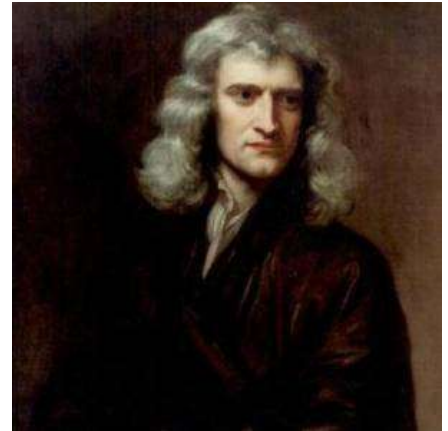


Plant and Animal Colorations: Iridescence, Warning Coloration, Sexual Selection, and the Wave Nature of Light

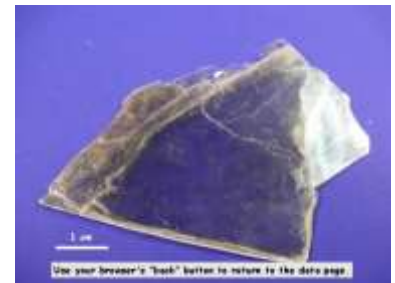
Sometimes *less is more*, and it is really pretty amazing how transparent objects such as a solution of soap or gasoline become colored when it becomes thin enough. Isaac Newton (1730) wrote, “*It has been observed by others, that transparent Substances, as Glass, Water, Air, &c. when made **very thin** by being blown into **Bubbles**, or otherwise formed into **Plates**, do exhibit various Colours according to their various thinness, altho’ at a greater thickness they appear very clear and colourless.*”



Demonstration: Blow soap bubbles and observe and describe the colors and order of colors on the top, bottom, and the rest of the surface of the bubble. How does the angle you view the soap bubble affect the colors that you see?

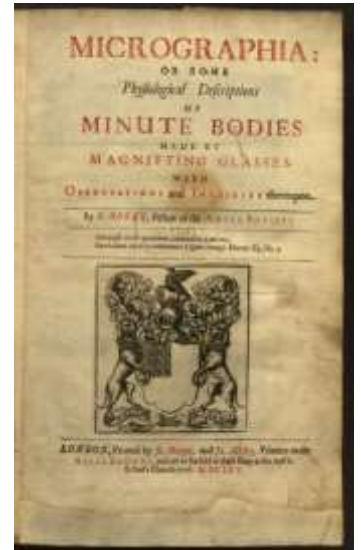


Demonstration: Look at the transparent mica (muscovite, Muscovy glass), then peel off a thin sheet and observe the colors and the order of colors. Are the colors more intense at the torn edges? How does the angle you view a thin sheet of mica affect the colors that you see?



How is it possible that a transparent soap solution or a transparent thin piece of mica can produce colors at all—never mind such vibrant and beautiful colors? Is this a case where we are producing something out of nothing?

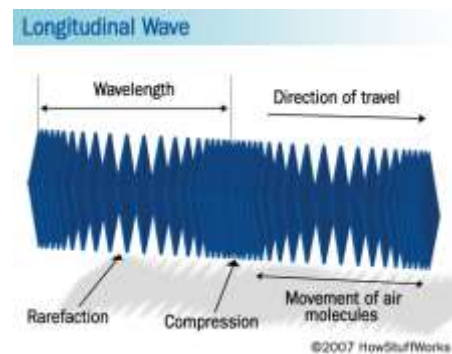
The observation of colors produced by thin plates of mica was first reported by **Robert Hooke** (1665) in his book **Micrographia**: “*Moscovy-glass, or lapis specularis, is a Body that seems to have as many curiosities in its fabrick as any common mineral I have met with: for first, it is transparent to a great thickness: next, it is compounded of an infinite number of thin flakes joyned or generated one upon another so close & smooth, as with many hundreds of them to make one smooth and thin plate of a transparent flexible substance.... This stone...exhibits...all the colours of the rainbow...but the order of the colours...was quite contrary to the primary or innermost rainbow, and the same with those of the secondary or outermost rainbow.....the phenomena of colours...I had often observed in those **bubbles which children use to make soap-water**, ...I was able to produce the same phenomena in thin bubbles made with any other transparent substance.*”



Robert Hooke (1665) observed similar colors in animal bodies such as pearls, **mother of pearl** shells, oyster shells, and concluded, “*wheresoever you meet with a **transparent body thin enough**, that is terminated by **reflecting** bodies of different **refractions** from it, there will be a production of these pleasing and lovely bodies.*” With his **microscope**, Robert Hooke could see that the colorful parts of these objects, as well as the **fantastical** and colorful regions of peacock and duck feathers, like the mica, also consisted of thin plates or lamina.



