Color and Color Vision

We live in a happy and joyous world of color. Sunlight before it even reaches the earth is scattered by small gas molecules in the atmosphere to give rise to the blue sky as well as warm sunrises and sunsets. Sunlight refracted through water droplets give rise to rainbows.

Sunlight falling on pigment-containing rock formations in the rainbow mountains in Danxia China is differentially reflected from the rocks in a manner that depends on the mineral content of the sandstone and conglomerates that make up the rock formations. [http://www.huffingtonpost.com/2013/07/31/rainbow-mountains-china-danxia-landform_n_3683840.html](http://www.huffingtonpost.com/2013/07/31/rainbow-mountains-china-danxia-landform_n_3683840.html)

Sunlight falling on pigment-containing flowers, fruits and autumn leaves is transmitted through and reflected from plants creating a spectrum of living color.
Leigh Hunt (1840) wrote in *The Seer; or Common-Places Refreshed*, that “Colours are the *smiles of nature*. When they are extremely smiling and break forth into other beauty besides, they are her laughs; as in the flowers.” Edwin Matzke (1942) wrote in an article on autumn colors entitled, “The Finest Show on Earth,” that “Perhaps this [autumn colors] is the *botanical expression of ‘art for art’s sake’*.”

Sunlight falling on pigment-containing bird feathers is reflected to produce reds. The red color results from the *carotenoid pigments* in the food the birds eat.

The blue in the plumage of birds and the wings of butterflies is not due to pigments. The blue is due to the laminated structure that makes up the feather or wings. We will talk about *iridescence* later in the semester.
Human beings mimic the colors of nature by creating natural and synthetic **dyes**, such as tekhelet, cochineal, madder, indigo, and mauveine to further color our world. We will learn about the histories (natural and otherwise) of the production of dyes later this semester.

**Popularity by Robert Browning**

*Who has not heard how Tyrian shells
Enclosed the blue, that dye of dyes
Whereof one drop worked miracles,
And coloured like Astarte's eyes
Raw silk the merchant sells?*

Color inspires wonder. Giovanni Dondi dell'Orologio (ca. 1382) wrote, “*To whatever object the eye first turns, the same is a wonder and full of wonder, if only we examine it a little.*”

Painters have captured the colors of nature using ground-up rocks, minerals, twigs, roots, leaves, animal exudates and bugs. Tyrian purple comes from an exudate of a snail, Ultramarine and Klein blue came from the ground gemstone, lapis lazuli, indigo from the *Indigofera* plant, Prussian blue from iron ferrocyanide, cobalt blue from cobalt salts, green vertigris from arsenic, Indian Yellow from the
urine of cows that had been fed mango leaves, Cadmium yellow from ground cadmium, Chrome yellow from acidified chromium, Chrome orange from alkaline chromium, and cochineal from ground scale insects.
David Hockney has come full circle creating paintings with light itself using a program called Brushes on his iPad.

**Demonstration:** Look at the colors in the photographs you sent me.

**Isaac Newton** (1675) discovered that sunlight carried the colors of the rainbow, of the sky, and of the sunrises and sunsets within itself. Newton found this out by showing that sunlight streaming through a pinhole in the window can be resolved with a glass prism into a **spectrum** of **seven colors**. At the December 9, 1675 meeting of the Royal Society, Newton explained that a prism separated white light into light of “unequal bignesses...the largest beget a sensation of a red colour; the least, or shortest, of a deep violet; and the intermediate ones, of intermediate colours; much after the manner that bodies...which according to those bignesses, make several tones in sound...colours, like sounds, being various, according to the various bigness of the pulses.” He
went on to say that “…colour may be distinguished into its principal degrees, red, orange, yellow, green, blue, indigo, and deep violet, on the same ground, that sound within an eighth is graduated into tones.”

Demonstration: Observe light coming through pinhole and candle light with large water-filled prism.

Newton added, “Now for the cause of these and such colours made by refraction, the biggest or strongest rays must penetrate the refracting superficies more freely and easily than the weaker, and so be less turned awry by it, that is, less refracted; which is as much as to say, the rays, which make red, are least refrangible, those which make blue and violet, most refrangible, and others otherwise refrangible according to their colour: whence, if the rays, which come promiscuously from the sun, be refracted by a prism, as in the aforesaid experiment, these of several sorts being variously refracted, must go to several places on an opposite paper or wall, and so parted, exhibit every one their own colours, which they could not do while blended together. And, because refraction only severs them, and changes not the bigness or strength of the ray, thence it is, that after they are once severed, refraction cannot make any further changes in their colour.”

