HE11 mode exhibits a maximum at V-1.08 while the HE21 mode derivative increases asymptotically at V=2.405. Note that the HE21 mode derivative is scaled by a factor of 1/10 for this display. The range of waveguide parameters between about 0.6 and 2.5 is the suggested optimum operating range for the cone spectrometer.

this mode cutoff effect, it would make sense to center your operating range about this point. This maximum dispersion occurs for a waveguide parameter value of V=1.08 at which point the waveguide mode efficiency is approximately 0.24 so that about a quarter of the incident light is still within the cone interior.

Now I would suggest that there is every reason to believe that the retinal cones do exactly this and use their physical parameters (diameter and refractive index) to position the middle of its operating range at precisely this point, namely the yellow wavelength of approximately 580 nm. This would have the consequence that a specific wavelength, namely unique yellow, is tied to a physical feature of the cones so that its location should remain relatively fixed and stable. It would also correspond to the position of best color discrimination and minimal spectral purity as yellow indeed does so correspond (discussion of spectral purity is beyond the scope of the current document and the saturation function is derived and discussed extensively in the book, Cone Shape and Color Vision where it is compared to the standard data). Note also that centering the cone operating range about this maximum derivative point also suggests some features to look for when cone spectrometer operation is mistuned - a defect that I suggest occurs in some forms of color deficit vision (see below).

Another notable feature of the mode derivative curves is the very large values of the derivative of the HE_{21} curve, reflecting its abrupt cutoff. Note that this cutoff terminates abruptly at the waveguide parameter value of V=2.405. Values this large will occur for the shortest wavelengths propagating in the largest (entrance) portion of the cone. What will happen in this case is that short wavelength violet light will then propagate (at least in the wide part of the cone) in two modes, both the HE_{11} and the HE_{21}. The HE_{21} portion will cutoff very rapidly and behave, in fact, like long wavelength red light. That is, violet will propagate in the cone like a mixture of red and blue light (the HE_{11} portion of the violet will continue down the cone and attenuate like blue light) . A mixture of red and blue light is, of course, the color purple and this effect thus explains the long puzzling similarity of violet and purple. The separation process as it



Why purple and violet look the same in the CSM explanation. The purple mixture of red and blue has a component that separates early (red) and a component that separates late (blue). Simillarly, violet has early and late separating components consisting of violet in the HE21 mode (early) and violet in the HE11 mode (late).

will occur in the two separate cases of either purple or violet incident on a given single cone is schematically illustrated in the cartoon figure.

The rapid cutoff of violet light in the HE_{21} mode accounts for the secondary minimum in the color discrimination curve plotted above. That secondary minimum is not more abrupt in the curve simply because a smooth line is drawn between only a few values of the wavelength pairs that I computed for the plot.

Color Deficit Vision

No discussion of color vision models can be complete without an accounting of how color vision function can go wrong and "color blindness" results. There are a number of ways in which color vision function fails, but by far the most common are the two types of red-green deficit vision, protanopia and deuteranopia. Both of these forms exhibit a gradation from nearly normal color vision through their anomalous variations (protanomalous or deuteranomalous) to the near complete loss of the ability to distinguish reds and greens. These forms have X-linked recessive genetics and affect around 8% of the male population and a much smaller percentage of females.

Color deficit vision is by itself a major topic of investigation with a vast body of research and published literature. I can hardly hope to do justice to all of that work in this short monograph. However, I will address a couple of topics about color blindness in terms of the CSM model, most of which is covered in more detail in the book, **Cone Shape & Color Vision.**

Within the CSM model, a direct way in which the cones will fail to provide the necessary time-ordered color information for the retinal neural circuitry to interpret appropriately is for the cones to be the wrong size to optimally disperse the spectrum along their length. This could happen in either of two ways; they could be too small or they could be too large. Either would cause deficient color vision in subtly different ways. It should be noted that this incorrect sizing might have nothing to do with the cone's physical size but be caused by incorrect values of the refractive index difference between the cones and their surrounding interstitial medium. Recall that the index of receptor "size" is the dimensionless waveguide parameter V,