From his observations of thin plates of mica, soap bubbles, the feathers of peacocks and ducks, the spark from flint and steel, the luminescence of rotten wood and fish, the thermoluminescence of the Bologna stone, the triboluminescence of a diamond, the bioluminescence of sea water, the light reflected from cats' eyes and the light coming from the bellies of glowworms, Robert Hooke (1665) tried to **understand the properties of light itself**. Robert Hooke (1665) concluded that the motion of light was “*exceedingly quick, such as those motions of fermentation and putrifaction, whereby, certainly, the parts are exceedingly nimbly and violently mov'd...Next, it must be a vibrative motion. And for this the newly mention'd diamond affords us a good argument; since if the motion of the parts did not return, the diamond must after many rubbings decay and be wasted.... And thirdly, that it is a very short vibrating motion...for a diamond being the hardest body we yet know in the world, and consequently the least apt to yield or bend, must consequently also have its vibrations exceeding short. And these, I think, are the three principle properties of a motion, required to produce the effect call'd light in the object.*”



Demonstration: Turn the crank of the wave demonstration apparatus to see both **transverse waves** and **longitudinal waves**. Although Robert Hooke did not clarify the type of vibration he thought light was, he was probably thinking of a sound wave analogy and sound waves are longitudinal waves that compress and rarefy the medium through which they travel.



Aside: The Great Fire of London occurred the year following the publication of Robert Hooke's *Micrographia*. Robert Hooke was a polymath who helped Christopher Wren design some of the monuments and buildings, including the **Monument to the Fire**, the **Royal Greenwich Observatory**, and **Bethlem** (known as Bedlam) **Royal Hospital** that would be built following the fire.



As we see, Robert Hooke (1665) considered light to be **vibrations with very short periods**. On the other hand, when we discussed color vision, we learned that **Isaac Newton** (1675) considered light to be composed of corpuscles and that a prism separated sunlight into corpuscles 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....*”

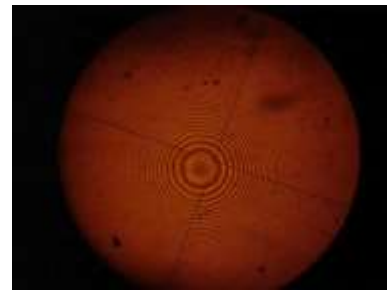
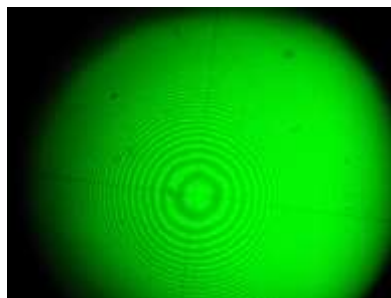


Isaac Newton was able to turn qualitative observations like we all make when we see the colors generated by soap bubbles into **quantitative experimental observations**. According to Isaac Newton (1730), “*If a Bubble be blown with Water first made tenacious by dissolving a little Soap in it, 'tis a common Observation, that after a while it will appear tinged with a great variety of Colours. As soon as I had blown any of them I cover'd it with a clear Glass, and by that means its Colours emerged in a very regular order, like so many concentrick Rings encompassing the top of the Bubble. And as the Bubble grew thinner by the continual subsiding of the Water, these Rings dilated slowly and overspread the whole Bubble, descending in order to the bottom of it, where they*



vanished successively. In the mean while, after all the Colours were merged at the top, there grew in the center of the Rings a small round black Spot.”

