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HUMAN COLOR PERCEPTION

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Abstract

Sir Isaac Newton's prism experiments were fundamental to the development of two distinct areas of modern science. The first was the physics of light and the second was the biology of color vision. While discussing color and color imaging systems it is important to distinguish between the domain of physics and the domain of biology. To illustrate that distinction, this paper will review historic experiments in color perception and discuss the varieties of color sensations that can be produced by a single physical stimulus.

When Sir Isaac Newton sent a pencil of sunlight through a prism, he initiated two distinct but closely intertwined sciences. The first was the physics of light; the second was the biology of vision. The study of light describes what light is, how it is produced, propagated, reflected, refracted, transmitted, and absorbed. The other science, the study of vision, starts with the human sensations produced by light, and tries to understand the way particular sensations are produced by particular light stimuli falling on the eye.

Although these two subjects are distinct areas of science searching for solutions to different problems, they are closely intertwined. In the 17th century, the human visual system was the only radiometer available. This meant that physical measurements had to be made with a biological system. Today there is an abundance of radiance measuring devices. They are necessary for precisely describing the stimuli that generate a particular sensation.

The main concern of this chapter is the development of ideas about the biology of human vision. In the beginning, the important ideas were not easily separable from those of physics. To begin let us see how Newton summarized his prism experiments.

> *"In the Experiments of the fourth Proposition of the first Part of this first Book, when I had separated the heterogeneous Rays from one another, the Spectrum pt formed by the separated Rays, did in the Progress from its End p, on which the most refrangible Rays fell, unto its other End t, on which the least refrangible Rays fell, appear tinged with this Series of Colours, violet, indigo, blue, green, yellow, orange, red together with all their intermediate Degrees in a continual Succession perpetually varying. So that there appeared as many Degrees of Colours, as there were sorts of Rays differing in Refrangibility. "* [1]

Newton made an important distinction between refractability and sensation.

> *"The homogeneal Light and Rays which appear red, or rather make Objects appear so, I call Rubrifick or Red-making; those which make Objects appear yellow, green, blue, and violet, I call Yellow-making, Green-making, Blue-making, Violet-making, and so of the rest. And if at any time I speak of Light and Rays as coloured or endued with Colours, I would be understood to speak not philosophically and properly, but grossly, and accordingly to such Conceptions as vulgar People in seeing all these Experiments would be apt to frame. For the Rays to speak properly are not coloured. In them there is nothing else than a certain Power and Disposition to stir up a Sensation of this or that Colour."* [2]

Then eight propositions later he describes the variation in colors of natural bodies.

> *"These Colours arise from hence, that some natural Bodies reflect some sorts of Rays, others other sorts more copiously than the rest. Minium reflects the least refrangible or red-making Rays most copiously, and thence appears red. Violets reflect the most refrangible most copiously, and thence have their Colour, and so of other Bodies. Every Body reflects the Rays of its own Colour more copiously than the rest, and from their excess and predominance in the reflected Light has its Colour."* [3]

There are two parts of this hypothesis. The first is that different bodies reflect different portions of the spectrum. The second is that the composition of the light coming to the observer's eye from that body determines its color. If Newton had been using current terminology, he would have said that color sensations simply depended on the wavelength-energy distribution of the light. Extending that statement we might say Newton believed that a unique color sensation was associated with a particular wavelength-energy distribution. The validity of this second part of Newton's hypothesis is carefully examined throughout this chapter.

In 1802, Thomas Young proposed a fundamental change in Newton's theory of how humans saw color sensations. He suggested that there were three kinds of receptors in the human eye. This was a very important hypothesis because it maintained the distinction set forth by Newton between the properties of light and the properties of human sensations. Lomonosov and Palmer in that period failed to maintain this distinction and suggested that there were only three kinds of light and three kinds of visual receptors." Young recognized that Newton's theory of light was accurate and that the properties of color mixing need only apply to human vision.

> *"Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colours, red, yellow, and blue, ... : and each sensitive filament of the nerve may consist of three portions, one for each principal colour."*[5]

Young proposed that there were three receptors at each color sensitive point in the retina. The wavelength-energy distribution at each point determines the integrated response (over the bandwidth of receptor sensitivity) of each of these receptors. The relative response of each receptor at each point determines the color sensation. Finally, we would expect Young to believe that for each unique triplet of integrated receptor responses, there would be a unique color sensation.

There were really two distinct parts of Young's hypothesis. The first was that there are three kinds of receptors. The second was that these three receptors work as a triplet at a point. One hundred sixty-six years after Young proposed the idea, Brown and WaId[6] and Marks, Dobelle, and MacNichol[7] measured the spectra of cones in the human retina. They found three different pigments in the cone receptors. The hypothesis that these three kinds of receptors must work at a point has yet to be proven true. In fact, there is substantial evidence to be discussed later that the second part of Young's hypothesis is not true.

The next major addition to the history of color science was made by

James Clerk Maxwell and Hermann von Helmholtz. They took the suggestion made by Young and established it as experimentally tested theory. Maxwell invented the color top that enabled the quantitative measurement of color mixing, wrote the first color mixing equations, and proceeded from Newton's color circle to set up the first color triangle defined by experiments.