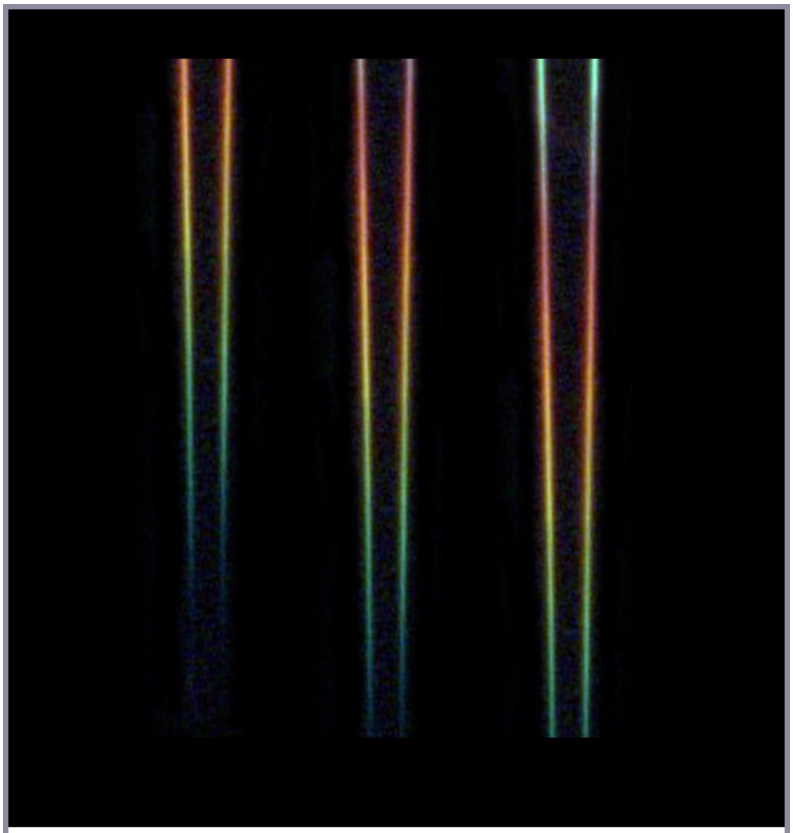
$$V = (\pi d/\lambda)(n_1^2 - n_2^2)^{1/2}.$$

For a given cone diameter, d, at a particular location along its length and for cone refractive index n_1, then if the surrounding medium refractive index, n_2, is larger (smaller) than normal, the cones will be smaller (larger) than they should be for optimum operation.

If the cones are too small, than long wavelength (red) light will be very inefficiently coupled into the cone's photosensitive outer segment. This will have two immediately obvious consequences: a lower sensitivity to red light and inefficient use of the cone length for discrimination. Both of these characteristics are signatures of one type of color deficit vision, protanopia, where there is both low sensitivity to red light and poor color discrimination.

If the cones are too large, then all colors will couple efficiently to the cone's photosensitive outer segment, but the spectrum will be dispersed (at least in the lowest-order, HE11 mode) inefficiently over the cone with mode cut off dispersing the spectrum only over the lower portions of the cone. The immediately obvious consequences of this mistuning will be reduced color discrimination and no reduction in spectral sensitivity, both of which are signature characteristics of deuteranopia.

An idea of how this cone mistuning might look is provide by the accompanying figure. Here, I have taken the photograph of spectral dispersion in a tapered fiber (shown at the beginning of this document) and simply cut a section from the photo and pasted it three different times into the figure. The portion pasted in the middle is meant to represent what the span of spectral dispersion due to mode cutoff would look like for optimum operation in the normal cones. The cone on the left is a portion cut out further down the fiber showing the spectral dispersion span if the cone is too small for optimum operation as in protanopia. On the right is the representation for the cone being too large as in deuteranopia. Note that in the too-small case, red light is not efficiently coupled into the cone and its spectral span is limited. In the too-large case, while the entire spectrum is coupled into the cone, the span is not ideally placed for optimum operation



Cone mistunings: Left to right, cones are too small, just right, and too large for optimum operation in CSM.

and there will be confusions due to second-order mode coupling, even for wavelengths that are not in the violet as in the normal cones.