Demonstration: Observe **Newton’s rings** using the Newton’s ring apparatus on a light table using a measuring loupe. What happens to the position of the rings when you filter the light with various colored filters?



Throughout this semester, we have assumed that light is **absorbed** and **emitted** by atoms and molecules as **infinitesimally small corpuscles** that travel between the emitter and absorber along infinitesimally thin rays. This hypothesis has been very productive; having allowed us to predict, using **geometrical optics** and the laws of **reflection** and **refraction**, the position, orientation, and magnification of images formed by the *camera obscura*, **mirrors** and **lenses**. In the words of **Christiaan Huygens** (1690): *“As happens in all the sciences in which Geometry is applied to matter, the demonstrations concerning Optics are founded on truths drawn from experience. Such are that the rays of light are propagated in straight lines; that the angles of reflexion and of incidence are equal; and that in refraction the ray is bent according to the law of sines, now so well known, and is no less certain than the preceding laws.”*



However, **Christiaan Huygens** (1690) not only saw the **value** of the corpuscular theory of light, but he also saw its **limitations**. He realized that if light were composed of material particles then the corpuscles composing a light ray crossing the corpuscles composing an intersecting light ray would **collide** with each other, causing each one to scatter and making it difficult for two people to see two different objects and even difficult for two people to see each other.

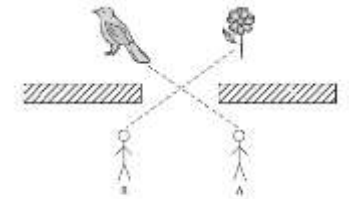
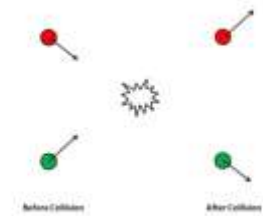
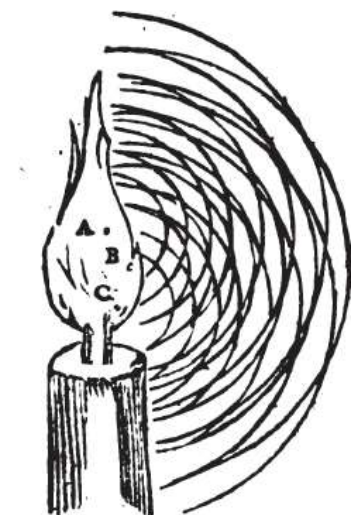


FIGURE 3.7 If light were composed of Newtonian corpuscles, corpuscles propagating from the bird to observer A should make it more difficult for observer B to see the flower, since the corpuscles from the flower will cause the corpuscles coming from the bird to scatter.

Christian Huygens (1690) wrote in his *Treatise on Light*, “I do not find that any one has yet given a probable explanation of the first and most notable phenomena of light, namely why is it not propagated except in straight lines, and how visible rays, coming from an infinitude of diverse places, cross one another without hindering one another in any way.”