> *"Let it be granted that the three pure sensations correspond to the colours red, green, and violet, and that we can estimate the intensity of each of these sensations numerically.*
>
> *"Let v, r, g be the angular points of a triangle, and conceive the three sensations as having their positions at these points. (See Figure 1-1) If we find the numerical measure of the red, green, and violet ports of the sensation of a given colour, and then place weights proportional to these parts at r, g, and v,*

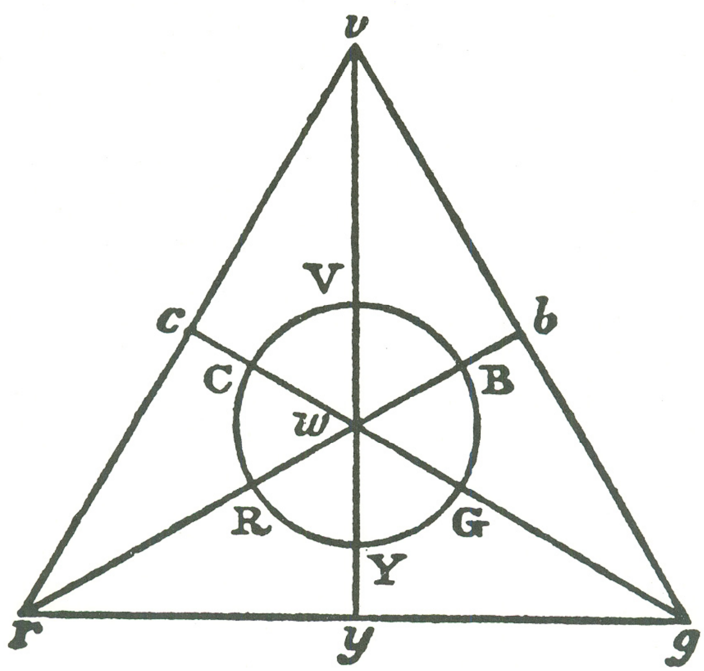

Figure I-I - One of Maxwell's color triangles from a letter to Dr. G. Wilson, 1855.

and find the centre of gravity of the three weights by the ordinary process, that point will be the position of the given colour, and the numerical measure of its intensity will be the sum of the three primitive sensations.

"In this way, every possible colour may have its position and intensity ascertained; and it is easy to see that when two compound colours are combined, their centre of gravity is the position of the new colour.

"The idea of this geometrical method of investigating colours is to be found in Newton's Opticks (Book I., Part 2, Prop. 6), but I am not aware that it has been ever employed in practice, except in the reduction of the experiments which I have just made. The accuracy of the method depends entirely on the truth of the theory of three sensations, and therefore its success is a testimony in favour of that theory.

"Every possible colour must be included within the triangle rgv. White will be found at some point, w, within the triangle. If lines be drawn through w to any point, the colour at that point will vary in hue according to the angular position of the line drawn to w, and the purity of the tint will depend on the length of that line.

"Though the homogeneous ray s of the prismatic spectrum are absolutely pure in themselves, yet they do not give rise to the 'pure sensations' of which we are speaking. Every ray of the spectrum gives rise to all three sensations, though in different proportions; hence the position of the colours of the spectrum is not at the boundary of the triangle, but in some curve CRY G B V considerably within the triangle. The nature of this curve is not yet determined, but may form the subject of a future investigation.

"All natural colours must be within this curve and all ordinary pigments do in fact lie very much within it. The experiments on the colours of the spectrum which I have made are not brought to the same degree of accuracy as those on coloured papers. I therefore proceed at once to describe the mode of making those experiments which I have found most simple and convenient.

"The coloured paper is cut into the form of discs, each with a small hole in the centre, and divided along a radius, so as to admit several of them being placed on the same axis, so that

part of each is exposed. By slipping one disc over another, we can expose any given portion of each colour. These discs are placed on a little top or teetotum, consisting of a flat disc of tin-plate and a vertical axis of ivory. This axis passes through the centre of the discs, and the quantity of each colour exposed is measured by a graduation on the rim of the disc, which is divided into 700 parts. (See Figure 1-2.)

"By spinning the top, each colour is presented to the eye for a time proportional to the angle of the sector exposed, and I have found by independent experiments, that the colour produced by fast spinning is identical with that produced by causing the light of the different colours to fall on the retina at once.

"By properly arranging the discs, any given colour may be imitated and afterwards registered by the graduation on the rim of the top. The principal use of the top is to obtain colour equations. These are got by producing, by two different combinations of colours, the same mixed tint. For this purpose there is another set of discs, half the diameter of the others, which lie above them and by which the second combination of colours is formed.

"The two combinations being close together, may be accurately compared, and when they are made sensibly identical, the proportions of the different colours in each is registered, and the results equated." [8]

In the following quotation from a paper presented to the Royal Society of Edinburgh, Maxwell reviews the contributions of Newton and Young and describes his invention of color photography. (In 1861 Maxwell exhibited the first trichromatic photograph during a lecture before the Royal Institution [9].)

"Newton, who was the first to demonstrate the actual existence of a series of kinds of light, countless in number, yet all perfectly distinct, was also the first to propound a method of calculating the effect of the mixture of various coloured light; and this method was substantially the same as that which we have just verified. It is true, that the directions which he gives for the construction of his circle of colours are somewhat arbitrary, being probably only intended as an indication of the general nature of the method, but the method itself is mathematically reducible to the theory of three elements of the colour-sensation.