In any case, in the context of the CSM model, if one can purposefully alter the refractive index of the cone's surrounding medium appropriately, it is not difficult to imagine that useful color vision function could be restored for "color blind" individuals. To "cure" protanopia one would need to increase the refractive index difference between the cones and its surround. This could be accomplished by increasing the refractive index of the interstitial medium by increasing the amount of included solids or suspended complex molecules in the medium. Conversely, to treat a deutan defect, it would be necessary to decrease that refractive index difference by reducing the refractive index of the surrounding medium by removing suspended solids or complex molecules.

It may be of interest that this may actually have already been successfully demonstrated. In a number of papers published in the 1970's, Louis F. Raymond reported on the treatment of a number of patients with allergies who were also colorblind (Raymond, 1971, 1972, 1975). He cites one case (Raymond, 1975) of a patient who tested as red-green color deficit on both Ishihara plates and Hardy-Rand-Rittler Plates. The patient tested positive for allergies to bacterial endotoxins and air-borne pollens in intradermal tests. Hyposensitization treatment, consisting of administration of diluted antigenic solutions of the items to which he was allergic cured the colorblindness. He claimed that the patient's color vision was normal on testing after two months, one year, and at two years later. He noted that he treated a total of 24 such cases with similar results.

There are a number of identifiable antibodies in human sera. Chemically, these are glycoproteins with molecular weights of around 150 to 200 kDa. These antibodies are a variety of immunoglobulins, including immunoglobulin E (IgE). It has been shown that IgE levels are reduced following hyposensitization treatments. Since the immunoglobulins are chemical similar to the mucopolysaccharides that are known to be present in the interstitial medium of the retina, conceivably, the hyposensitization treatments may have altered (decreased) the refractive index of the interstitial medium and thereby restored color discrimination function.

If these results can be confirmed, and, if this is indeed a mechanism for restoration of color vision function, then the patients that would have benefited from this particular approach should be those with protanopia. That is, decreasing the density of the interstitial medium through the injections should decrease the refractive index of surrounding medium and thus increase the effective size of the cones. This could be expected to restore the subject's color vision function so long as the appropriate retinal circuitry was still present. Unfortunately, Raymond never specified which type (or types) of the red-green color deficit vision he was able to treat. In any event, given the large number of individuals in the general population afflicted with color deficit vision, this is clearly an area of clinical research that should be further explored.

Another version of color deficit vision is true color blindness or achromatopsia. There have been a number of cases of complete color blindness where the subjects donated their eyes for scientific research after death. The autopsy results showed, in some cases, a normal population of cones, and in others a drastically reduced number of cones (Alpern et al, 1960; Falls, et al, 1965; Glickstein & Heath, 1975; and Harrison et al, 1960) . However, one common feature found by all the studies was that what cones were present were abnormal in shape with outer segments that were either grossly misshapen or abnormally squat and short. Whatever else may have been wrong in these eyes, it is quite clear that in the context of the CSM model such cones could not have provided useful color discrimination.

Summary, Final Note

I have covered a wide range and large number of issues related to human color vision. I hope that in the process I have shed some light on the topic, Color Vision: A New Understanding. While I have made what I believe is a very strong case for the inadequacy (at least) of the three-cone model of color vision as based on "red", "green" and "blue" photopigments uniquely sequestered within each cone type, there is still, of course, a very important role for photopigments in any model of color vision. The photopigments provide the first step in the transduction of light into a visual sensation. However, I am suggesting that the role for photopigments is ancillary to the basic spectral dispersion mechanism of waveguide mode cutoff. Photopigments do the work of absorbing and converting the light into an electrical signal and a differential distribution of photopigments with different absorption curves could well enhance and improve the operation of the basic mechanism proposed here.

By way of a summary, some of what has been covered in this document includes:

> A description of the approximate three dimensional nature of human color vision: how that dimensionality plays in metameric matches, how the ratio of cone bipolar cells to cones varies from 3:1 in the central retina where color vision is trichromatic, to 2:1 in the intermediate retina where color vision is dichromatic and to 1: 1 in the peripheral retina where color vision is essentially monochromatic. The bottom line is that the dimensionality of color perception is evidently more closely tied to the processing circuitry of the retina rather than to separate cone classes.
>
> A description of the Ives' experiment that invalidates the basic premise of the standard three-cone model through the demonstration of the breakdown of statically established metameric matches under dynamic presentation and the validation of that result in our own repetition of the experiment.