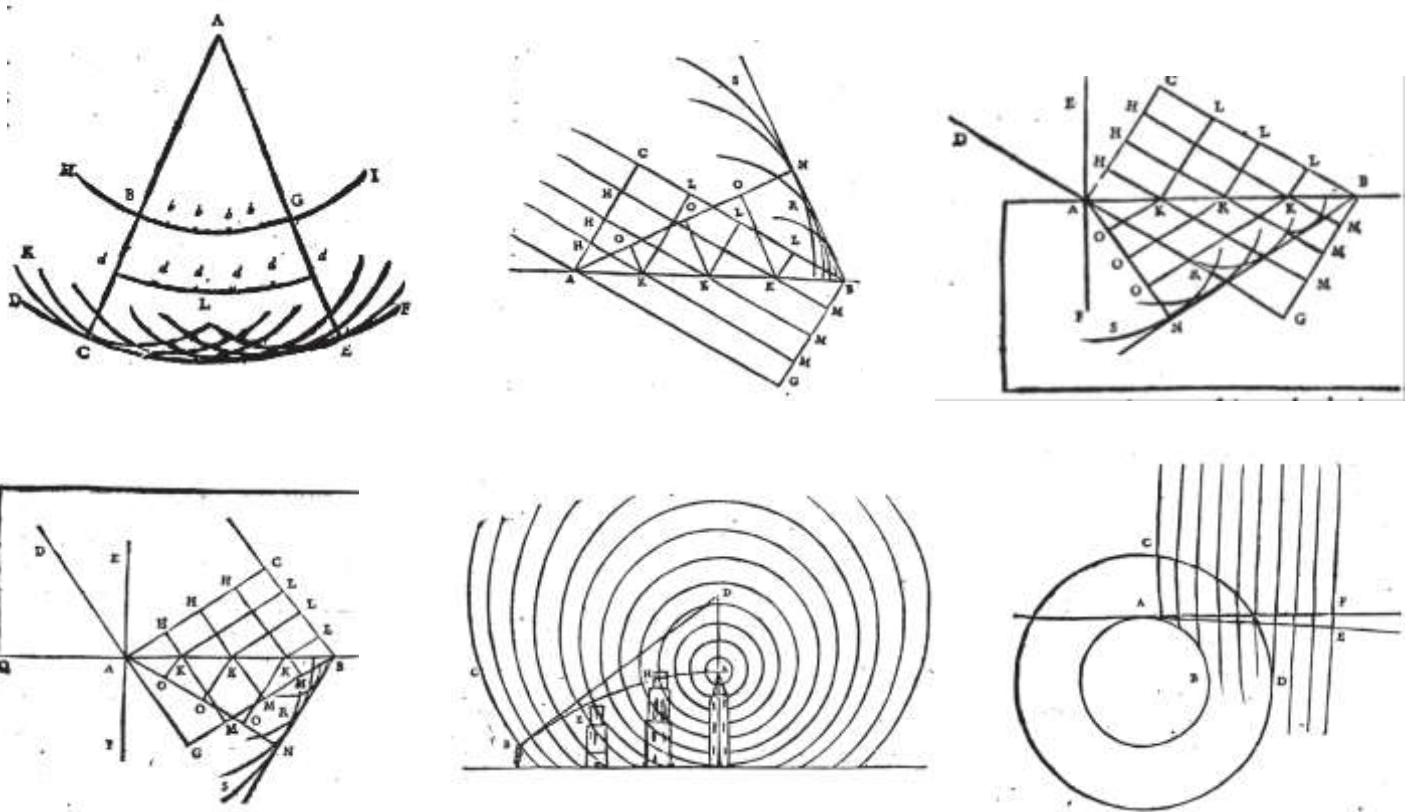
Christian Huygens decided that since particulate light corpuscles would collide with each other and interfere with each other’s propagation, light must be **immaterial and consist of the motion of an ethereal medium**. Here is how he came to the conclusion that light is the motion of the ether. Fire produces light, and likewise, light, collected by a concave mirror, is capable of producing fire. Fire is capable of melting, dissolving, and burning matter, and it does so by disuniting the particles of matter and sending them in motion.

According to the mechanical philosophy of nature championed by **René Descartes**, **anything that causes motion must itself be in motion**, and therefore, **light must be motion**. Since two beams of light crossing each other do not hinder the motion of each other, the components of light that are set in motion must be immaterial and imponderable. According to Huygens, light impels the so-called

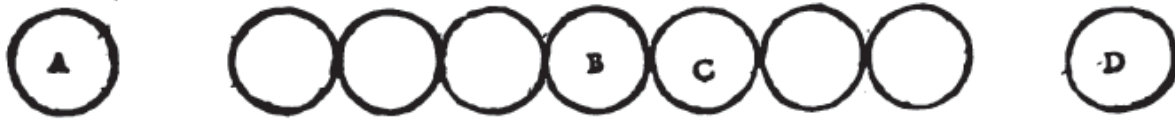


luminous ether through which the light propagates into motion. Then the motion of the ether causes an impression on our retina; resulting in vision much like vibratory motion of the air causes an impression on our eardrum; resulting in hearing.

Christian Huygens (1690) explained the inverse square law, reflection, refraction and even some atmospheric optical illusions with his wave theory of light. Notice that the prominent wave fronts and rays are related in that the prominent wave fronts are perpendicular to the rays.