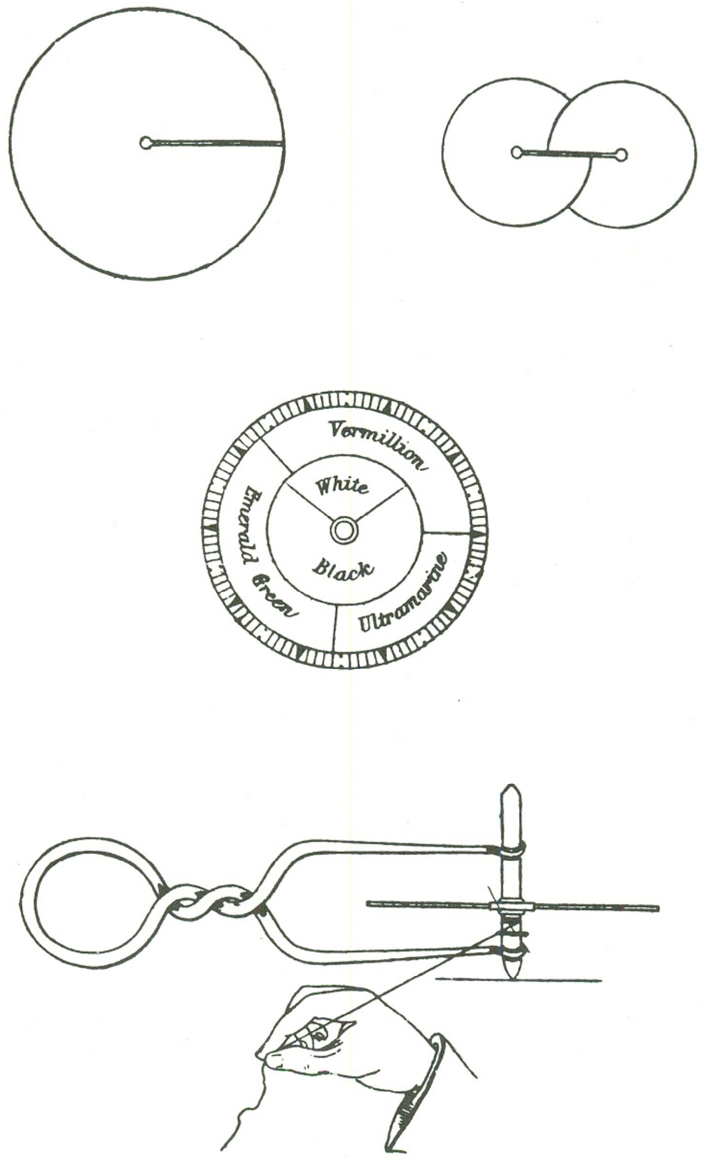

Figure 1-2 - Diagram of Maxwell's color top from his 1857 article in the transactions of the Royal Society of Edinburgh. At the top of the figure are paper discs of different sizes with slits to allow them to slide over one another. These discs were arranged and calibrated by the 100 divisions around the outside (center diagram). The top itself is shown at the bottom of the figure.

"Young, who made the next great step in the establishment of the theory of light, seems also to have been the first to follow out the necessary consequences of Newton's suggestion on the mixture of colours. He saw that, since this triplicate has no foundation in the theory of light, its cause must be looked for in the constitution of the eye; and, by one of those bold assumptions which sometimes express the result of speculation better than any cautious trains of reasoning, he attributed it to the existence of three distinct modes of sensation in the retina, each of which he supposed to be produced in different degrees by the different rays. These three elementary effects, according to his view, correspond to the three sensations of red, green, and violet, and would separately convey to the sensorium the sensation of a red, a green, and a violet picture; so that by the superposition of these pictures, the actual variegated world is represented.

"In order fully to understand Young's theory, the function which he attributes to each system of nerves must be carefully borne in mind. Each nerve acts, not, as some have thought, by conveying to the mind the knowledge of the length of an undulation of light, or of its periodic time, but simply by being more or less affected by the rays which fall on it. The sensation of each elementary nerve is capable only of increase and diminution, and of no other change. We must al so observe, that the nerves corresponding to the red sensation are affected chiefly by the red rays, but in some degree al so by those of every other part of the spectrum; just as red glass transmits red rays freely, but al so suffers those of other colours to pass in smaller quantity.

"This theory of colour may be illustrated by a supposed case taken from the art of photography. Let it be required to ascertain the colours of a landscape, by means of impressions taken on a preparation equally sensitive to rays of every colour.

"Let a plate of red gloss be placed before the camera, and an impression taken. The positive of this will be transparent wherever the red light has been abundant in the landscape, and opaque where it has been wanting. Let it now be put in a magic lantern, along with the red glass, and a red picture will be thrown on the screen.

"Let this operation be repeated with a green and a violet glass, and, by means of three magic lanterns, let the three images be superimposed on the screen. The colour of any point

on the screen will then depend on that of the corresponding point of the landscape; and, by properly adjusting the intensities of the lights, &c., a complete copy of the landscape, as far as visible colour is concerned, will be thrown on the screen. The only apparent difference will be, that the copy will be more subdued, or less pure in tint, than the original. Here, however, we have the process performed twice - first on the screen, and then on the retina.