The explanation of the Ives' result in terms of the chromatic latency of color perception as measured in our experiments where we made use of the separate and simultaneous observation of rod and cone responses using moving slits of light.

A cursory review of the evidence from molecular genetics and microspectrophotometry that shows that the evidence does indeed suggest the existence of multiple pigments but that these are not necessarily the same thing as multiple cones.

Reviewed the anatomical evidence that shows that instead of separate classes of cones, all the cones in a given area of the retina are essentially identical and that there is a systematic change in the shape of the cone photosensitive outer segments from being long and gently tapering in the central retina where color vision is best to being short, squat and more evidently tapered in the periphery where color vision is diminished.

Described a spectroscopic property of small tapered fibers where low-order waveguide mode cutoff disperses light in a systematic spectral order along the length of a cone.

Pointed out that the cones of the human retina have precisely the right parameters (size, shape and refractive index) to optimally exhibit the spectral dispersion effect.

Described an experimental demonstration of this spectral dispersion in tapered fibers and showed photographs of the spectral dispersion of light emerging from a cone as a result of mode cutoff.

Described the induction of subjective colors with purely black and white illumination presented in the appropriate temporal order, and how the temporally ordered colors match the measured chromatic latency of color perception.

Described how the photoabsorption event within a cone is local, so that information on absorption as a function of position along the length of the cone is available for some read-out mechanism. The absorption event is, in fact, localizable to less than one μm so that for the the 40 μm long foveal cones, the potential wavelength discrimination (for a single cone) is 1/40th of the 650 to 450 nm range of vision or 5 nm.

Described the existence of a mechanism (microscaddic eye movements) to provide the synchronization signal to convert the spectral dispersion of color information along the length of the cones into a temporal code with the characteristics matching the induction of subjective colors.

Provided a list of 42 items, including anatomical features of the cones and retina and of color vision functions and effects. that any model of color vision must explain or at least with which it must be consistent. The proposed cone spectrometer model accounts well for virtually the entire list, while the standard three-cone model predominantly fails.

Described a photpigment-independent calculation that accounts for the hue discrimination function on the basis of the cone spectrometer action alone.

Described how the model accounts for the similarity of the perception of violet and purple as a result of second order mode propagation for light of sufficiently short wavelength.

Described how mistuning of the cone parameters can lead to the common forms of color deficit vision and discussed how the understanding of this process might lead to new ways to clinically address color blindness.

The bottom line to all this is that the eye is indeed a marvelous instrument of seeing, perhaps even more cleverly constructed than had been previously imagined. There is reason, after all, that we can each detect seven million different colors or so and do it over a dynamic range of light intensity that spans some ten orders of magnitude, a feat no invention of technology has yet achieved. Each human eye is composed of an array of millions of sublimely constructed spectroscopic detectors that can each resolve the world of colors in a way no mere gross partitioning into three buckets of color could ever hope to accomplish.

Given the scope of what I have covered here, I can hardly do justice to the vast body of scientific research, studies, publications, and data that has been generated about human color vision over the last two hundred years. There is clearly very much more to do, but perhaps the framework of the cone spectrometer model described both here and in the book, **Cone Shape and Color Vision**, can help with the process of understanding human color vision.

Afterword

I apologize in advance to any whose pet project or effect or issue I did not address (although, perhaps I should be apologizing to those whose issues I did address!). The subject is simply much too vast to cover everything in one document or even one book. I do really feel that what is discussed here, as comprehensive as I have tried to make it, is only a beginning. My greatest joy after so many years of working on this issue would be to see a revitalization of the field of color vision with a new understanding that I may have had a small part in generating.

Anyway, thanks to Nancy for discussions and in helping to proof all this and to Dave for some excellent ideas for making this a better document. Any omissions, errors, or gaffs, unintended as they may be, are entirely my own responsibility.