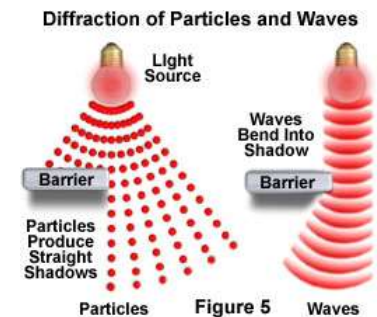


Interestingly, in order for his wave theory of light to explain the rapidity of light propagation and the fact that you can see very tiny things, Christian Huygens had to postulate that the ether itself was particulate.



While Christian Huygens chose to see light as waves traveling through a particulate ether, ironically, Isaac Newton chose to see light as corpuscles traveling through a waving ether whose periodic density variations resulted in the colors of thin plates. Isaac Newton (1730, Query 3) asked, “*Are not rays of light in passing by the edges and sides of bodies, bent several times backwards and forwards, with a motion like that of an eel? And do not the three fringes of colour’d light above-mention’d arise from three such bendings?*”

Isaac Newton considered light itself to be particulate because, if light indeed were primarily a wave, he should have seen light **bend behind an obstruction** the way sound waves and water waves bend around an obstruction. He did not see any light behind a small obstruction.



The bending of light by an obstruction was first observed by **Francesco Maria Grimaldi** in 1665. He called this phenomenon **diffraction**, from the Latin words *dis* and *frangere* which mean “apart” and “to break.” Unfortunately, Francesco Maria Grimaldi’s observation that light does not always travel in straight lines in a single medium was lost to obscurity.



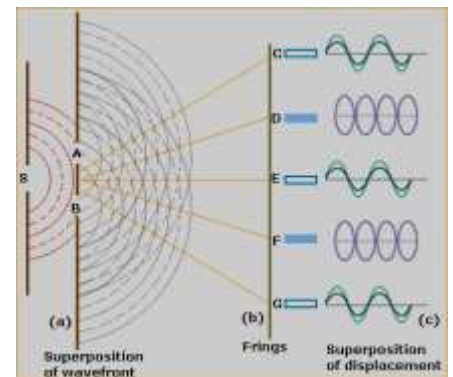
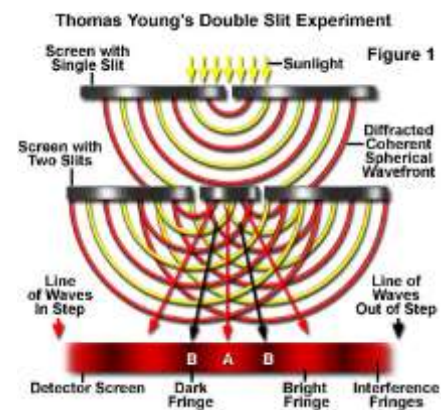
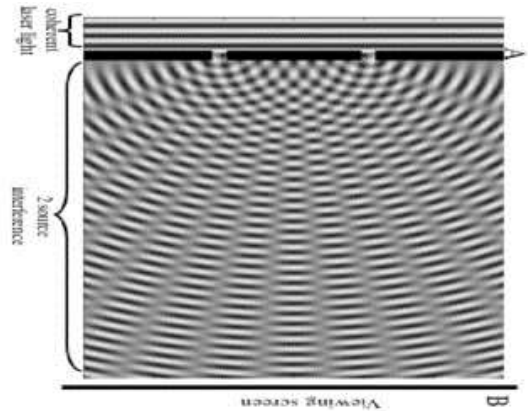
As a consequence of the great achievements of Isaac Newton and the hagiographic attitude and less than critical thoughts of the followers of this great man, the corpuscular theory of light predominated, and Robert Hooke’s and Christiaan Huygens’ wave theory of light lay fallow for about a century until it was