Are there really seven discrete colors or do colors vary continuously? Mendel chose to look at seven discrete characteristics of peas. Why seven? Could it be that in the Bible, seven symbolizes completeness or perfection? Some examples include:
“By the seventh day God had finished the work he had been doing; so on the seventh day he rested from all his work. Then God blessed the seventh day and made it holy, because on it he rested from all the work of creating that he had done” (Genesis 2:2-3); “But in the days when the seventh angel is about to sound his trumpet, the mystery of God will be accomplished, just as he announced to his servants the prophets” (Revelation 10:7); and “I saw in heaven another great and marvelous sign: seven angels with the seven last plagues—last, because with them God’s wrath is completed” (Revelation 15:1); and “The seventh angel poured out his bowl into the air, and out of the temple came a loud voice from the throne, saying, “It is done!” (Revelation 16:17).

While there may be no scientific reason to divide the infinite array of spectral colors into seven artificial colors, there is a natural reason to divide the infinite array into three primary colors.

Demonstration: Look at the sky through your spectroscope, which uses a diffraction grating to separate the differently-colored light rays. Describe the spectrum of sunlight. Is it continuous, discrete or both?

Demonstration: Look at colorful items in the room when the curtains are open and the lights are on. Describe the colors you see when you use your photopic vision. Now dim the lights and close the curtains.
Describe the colors you see when you use your _scotopic vision_.

Since the _three primary colors_ are capable of mixing all the other colors, _Thomas Young_ (1802), *The Last Man Who Knew Everything*, guessed that there must be _three color receptors_ in the retina. We now know that there are three types of _cones_, each with a different _spectral sensitivity_.

**Color vision** depends on the _cones_. There are three types of cones in the _retina_: Short (S or Type I) wavelength cones, most sensitive to short wavelengths and bluish (B) colors; mid (M or Type II) wavelength cones, most sensitive to mid wavelengths and greenish (G) colors; and long (L or Type III) wavelength cones, most sensitive to long wavelengths and reddish (R) colors. Here is the original data from George Wald (1964). Note that the sensitivity of the blue cones is less that the sensitivity of the green and red cones.

The sensitivity to blue in the subject (R.H.) shown was about three times greater than that of the average observer. Again, I believe that there is only one reality, but individually, we picture it differently in our mind’s eye, in part due to having a greater or fewer number of a given type of cone.
How the absorption of light by the cones results in our perception of color is still a mystery. However we understand more as a result of studying vision in various animals. For example, the ground squirrel (*Spermophilis tridecemlineatus*) is one animal where color vision is studied because it has a **cone-dominated retina** that resembles the **fovea** of humans. The ground squirrel retina differs from the human retina in that it only has only two cone types, one that is blue sensitive and one that is green sensitive.

Here is a **tissue slice** of a ground squirrel **retina** showing many **cones**. The **cones** that are most sensitive to blue light are stained with an antibody that fluoresces blue. When the blue light-sensitive cones are injected with a red fluorescent dye, the dye stays in the injected cones, showing that each **blue-sensitive cone** is isolated.

On the other hand, when a fluorescent green dye (neurobiotin) is injected into one green-sensitive cone, it diffuses into nearby green-sensitive cones, but not the blue-sensitive cones showing that the **green-sensitive cones are isolated from blue sensitive cones but interconnected to other green sensitive cones**. The coupling of similar cells increases the **signal-to-noise ratio** when light is limiting but also causes **blurring**, resulting in a decrease in **visual acuity**.
The neural processing of the outputs of the Type I, Type II and Type III cones of humans must be considered as a **black box** in terms of the connections and functions of the various neurons that connect the cones to the visual cortex. The initial effect of light on the cone is to make the electrical potential of the plasma membrane more negative (**hyperpolarized**).

In a cone cell in the **dark**, the **sodium channels** in the plasma membrane are **open**. Sodium ions, with a positive charge, enter the cell along their concentration gradient which causes the plasma membrane of the cone to stay **depolarized**. When the membrane is depolarized, glutamate is released. The glutamate is a **neurotransmitter** and the released glutamate causes the plasma membrane of some neurons to depolarize and the plasma membrane of other neurons to hyperpolarize.