"This illustration will shew how the functions which Young attributes to the three systems of nerves may be imitated by optical apparatus. It is therefore unnecessary to search for any direct connection between the lengths of the undulations of the various rays of light and the sensations as felt by us, as the threefold partition of the properties of light may be effected by physical means. The remarkable correspondence between the results of experiments on different individuals would indicate some anatomical contrivance identical in all. As there is little hope of detecting it by dissection, we may be content at present with any subsidiary evidence which we may possess. Such evidence is furnished by those individuals who have the defect of vision which was described by Dalton, and which is a variety of that which Dr. G. Wilson has lately investigated, under the name of Colour-Blindness." [10]

It is easy to see that the entire scope of this book is directly traceable to the work of James Clerk Maxwell. He found experimental evidence supporting Young's three receptor theory; he wrote the first equations of colorimetry; he invented the first color photograph. In addition, he initiated the quantitative study of color-blindness. II It is fun to imagine what his reaction might be if he were reading this book.

Many things have happened in the science and applications of color technology since 1879. Although most of the basic ideas were known while Maxwell was alive, the successful applications of those ideas came later. Additive color reproduction, while started by Maxwell in his triple projection system, needed a variety of different techniques before becoming practical. Today, additive color reproduction is used primarily in color television. The subtractive color principle, first described by du Hauron in 1862, is the basis of most present day color photography. As such, its use has spread to the diversified areas of color printing, microfilming, aerial photography, etc. It is also the principle used in instantaneous color processing introduced by Land in 1963. Concurrent with these developments came the need for establishing standards of color matching for use in science and industry. In 1931 the Commission

International d'Eclairage first established such standards. One hopes that Maxwell would enjoy seeing the wide variety of technological branchings which have grown from his fruitful ideas.

based more on the biology of vision. I can well afford to do this because the continuation of Maxwell's experiments leads to colorimetry and we are very fortunate in that the next chapter on colorimetry is by Dr. Gunter Wyszecki.

Maxwell did not experiment with what we described as the second half of Young's hypothesis. That is, he did not test the idea that the three receptors worked at a point to determine color. If you assume, as Maxwell must have, that the comparison of red, green, and blue responses are compared at a point, then a unique triplet of red, green, and blue should produce a unique color sensation. It would follow then that a single wavelength-energy distribution should always look the same color. Helmholtz realized that this was not always true. He devoted a chapter in the Physiological Optics on the subject, which he called contrast. In the introduction to the chapter, Helmholtz says,

> *“... what we have to do now is to investigate the mutual influence of different luminosities and colours appearing together in the visual field side by side with each other.*
>
> *"The result of such a juxtaposition usually is that each portion of the visual field next (to) a brighter one looks darker, and vice versa; and a colour alongside another colour resembles more or less the complementary colour of the latter. The opposition thus manifested is implied in the term contrast."* [12]
>
> At the end of the chapter he summarized the history of the subject.
>
> *"Leonardo da Vinci was quite familiar with contrast phenomena. He says that of all colours of equal purity those are the most beautiful that are placed side by side with their opposites; that is, white with black, blue with yellow, red with green. Later the contrast phenomena that especially attracted attention more than all others were coloured shadows. Otto v. Guericke knew about them and tried to utilize them to prove Aristotle's statement, that blue could be obtained by mixing white and black ... The subjective nature of the colour of one of the shadows seems to have been discovered first by RUMFORD, by observing it through a narrow tube. GOETHE, GROTTHUSS, BRANDES, and TOURTUAL adopted the same view ... PLATEAU included contrast phenomena in his theory of afterimages ... The modifications of individual colours by their juxtaposi-*

tion to others were accurately described by CHEVREUL." [13]

It is worthwhile to pause here and review in somewhat greater detail the accumulated evidence from da Vinci, von Guericke, Rumford, Goethe, Plateau, and Chevreul that a particular wavelength-energy distribution does not give a unique color sensation. In the following quotation, Rumford described how he obtained colored shadows.

> *"Desirous of comparing the intensity of the light of a clear sky, by day, with that of a common wax candle, I darkened my room, and letting the daylight from the north (coming through a hole near the top of the window-shutter) fall at an angle of about 700 upon a sheet of very fine white paper, I placed a burning wax candle in such a position that its rays fell upon the same paper, and, as nearly as I could guess, in the line of reflection of the rays of daylight from without; when, interposing a cylinder of wood, about half an inch in diameter, before the centre of the paper, and at the distance of about two inches from its surface, I was much surprised to find that the two shadows projected by the cylinder upon the paper, instead of being merely shades, without colour, as I expected to find them, the one of them-that which, corresponding with the beam of daylight, was illuminated by the candle,- was yellow; while the other, corresponding to the light of the candle -- and consequently illuminated by the light of the heavens, - was the most beautiful blue that it is possible to imagine."* [14]

After a number of different experiments he said:

> *" ... I began to suspect that the colours of the shadows might in many cases, notwithstanding their apparent brilliancy, be merely an optical deception, owing to contrast or to some effect of the other real and neighbouring colours upon the eye. "* [15]

He then set up two Argand's lamps that emitted the same color light and hence did not produce colored shadows. He looked through a blackened tube at one of the shadows while an assistant placed a sheet of yellow glass before the lamp. He wrote,