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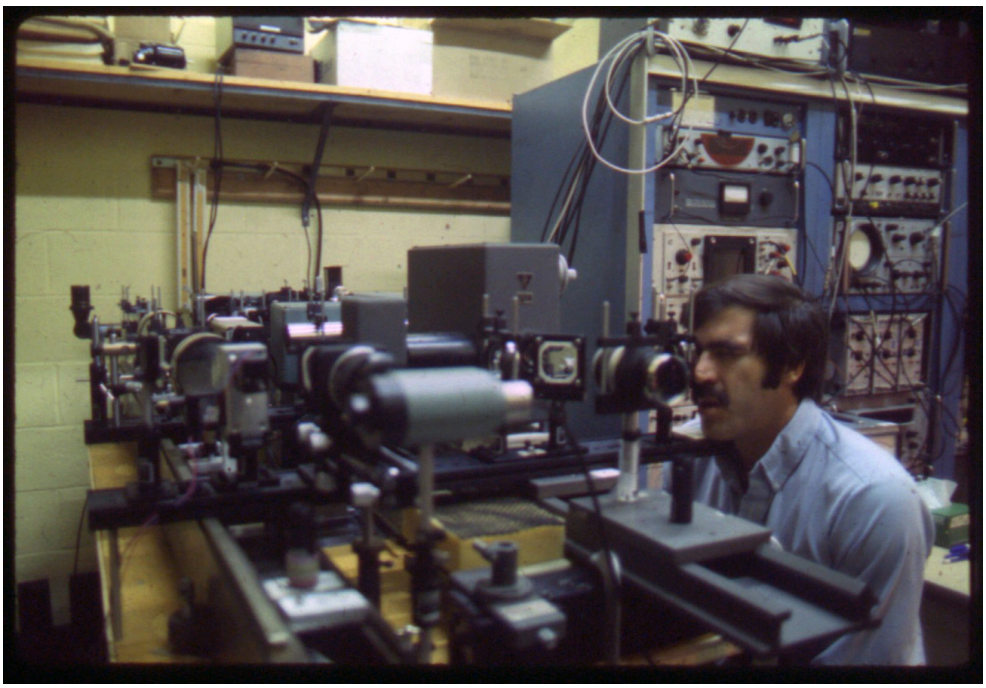
About the Author: John A. Medeiros

So what about me and why should you be spending your valuable time reading what I have to say about how your eyes see color?

Well, other than that I think the evidence will show that what I have covered on this web site is indeed valid, it does represent over thirty years of professional work by a number of colleagues and myself.

I have a doctorate in physics from the University of Massachusetts (Amherst) where I did experimental work on atomic collisions (Thesis: Metastable Hydrogen Atom Collision Processes). Subsequently, I worked for some five years or so as a postdoctoral fellow and then as a research associate at the University of Western Ontario investigating both the anatomical structure of the retina and damage mechanisms of laser irradiation in the eye. That work contributed in a small way to the current routine clinical treatment by ophthalmologists of retinal problems using lasers. That's also where I got the basic idea of the cone spectrometer model as a consequence of using a physicist's perspective in studying the eye and vision.

Following that work, I took an assistant professorship in the physics department at The Pennsylvania State University (York campus) for six years. My research there included the study of arterial branching in the retina and the work on the separation of rod and cone perception. The photograph below shows me at the business end of the moving slit apparatus we put together in my lab at Penn State during that period. I was awarded tenure at Penn State but I subsequently decided to leave to work in industry.



After six years in the deserts of New Mexico as Chief Optical Engineer for Pacific Sierra Research on some optical physics projects that I still can't talk about, I went to work for COLSA Corporation in Huntsville, AL as a Senior Scientist where I've been for the last (nearly) twenty years. My day job involves playing with large toys (some of the biggest computers on the planet) and no; we don't use them for investigating color vision. Instead, they are used for computational fluid dynamics calculations investigating hypersonic flight.

I have had the great privilege over the years of working with some very good and very smart people on a number of different projects. As you might expect, these very competent colleagues are not necessarily in the mainstream of vision research on the standard trichromatic model. Simply put, most of those supporting the traditional model have not been very welcoming of any efforts to point out the need for a radically new approach to the understanding of color vision. Hopefully, what I have put together here on this web site and in my book, Cone Shape & Color Vision, will help in starting some very needed discussion of just how color vision really works.