When light is **absorbed** by a **photopsin photoreceptor pigment** in the cone, the pigment becomes active. **Photopsin** is composed of a **chromophore**, known as **11-cis retinal**, which is a derivative of **vitamin A** and the protein **opsin**.
The Type I, Type II and Type III cones in humans have the same retinal chromophore, but the amino acid sequence of the opsin protein in each type of photoreceptor cell is different enough to cause the three different spectral sensitivities. In humans, Type I cones are sensitive to violet, blue and green light; Type II cones are sensitive to blue, green, yellow, orange and red light; and Type III cones are sensitive to green, yellow, orange and red light.

When photopsin absorbs light, the 11-cis retinal is converted into all-trans retinal. The all-trans retinal form of photopsin activates a G protein known as transducin that eventually causes the sodium channels to close. The inhibition of the movement of positively-charged sodium ions into the cell causes the plasma membrane to hyperpolarize, and the hyperpolarization inhibits the release of glutamate. The inhibition of glutamate release results in a change in the neural activity of the nearby ganglion cells and a message that light was absorbed by a particular cone is sent to the brain. The neural message carried by the ganglion cell encodes the brightness of the light that hits a cone that is sensitive to a given color region, and the mind sees the neural message as a color at the point. It takes the neural messages of three different cone types for the mind’s eye to see white. The mind can see a million different colors in a given point by
reconstructing the neural signals that come from three nearby cones with different spectral sensitivities.

Let’s look at the response of a Type II cone to four particular wavelengths: 500 nm (cyan), 522 nm (green), 580 nm (yellow) and 590 nm (orange). The Type II cone has the same response to equal intensities of 500 nm and 590 nm light. It also responds identically to equal intensities of 522 nm and 580 nm light. If we only had Type II cones, we could not distinguish cyan from orange or green from yellow.

However, by having three types of cones, each with a different spectral response, we can differentiate approximately a million colors. Now you can see how: green (500 nm) and orange (590 nm) generate a response of 8 on Type II cones, but green generates a response of 3 on Type III cones while orange generates a response of 17. Green generates a tiny response on Type I cones while orange generates no response on Type I cones. The three types of cones send three messages, encoded into neural pulses, to the brain. The set of three messages define a wavelength: The complete message for 500 nm light is (0.1, 8, 3) and for 590 nm light it is (0, 8, 17).
**Demonstration:** Look at the spots made by the red and green lights. The peak of the green spot is about 532 nm and the peak of the red spot is about 633 nm. The green spot generates a response of 17 in the Type II cone and a response of 9 in the Type III cone. The red spot generates a response of 2 in the Type II cone and a response of 8 in the Type III cone. The message for the 532 nm light is (0, 17, 9) and for the 633 nm light, it is (0, 2, 8).

When the green and red spots overlap, they will generate yellow and the total number of neural responses will be 0 from the Type I cone, 19 from the Type II cone and 17 from the Type III cone. This neural response (0,19,17) is similar to the neural response that would be generated by a single wavelength of yellow light just under 560 nm. Thus the neural signal that is sent to the brain and decoded into color is the same whether a **pure spectral color** is observed or two or more pure colors that give the **exact same neural response** are mixed. This is why we cannot tell the difference between a pure spectral color and a mixed color. Some humans may have four types of cones (**tetrachromats**) instead of three types of cones (**trichromats**). Tetrachromats can differentiate between pure and mixed colors even better than trichromats.
**Demonstration:** Use the color Addition Spotlights to see the three primary colors and how they add. What color do you get when you add red and green? Blue and green? Red and Blue? A color and its complementary color make white. Which pairs are complementary colors?

**Demonstration:** The color of an object not only depends on the chemical composition of its surface, but on the spectral quality of the illumination. What color is the red or green apple when it is placed in each color zone?

**Demonstration:** Arrange the three lights to that they make one big white spot. Use your hand to make a shadow by blocking one of the colored lights at a time. The shadow will be the color of the two colors that were not blocked.