> *"The result of the experiment was very striking, and fully confirmed my suspicions with respect to the fallacy of many of the appearances in the foregoing experiments.*
>
> "So for from being able to observe any change in the shadow upon which my eye was fixed, I was not able even to tell when the yellow glass was before the lamp and when it was not; and,

> *though the assistant often exclaimed at the striking brilliancy and beauty of the blue colour of the very shadow I was observing, I could not discover in it the least appearance of any colour at all. But as soon as I removed my eye from the tube, and contemplated the shadow with all its neighbouring accompaniments, - the other shadow rendered really yellow by the effect of the yellow glass and the white paper, which had likewise from the same cause acquired a yellowish hue, _ the shadow in question appeared to me as it did to my assistant of a beautiful blue colour."* [16]

Clearly the wavelength-energy distribution of the light was not affected by viewing the shadows through a black tube. It follows then that a single physical stimulus at a point does not generate a unique color sensation.

Da Vinci, Goethe, Chevreul and many others up to the modern work of Albers[17] have studied the effect of colors surrounding other colors. This mass of evidence also shows us that a single wavelength-energy distribution need not and does not generate a unique color sensation.

Helmholtz's response to this realization was to suggest that pure simultaneous contrast was due to a change, not of sensation, but of judgment. Helmholtz also realized that the color of objects remained essentially constant, even though the wavelength distribution of the illumination changed dramatically. Again, he argued that it was judgment that made the visual system indifferent to large changes in wavelength-energy distribution.

> *"By seeing objects of the same colour under these various illuminations, in spite of difference of illumination, we learn to form a correct idea of the colours of bodies, that is, to judge how such a body would look in white light; and since we are interested only in the colour that the body retains permanently, we are not conscious at all of the separate sensations which contribute to form our judgment."* [18]

Helmholtz rejected the idea proposed by Hering[19] that the responses of one region of the retina affected the responses of other regions. In this century, experiments in neurophysiology have unequivocally shown that interactions between adjacent parts of the retina are found in almost every type of visual system. Experiments from those of Hartline and Ratliff's[20] on "the horseshoe crab to those of Werblin and Dowling's[21] on the vertebrate Necturus have shown interactions between widely spaced receptors.

If we take the results of the different contrast experiments and juxtapose them with the ideas discussed by Newton, Young, and Maxwell, we arrive at a fundamental paradox. In all these contrast experiments the triplets of Young's receptors receive the same physical stimulus. Yet, a variety of sensations are produced by this single stimulus. All of these experiments indicate that a particular wavelength-energy distribution need not produce a single color sensation. It is obvious that something else is needed beyond Young's hypothesis for a sufficient description of the visual system. Are we looking for a minor addition or are we looking for a fundamental change? When we study the contrast experiments and the real everyday visual environment, do we find that a. particular wavelength-energy distribution is always nearly the same sensation, or do we find that it can be any color sensation? If we could prove the latter, namely that a particular stimulus ca n produce any sensation, then we would have to look for a fundamental change in our ideas about the biology of vision.

Land [22,23] performed an experiment in which a single mixture of red, green, and blue light produced many different color sensations. The observers reported white, pink, green, red, brown, yellow, purple, blue, and black sensations from one and the same wavelength-energy distribution coming to their eyes from the points in question. The experiment used a large complex display called the Mondrian. The display had about 100 different colored matte papers arranged arbitrarily so that no particular color surrounded another. In fact, there were over five or six different papers around each other. The display was illuminated by three projectors, each with a broad-band interference filter. One filter transmitted part of the long waves, or red-making portion of the spectrum. The second transmitted part of the middle-length waves, or green-making rays, and the third transmitted part of the short waves, or blue-making rays. Each projector had an independent brightness control. The observers picked an area - say a white one - and measured the radiance from that area in each of the three illuminations. Then the observers picked a second area - say a red one - and measured the three radiances from it. These measurements showed that there was about the same amount of long-wave light coming from the red paper as from the white, but there was much less middle- and short-wave light. The illumination was then changed so that the same radiances came from the red paper us came previously from the white paper. This was accomplished by increasing the middle- and short-wave illuminations by the amounts that they were poorer reflectors than white. All three illuminations were turned on together and the red area still looked red even though it sent the same wavelength-energy distribution to the eye as the white had a moment before. In the same manner, Land went from paper to paper in the display and produced very nearly the full gamut of color sensations with a single wavelength-energy distribution.

This experiment led Land to propose that something fundamental was wrong with the idea that the biological system used the physical stimulus at a point. Instead of the long-, middle-, and short-wave receptors comparing responses at a point, Land proposed that all the long-wave receptors interacted to compute a biologic equivalent of reflectance from the long-wave flux. Similarly the middle- and short-wave receptors acted as independent sets to compute biologic reflectances for middle- and for short-wave flux.[24] This biologic correlate of reflectance integrated over a band of wavelengths is called lightness.[25] It is what we see if we look at the world in a single band of wavelengths. Land proposed that there exist systems which he called Retinexes that generate the lightnesses in each of the long, middle, and short wave bands. Color sensations are generated by comparing the three different biologic reflectances or lightnesses.