revived by **Thomas Young**, a botanist, a translator of the Rosetta stone, and a physician who was trying his hand at teaching Natural Philosophy at the Royal Institution. While preparing his lectures, Thomas Young reexamined the objections that Isaac Newton had made to the wave theory of light. Thomas Young, who studied the master, not the followers, apes, epigones, imitators, or votaries, concluded that the wave theory in fact could describe what happens to light when it undergoes diffraction as well as reflection and refraction. Here is how Thomas Young (1804) came to this conclusion: *“I made a small hole in a window-shutter, and covered it with a piece of thick paper, which I perforated with a fine needle. For greater convenience of observation, I placed a small looking glass without the window-shutter, in such a position as to reflect the sun’s light, in a direction nearly horizontal, upon the opposite wall, and to cause the cone of diverging light to pass over a table, on which were several little screens of card-paper. I brought into the sunbeam a slip of card, about one-thirteenth of an inch in breadth, and observed its shadow, either on the wall, or on other cards held at different distances. Besides the fringes of colours on each side of the shadow, the shadow itself was divided by similar parallel fringes, of smaller dimensions, differing in number, according to the distance at which the shadow was observed, **but leaving the middle of the shadow always white.**”*



Thomas Young observed something that the great Newton had missed. Young noticed that the light in fact did bend into the geometrical shadow of the slip of card. According to Thomas Young (1804), *“It was in May of 1801, that I discovered, by reflecting on the beautiful experiments of Newton, a law which*

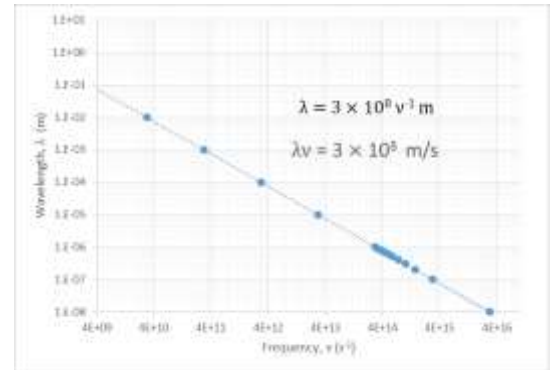
appears to me to account for a greater variety of interesting phenomena than any other optical principle that has yet been made known. I shall endeavour to explain this law by a comparison: **Suppose a number of equal waves of water to move upon the surface of a stagnant lake, with a certain constant velocity, and to enter a narrow channel leading out of the lake; suppose, then, another similar cause to have excited another equal series of waves, which arrive at the same channel with the same velocity, and at the same time with the first. Neither series of waves will destroy the other, but their effects will be combined; if they enter the channel in such a manner that the elevations of the one series coincide with those of the other, they must together produce a series of greater joint elevations; but if the elevations of one series are so situated as to correspond to the depressions of the other, they must exactly fill up those depressions, and the surface of the water must remain smooth; at least, I can discover no alternative, either from theory or from experiment. Now, I maintain that similar effects take place whenever two portions of light are thus mixed; and this I call the general law of interference of light.**”



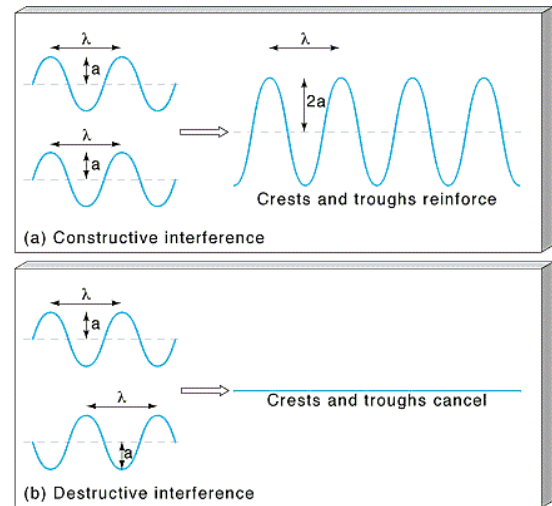
Let's look at the interference of light waves. Note that just like the mathematical waves we used to describe **circadian rhythms**, a light wave has a **phase** relative to a reference, an **amplitude**, a **period** and its inverse (a frequency),

and a **wavelength**. The product of the frequency (ν) and the wavelength (λ) is the **speed of the wave**. For light, the speed in a vacuum is called c , which is 3×10^8 m/s. The relation between the speed and wavelength of light in a single inertial frame, that is, when the source of light and observer are not moving relative to each other, is given by the **dispersion relation**:

$$\nu\lambda = c$$



When two nearby waves have the **same phase**, they **constructively interfere** to produce a resultant wave that has twice the amplitude. Since the intensity (I) of the resultant is proportional to the square of the amplitude (a), the resultant intensity ($I = (2a)^2 = 4a^2$) is greater than the intensity of the individual waves that make up the resultant wave ($I = a^2 + a^2 = 2a^2$). **That is, the square of the sum is greater than the sum of the squares.**