Adding equal intensities of the **three primary colors**, red, blue and green results in white. A primary color cannot be matched by any mixture of the other two primaries. Adding red and blue produces **magenta**, adding red and green
produces **yellow** and adding blue and green produces **cyan**. A **complementary** color is defined as the color that when added to another color produces white. Magenta is the complementary color of green, yellow is the complementary color of blue, and cyan is the complementary color of red.

Red, green and blue light can be added together in various proportions to make any color. This can be clearly seen with the color vision program from PhET Interactive Simulations: [http://phet.colorado.edu/en/simulation/color-vision](http://phet.colorado.edu/en/simulation/color-vision). The color (C) formed is described by the following equation:

\[ C = aR + bG + cB \]

where a, b, and c are the intensities of Red, Green and Blue light, respectively.

The fraction of the light that is red is given by \( r = \frac{a}{a+b+c} \), and the fraction of the light that is green is given by \( g = \frac{b}{a+b+c} \). Since all the colors can be made by R, G, and B, then \( r, g, \) and \( b \) must add up to 1 and \( b = 1 - r - g \). Therefore we do not have to calculate \( b \) directly and we can characterize any color spot with \( r \) and \( g \).

The total intensity of the spot is given by \( I = a + b + c \).

We can use a **color triangle** to characterize most of the colors that a human can see. To use the **color triangle**, plot the value \((r, g)\) for each color to be added. Then draw a line between them. The resulting color is the middle of the line. Magenta is the midpoint between \((0,0)\) and \((0,1)\); yellow is the midpoint between \((0,1)\) and \((1,0)\); Cyan is the midpoint between \((0,0)\) and \((0,1)\). White is the point \((0.33, 0.33)\).
Any mixed color can be considered to be the **sum of any spectral color** or **hue plus white**. A **high-saturation** color contains no white whereas a **lower-saturation** or pastel color contains more white.

One can draw a line *from* the white spot *to* any of the spots representing the primary or secondary colors. Along the line, the **hue** (or **spectral color**) stays the same, but the **saturation** increases. A **hue** or **spectral color** is defined by a single wavelength.

A line drawn from the white spot to any pure spectral color represents a single **hue** with increasing **saturation**.

Pink is a very low saturation red and falls on the line between white and red.
The color triangle can be used to predict the color made by mixing any two colors of light. In order to predict the outcome of the mixture, we must find the position of the colored light that will be mixed on the color triangle. If we want to mix equal parts of high-saturation green and high-saturation orange, we draw a line between the two colors and find the midpoint, which is yellow. If we want to mix 2 parts of high-saturation green with 1 part high-saturation orange, we find the point on the line that is one-third of the way from green and two-thirds of the way from orange. The resulting color is lime green.

http://phet.colorado.edu/en/simulation/color-vision Likewise, gray is low-intensity white and brown is low intensity orange, and beige is low-saturation brown or low-saturation and low-intensity orange.

Unfortunately, this simple color triangle does not show every color. For example it does not show olive green, which is just a low-intensity green. Check this with the color vision program.

http://phet.colorado.edu/en/simulation/color-vision
Let’s consider the two ways to make cyan. One is with a 480 nm spectral color (spot 2) and the other is to use a combination of RGB (spot 1). The two colors are matched when our visual system with our eyes and brain tell us that they are matched. Spot 2 sends a neural message produced by 480 nm light with the code (1, 4, 1). Spot 1 sends a neural message produced by a mix of 420 nm and 550 nm light with the code (2, 19.5, 14). Clearly, they are not matched!

We could get the two neural signals to match if we added red light to spot 2. Since red is the complement of cyan, this is equivalent to desaturating the cyan. Adding red to the cyan in spot 2 is mathematically equivalent to adding negative red to
the blue and green that makes spot 1. Adding negative red will “saturate” the unsaturated cyan to make spectral cyan.

\[
\text{Spectral Cyan} + xR = G + B
\]

\[
\text{Spectral Cyan} = G + B - xR
\]

We can represent the addition of negative red by using the area outside the color triangle as shown in this CIE Chromaticity Diagram. (CIE stands for International Commission on Illumination). The horseshoe shaped area is the area of human vision. The spectral colors that we can see and mix with RGB are inside the color triangle. The spectral colors that we can see, but cannot mix with just RGB are outside the triangle. I like talking about the RGB system because it matches the color sensitivities of our cones, but there are other systems of combining colors such as the Cyan-Magenta-Yellow-Black (CMYK) used in many printers.