The idea of the visual system sensing reflectance has its foundations back with Newton. Remember, he described that certain bodies reflect some sorts of rays more copiously than the rest, and hence their color. What Newton did not realize was the paradox that color sensations stayed the same when the illumination changed. Maxwell also was very close to the idea that reflectance in each wave band generated color sensations. He made the first color separation photographs. Looking at these separations, the observer sees the apparent reflectances integrated over each wave band. Maxwell, as well as Newton, did not discuss the effects of illumination. Namely, color sensations correspond to the reflectance of objects, even though the light in the natural environment coming to the eye from these objects is determined by an extremely variable and "unknowable" illumination.

The idea of an "unknowable" illumination is worth studying for a moment. Since the flux at the eye is the product of the reflectance times the illumination, one cannot determine the illumination from the total flux unless one knows the reflectance of the object. In studying the physics of light today, determining reflectance is a trivial matter. But remember, we are discussing the environmental problem confronting the evolving animal. The illumination varies in spectral composition, such as sunlight vs. skylight; in overall quantity, such as a bright day vs. a dark day; and in uniformity of illumination across the field of view, such as shadows cast by clouds or trees, etc. The animal visual system cannot use the same techniques the physicist would. The animal has neither reflectance standards nor illumination standards. His estimation of the reflectance of objects must be accomplished both instantaneously and internally. If within these constraints the illumination is "unknowable," then the animal must have developed a mechanism that can determine reflectance without separating illumination from the flux at the eye. This is the job of each Retinex. It must generate lightnesses that correspond to reflectances. Land and McCann [26] proposed a visual mechanism for computing reflectance regardless of the non-uniformities in illumination. This mechanism uses the ratio of flux at closely spaced points and sequentially multiplies them to form a product. This product is the mathematical model's approximation of reflectance. It is beyond the scope of this chapter to discuss the details of this mechanism, however the basic hypothesis is that taking the ratio of flux at closely spaced points eliminates the effect of gradual changes of illumination. The change in flux is so small from gradual illumination changes that it cannot be detected by the ratio measuring cells. Abrupt changes in flux are caused by edges between objects of different reflectance. The magnitude of the change in reflectance across an edge is measured by the ratio operation, thus establishing the relative reflectance of two adjacent areas. The ratio of reflectances is then sequentially multiplied to obtain the relative reflectance of each object in the field of view. Lightness, in principle, is also independent of overall changes in the level of illumination. This follows naturally from the fact that lightness correlates with reflectance and the reflectance of an object does not change with changes in illumination. The human system approaches total independence; however, there exists enough of a dependence on overall illumination to tell a bright day from a dark day.

Let us consider the effects of changing illumination from tungsten to zenith skylight. In tungsten illumination the long-wave receptors would interact with each other to form a lightness image that reported the biologic equivalent of reflectance for the long-wave portion of the spectrum. The middle-wave receptors would interact to generate a different set of lightnesses, as would the short-wave receptors to form a third set of lightnesses. The next stage in the processing would be to compare the three biologic correlates of reflectances of each area and to generate its color sensation. Now we change the illumination from tungsten to zenith skylight. (For simplicity we can assume that both illuminations have the same quantity of middle-wave light.) This change greatly diminishes the amount of long-wave light and greatly increases the amount of short-wave light. Again, according to Retinex theory the long-wave receptors interact to generate lightnesses or biologic reflectances for each area. These lightnesses will be nearly identical to those in tungsten illumination. The only difference will be that the overall level of long-wave light will be lower and that might produce very slight changes in lightness. Similarly the short-wave lightnesses will be the same except for slight shifts due to increasing amounts of short-wave light. The same explanation applies to the colored Mondrian experiments. Each Retinex computes lightnesses independent of the overall level of illumination.

It is clear that when one accepts the idea that each kind of receptor acts as a set to generate the correlate of reflectance, the problems of changing illumination and other contrast experiments are easily explained. The study of color vision shifts to new unexplored questions. How can a set of receptors compute reflectance? How do you simulate, calculate, and observe the lightnesses produced by those broad-band visual receptors? Is there a unique sensation associated with each triplet of I lightnesses?

Before we explore all these new questions, how sure can we be that the receptors are free to act as independent sets and not as three endings of a single nerve as Young suggested? The answer is that there is good evidence at certain neural stages that each set of cones is independent of the other sets of cones, as well as independent of the rods.