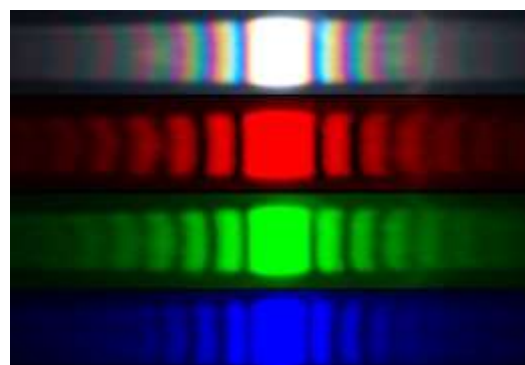


When **the peaks of one wave line up with the troughs of a nearby wave**, they **destructively interfere** to produce a resultant wave that has zero amplitude. Since the intensity (I) of the resultant is proportional to the square of the amplitude (a), the resultant intensity ($I = (a-a)^2 = (0a)^2 = 0$) is less than the intensity of the individual waves that make up the resultant wave ($I = a^2 + a^2 = 2a^2$). **That is, the square of the sum is less than the sum of the squares.** The averaged intensity of the waves that constructively and destructively interfere is equal to the intensity of the individual input waves, consistent with the **First Law of Thermodynamics**.

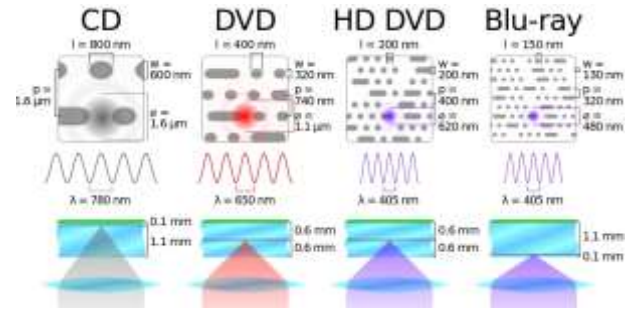
That is, **diffraction** does not lead to a change in the amount of energy but results in the **redistribution of energy in space**.

Thomas Young (1804) went on to say, “*The observations on the effects of diffraction and interference, may perhaps sometimes be applied to a practical purpose, in making us cautious in our conclusions respecting the appearances of **minute bodies viewed in a microscope**. The shadow of a fibre, however opaque, placed in a pencil of light admitted through a small aperture, is always somewhat less dark in the middle of its breadth than in the parts on each side. A similar effect may also take place, in some degree, with respect to the image on the retina, and impress the sense with an idea of a transparency which has no real existence: and, if a small portion of light be really transmitted through the substance, this may again be destroyed by its interference with the diffracted light, and produce an appearance of partial opacity, instead of uniform semitransparency. Thus, a central dark spot, and a light spot surrounded by a darker circle, may respectively be produced in the images of a semitransparent and an opaque corpuscle; and impress us with an idea of a complication of structure which does not exist.*” We will repeat Thomas Young’s experiments next week when we talk about microscopy.