The CIE Chromaticity Diagram can be rescaled so that all of the values are positive. The rescaled (0-0.8) CIE Chromaticity Diagram can be used to describe the spectral qualities of various sources of illumination with different color temperatures (from 1500 K to 10,000 K).
Under the same illumination, not everyone sees an object as having the same color. John Dalton, the founder of the atomic theory, noticed this in 1794. Dalton wrote, “It has been observed that our ideas of colours, sounds, tastes, &c. excited by the same object may be very different in themselves, without our being aware of it; and that we may nevertheless converse intelligibly concerning such objects, as if we were certain the impressions made by them on our minds were exactly similar. All, indeed, that is required for this purpose, is, that the same object should uniformly make the same impression on each mind; and that objects which appear different to one should be equally so to others. It will, however, scarcely be supposed, that any two objects, which are every day before us, should appear hardly distinguishable to one person, and very different to another, without the circumstance immediately suggesting a difference in their faculties of vision; yet such is the fact, not only with regard to myself, but to many others also, as will appear in the following account.”

“I was of the opinion, though I might not often mention it, that several colours were injudiciously named. The term pink, in reference to the flower of that name, seemed proper enough, but when the term red was substituted for pink, I thought it highly improper; it should have been blue, in my apprehension, as pink and blue appear to me very nearly allied; whilst pink and red have scarcely any relation.”
“In the course of my application to the sciences, that of optics necessarily claimed attention; and I became pretty well acquainted with the theory of light and colours before I was apprized of any peculiarity in my vision. I had not, however, attended much to the practical discrimination of colours, owing, in some degree, to what I conceived to be a perplexity in their nomenclature. Since the year 1790, the occasional study of botany obliged me to attend to colours more than before. With respect to colours that were white, yellow, or green, I readily assented to the appropriate term. Blue, purple, pink, and crimson appeared rather less distinguishable; being according to my idea, all referable to blue. I have often seriously asked a person whether a flower was blue or pink, but was generally considered to be in jest. Notwithstanding this, I was never convinced of a peculiarity in my vision, til I accidentally observed the colour of the flower on the Geranium zonale by candle-light, in the autumn of 1792. The flower was pink, but it appeared to me almost an exact sky-blue by day; in candle-light, however, it was astonishingly changed, not having then any blue in it, but being what I called red, a colour which forms a striking contrast to blue. Not then doubting but that the change in colour would be equal to all, I requested some of my friends to observe the phenomenon; when I was surprised to find they all agreed, that the colour was not materially different from what it was by day-light, except my brother, who saw it in the same light as myself. This observation clearly proved, that my vision was not like that of other persons; and, at the same time, that the difference between day-light and
candle-light, on some colours, was indefinitely more perceptible to me than to others.”

Dalton guessed that the difference between his and his brother’s color vision and the color vision of others was a result that the vitreous humor in his and his brother’s eyes must be bluish and if so, would imitate the effect of looking at the world through a blue filter.

**Demonstration:** Look at the world through a blue filter.

Dalton asked that his eyes would be dissected after his death in order to test his hypothesis. Dalton died on July 27, 1844 when he was 78. On the next day, Joseph Ransome performed an autopsy. Ramsome found that both the aqueous and vitreous humors of the eye were clear and transparent, although the crystalline lens was yellowish, like anyone’s of his age. Luckily Ransome saved and preserved the remains of the two eyes.
Now we know that color blindness usually arises from the lack of one of the three types of cones in the retina. **Deuteranopia** results from the lack of a functional mid wavelength sensitive Type II photoreceptor and **protanopia** results from the lack of a functional long wavelength sensitive Type III photoreceptor. Deuteranopia and protanopia are forms of **red-green colorblindness**.

Since the three photoreceptors are a result of three different versions of the opsin protein, the genes that code for Dalton’s cones could be determined from his preserved eye. Dalton was a deuteranope, who was missing the mid wavelength sensitive Type II photoreceptor.

Without a Type II photoreceptor, the world would be to Dalton a mixture of blue and red (left). Without a Type III photoreceptor, the world would be a mixture of blue and yellow (middle). The world of a trichromat is shown on the right.

![Colorblindness Diagram](image)
Do you see the number 37? If not, you may be missing Type III cones and have protanopia.