Stiles,[27] using increment threshold techniques, found almost complete independence between rods and each cone mechanism. He superimposed a test flash of one variable wavelength on a background of a second variable wavelength. For each mechanism, the increment threshold was lowered in proportion to that mechanism's sensitivity to the test spot and increased in proportion to its sensitivity to the surround. This simple proportional relationship indicates the absence of interactions of the different mechanisms. Alpern[28] reported that the threshold for a 5 msec. flash can be greatly increased by following it with a second flash surrounding the first. This phenomenon is called metacontrast. Using the different spectral sensitivities, directional sensitivities and rates of dark adaptation of rods and cones, Alpern designed metacontrast experiments to test the independence of rods and cones. For example, when the test flash excited only the rods, the surrounding after-flashes of different wavelengths but equal brightness to the rods raised the test threshold the same amount. This indicated the absence of rod-cone interactions in the metacontrast mechanism below cone threshold. Alpern also found metacontrast after light adaptation when the cones had recovered sensitivity to light, but the rods had not. This showed that cones affected cones as much as rods affected rods. Alpern and Rushton[29] extended the desensitizing metacontrast experiments to test the independence of the cone mechanisms from each other. They used test flashes of different various wavelengths and after-flashes of variable wavelengths. They found that if a test flash excites one cone mechanism, then the after-flash raises this threshold only by stimulating that mechanism in the surround. Stimulating the other cone mechanisms does not affect the test flash threshold. Westheimer[30] showed that illuminating the area surrounding a test flash either increased its threshold (desensitizing) or decreased its threshold (sensitizing) depending on whether the distance separating the surrounding flash and the test flash was large or small. He used the sensitizing interactions to show another type of rod-cone independence. He showed that sensitizing signals produced by the rods did not produce sensitization in the cones. McKee and Westheimer 31 measured the action spectrum of the sensitizing effect for the red and green color systems. They showed that the desensitizing and sensitizing adaptation zones are found in both red and green mechanisms. Further for each mechanism the surrounding sensitizing zone has the same action spectrum. This supports the idea that the red and green cone mechanisms are independent of each other at least at the levels that produce sensitizing and desensitizing interactions.

Duplicity theory states that the rods and cones are completely different systems: one for low-radiance, colorless vision and the other for high-radiance, color vision. The many different properties of images produced by rods and cones have accumulated substantial support for the idea that the rod and cone processes are different. The rods and cones have different shapes and distribution over the retina,[32] different rates of dark adaptation,[33] different spectral sensitivities,[34] different directional sensitivities,[35] different acuity properties,[36] different flicker fusion properttes,[37] and independent desensitizing[38] and sensitizing[39] "retinal interactions .

Despite all this evidence that the rods and cones are independent systems, experiments have shown that color sensations can be generated by the interactions of rods and cones. Blackwell and Blackwell found that a rare type of color-blind observer reported different color names even though he had only rods and short-wave cones.[40] Stabell reported" color sensations from the interactions of afterimages (produced by lights above cone threshold) and stimuli below cone threshold.[41]

McCann and Benton found that the rods and long-wave cones interact to produce color sensations.[42] The technique was to determine the 546 nm flux necessary for a threshold response of the rods and the 656 nm flux necessary for a threshold response of the long-wave cones. Figure 1-3 shows the plot of wavelength vs. radiance necessary for a threshold response of the rods and each type of cone. The shaded areas illustrate the technique of providing just enough 546 nm flux to excite the rods and just enough 656 nm flux to excite the long-wave cones. Using those quantities of 546 nm and 656 nm flux, McCann and Benton produced color sensations even though the 546 nm flux was a thousand times below cone threshold. They further showed that the color images produced by these interactions were nearly indistinguishable from images seen on two wavebands entirely above cone threshold.

Performing experiments with only rods and long-wave cones provides a test of the hypothesis that color depends on the lightnesses produced by independent systems. Certainly the rods are part of an independent system that forms an image in terms of lightness. We know this from the experiments supporting duplicity theory and from observing the colorless rod image in very low illumination. In addition, the image seen by the long-wave cones alone has no variety of color sensations, just an overall wash of red covering the entire field of view. Here again we have an image in terms of lightness, with a reddish wash that must interact with the colorless, rod lightness image. The interaction of these two images as already described is almost indistinguishable from an image seen on two wave bands entirely above cone threshold. This observation goes quite far in supporting the idea that color sensations are generated by the comparison of lightnesses formed by independent systems.

Can we press the hypothesis even further? Is it possible, in a complex image that excites only the rods, to produce two significantly different lightnesses from areas simultaneously sending the same radiance to the eye? Is it possible to combine such a rod image with an image