Do you see the number 49? If not, you may be missing Type II cones and have deuteranopia.

Do you see the 56? If not, you may be missing Type I cones and have tritanopia.
Take the Ishihara Color Vision Test. What numbers do you see?
Dalton and his brother both were colorblind; suggesting that color blindness is a **genetic trait**. The Human Genome Project tells us that **fifty six different genes** on 19 different chromosomes affect colorblindness. Because the major and common (red-green protanopia and deuteranopia) colorblind genes are on the **X-chromosome**, color blindness is often a **sex-linked trait** that is more common in men than in women since women; with two X chromosomes often have one normal copy of the gene that will cover for (or is **dominant** over) the colorblind version of the gene (which is **recessive**).

Color vision requires photopic vision. **Jan Purkinje** noticed that with scotopic vision, blue flowers appeared brighter than red flowers but as the dawn progressed, the red flowers appeared brighter than the blue as photopic vision was used. He wrote, “**Objectively, the degree of illumination has a great influence on the intensity of color quality. In order to prove this most vividly, take some colors before daybreak, when it begins slowly to get lighter. Initially one sees only black and grey. Particularly the brightest colors, red and green, appear darkest. Yellow cannot be distinguished from a rosy red. Blue became noticeable to me first. Nuances of red, which otherwise burn brightest in daylight, namely carmine, cinnabar and orange, show themselves as darkest for quite a while, in contrast to their average brightness. Green**
appears more bluish to me, and its yellow tint develops with increasing daylight only.”

During a full moon, the light is too bright for scotopic vision and too dim for photopic vision. Could this mesopic vision be involved in lunacy? Just asking!

The name of colors and the color itself is processed by our brain differently, and that is what makes the Stroop Test so fun. Say the name of the color the word is printed in, not what the word represents.

**Stroop Effect**

YELLOW  BLUE  ORANGE
BLACK  RED  GREEN
PURPLE  YELLOW  RED
ORANGE  GREEN  BLUE
BLUE  RED  PURPLE
YELLOW  RED  GREEN

George Wald discovered that vitamin A was necessary for making the visual pigments in the rods and cones. Here is the speech he gave at the banquet when he received the Nobel Prize in Stockholm, December 10, 1967.

Your Majesty, Royal Highnesses, Excellencies, Ladies, Gentlemen, and fellow students:
A scientist should be the happiest of men. Not that science isn't serious; but as everyone knows, being serious is one way of being happy, just as being gay is one way of being unhappy.

A scientist lives with all reality. There is nothing better. To know reality is to accept it, and eventually to love it.

I tell my students to try early in life to find an unattainable objective. The trouble with most of the things that people want is that they get them. No scientist needs to worry on that score. For him there is always the further horizon. Science goes from question to question; big questions, and little, tentative answers. The questions as they age grow ever broader, the answers are seen to be more limited.

A scientist is in a sense a learned small boy. There is something of the scientist in every small boy. Others must outgrow it. Scientists can stay that way all their lives.

I have lived much of my life among molecules. They are good company. I tell my students to try to know molecules, so well that when they have some question involving molecules, they can ask themselves, What would I do if I were that molecule? I tell them, Try to feel like a molecule; and if you work hard, who knows? Some day you may get to feel like a big molecule!

So we have much to be thankful for. With this great honor you cast a radiance upon our science. We who work in vision are happy to have it made so visible.

I am glad to be able to bring this offering to the memory of my teacher, Selig Hecht, whose widow Gelia is here with us tonight; to my wife, who is also my closest co-worker; and to my co-workers at home, particularly Paul Brown, who for twenty years has done so much himself, and with us all.
But there is something more. The grocer, the butcher, the taxi man, all seem delighted to share in our pleasure. The Nobel Prize is an honor unique in the world in having found its way into the hearts and minds of simple people everywhere. It casts a light of peace and reason upon us all; and for that I am especially grateful.

In his advice to youth, Albert Einstein said: “The important thing is not to stop questioning. Curiosity has its own reason for existence. One cannot help but be in awe when he contemplates the mysteries of the eternity, of life, of the marvelous structure of reality. It is enough if one tries to comprehend a little of this mystery each day. Never lose a holy curiosity. Try not to become a man of success but rather try to become a man of value.” (Life Magazine, May 2, 1955)