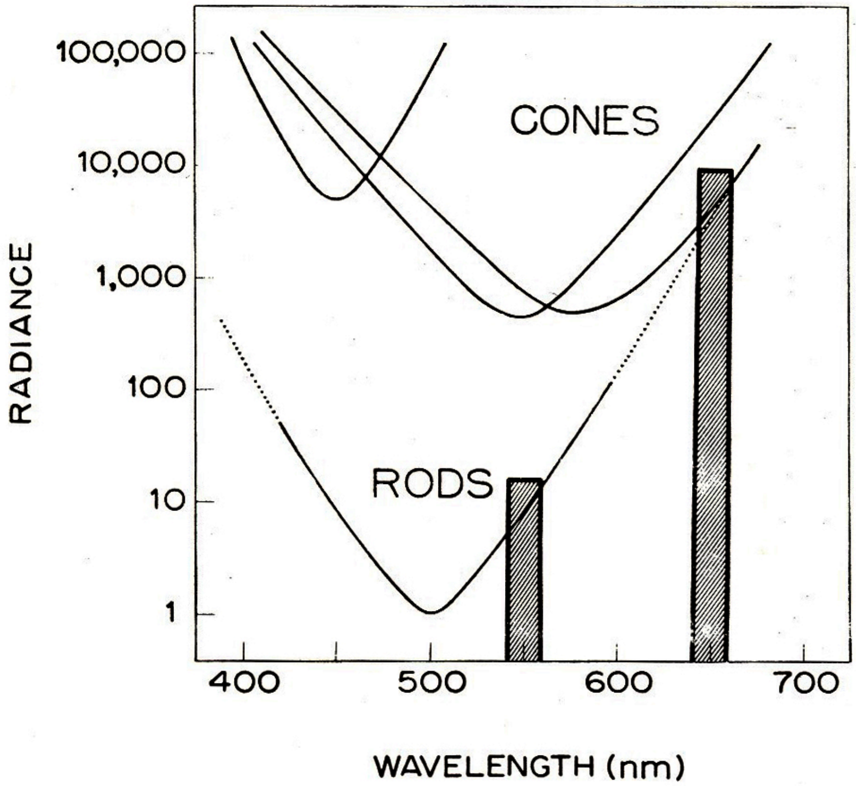

Figure 1-3 - Plot of wavelength vs. the radiance necessary to excite a threshold response of the rods and the various types of cones in the retina. The shaded lines indicate the radiances necessary for exciting the rods with 546 nm light, and the long-wave cones with 656 nm light.

seen by the long-wave cones, which has different lightnesses produced by areas having the same radiance? Do these areas produce different color sensations? Are the sensations consistent with the hypothesis that colors are determined by the comparison of lightnesses?

Land[43] set up an experiment in which one area appeared red and another area appeared green even though the radiations coming from both areas were identical. The experimental display was a pastel chalk drawing by Jeanne Benton, called the Street Scene (Figure 1-4), which included a green awning on the left side and a red door on the right side.

I set up the Street Scene display and repeated Land's experiment with only the rods and long-wave cones.[44] I used two projectors with narrow-band interference filters, one 656 nm the other 546 nm to illuminate the entire display. Figure 1-4 is a pair of photographs of the Street Scene taken with the 656 nm and 546 nm filters in uniform illumination. The door reflected a high percentage of long-wave radiation and

Figure 1-4 - Multicolored chalk drawings by Jeanne L. Benton. Top photograph was taken in uniform 656 nm illumination; the bottom in uniform 5046 nm illumination. This drawing was used with controlled non-uniform 656 and 546 nm illumination to produce two different color sensations from physically identical stimuli. The radiance for each wavelength was also controlled so that only the rods and long-wave cones were above threshold.

a low percentage of middle-wave radiation. A wedge transparency was chosen for one projector so that the same radiance at 656 nm came to the eye from the awning and the door. Similarly, another wedge was placed on the other projector so that the same radiance of 546 nm came to the eye from the awning and the door. Therefore, when both projectors were turned on together, exactly the same composite stimulus was coming from the center of both the awning and the door. The awning and the door sent only one-seventh the amount of 546 nm light necessary to obtain a threshold response from the middle-wave cones. The entire scene was below cone threshold for 546 nm light and slightly above long-wave cone threshold for 656 nm.

The observers reported that the awning was dark gray in 656 nm illumination and light gray in 546 nm illumination. They further described the door as being light gray in 656 nm and dark gray in 546 nm. The observers were then asked to describe the color sensations of the two areas in the combined long- plus middle-wave illumination. They reported that the sensations from those two areas were different from each other - green and red - even though the centers of the areas sent identical physical stimuli to the eye. Just as in Land's experiments entirely above cone threshold, the simultaneously identical sets of radiances produced very different color sensations. Therefore, color sensations from rod-cone interactions depend on the lightnesses of each area and not flux. Thus we have established a specific example of the mechanism proposed by Land's Retinex theory. Rods and cones act independently to form lightnesses which correlate with reflectance. Lightnesses of the two systems are compared to generate color sensations.

Now we have completed the long trip from Newton's prism to a small portion of the work that is taking place today. The physics of light is much more settled than the biology of vision. Even within the study of vision we have many different fields that differ because of their fundamental first assumptions. There is the domain of colorimetry that comes closest to physics. There is the romantic anti-physical tradition followed by Goethe and Hering. The problem most of us are concerned with is: What color sensation will a particular wavelength-energy distribution produce? This particular question is beyond the experimental definition of colorimetry, which is technically restricted to the problem of color matching. When you step from the rigor of this closest relative of physics into the world of the evolving animal, you find that visual sensations correspond with reflectance. The animal has a mechanism for finding the reflectance of each object from the light coming to his eyes. The mechanism does this even though the illumination is "unknowable." The lesson from the biology of vision is that one must be very careful when one leaves the orderly house of physics end ventures into our natural visual-environments.

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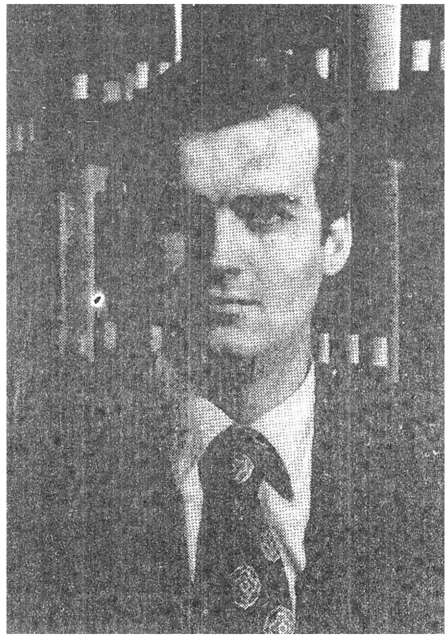

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