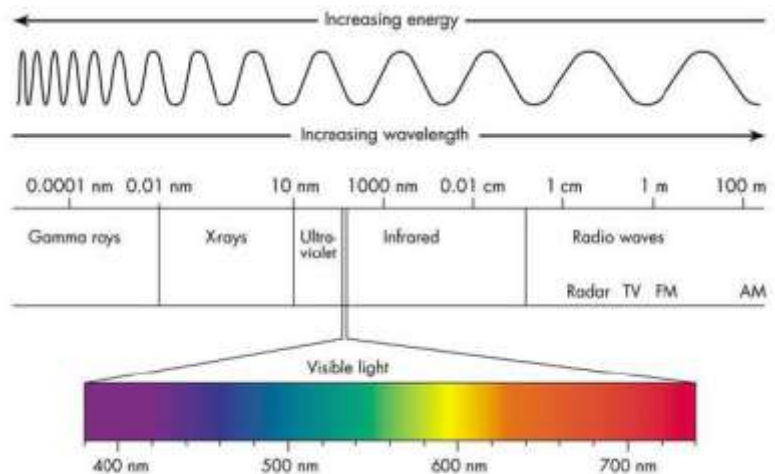
Thomas Young found that the position of the bright and dark bands depended on the color of light. By measuring the distances between the bright bands of each color, he determined the **wavelength** of each color that makes up the **spectrum** of visible light.



Demonstration: Look at the sunlight through you transmission diffraction grating and see how a transparent object with structures with a size on par with the wavelength of light can differentially diffract the spectral colors of sunlight. The lines on a compact disc (**CD**) are also sufficiently close and regular to act as a reflection diffraction grating that differentially diffracts the spectral colors of sunlight. Digital video discs (**DVD**) have closer lines and **blu-ray discs** have even closer lines.



Thomas Young’s work led to the description of the **spectrum** that we have alluded to all semester.



The colors produced by **thin film interference** of light waves and the **diffraction** of light waves are known as **structural colors**. Because the **colors we see vary** as we change our position of view, structural colors produce **iridescence**. That is, these structures with sizes close to the wavelength of light have the potential to produce all the colors of the rainbow. Iridescence is named after the Greek goddess **Iris**.



Despite or perhaps because of Thomas Young's accomplishments, he became a *persona non grata*, since he did not accept the corpuscular nature of light proffered a century before by his fellow Englishman Isaac Newton. Isaac Newton, is interred in **Westminster Abbey** with the following inscription on his monument, "*Here is buried Isaac Newton, Knight, who by a strength of mind almost divine, and mathematical principles peculiarly his own, explored the course and figures of the planets, the paths of comets, the tides of the sea, the dissimilarities in rays of light, and, what no other scholar has previously imagined, the properties of the colours thus produced. Diligent, sagacious and faithful, in his expositions of nature, antiquity and the holy Scriptures, he vindicated by his philosophy the majesty of God mighty and good, and expressed the simplicity of the Gospel in his manners. Mortals rejoice that there has existed such and so great an ornament of the human race! He was born on 25th December 1642, and died on 20th March 1726.*" Newton was held in high regard in England as can be seen by the epitaph written in 1727 by **Alexander Pope**: "*Nature and Nature's laws lay hid in night: God said, 'Let Newton be!' and all was light.*" **Edmund Halley** also wrote glowingly about Newton: "*So near the gods—man cannot nearer go.*" **John Draper** (1861) put a picture of Newton in his book, *Human Physiology*. The **Marquis de L'Hôpital** glorified Newton thusly, "*Does he eat, and drink, and sleep, like other people? I represent him to myself as a celestial genius entirely disengaged from matter.*"



Isaac Newton was beatified by the scientific community and Thomas Young was viciously attacked for being “Anti-Newtonian”. An anonymous reviewer, most likely **Lord Brougham**, wrote in the Edinburgh Review about Young’s lecture on the wave theory of light, *“A mere theory is in truth destitute of all pretensions to merit of every kind, except that of a warm and misguided imagination. It demonstrates neither patience of investigation, nor rich resources of skill, nor vigorous habits of attention, nor powers of abstracting and comparing, nor extensive acquaintance with nature. It is the unmanly and unfruitful pleasure of a boyish and prurient imagination, or the gratification of a corrupted and depraved appetite.”* The anonymous reviewer went on to say: *“We take our leave of this paper with recommending it to the Doctor to do that which he himself says would be very easy; namely, to invent various experiments upon the subject. As, however, the season is not favourable for optical observation, we recommend him to employ his winter months in reading the “Optics”, and some of the plainer parts of the “Principia”, and then to begin his experiments by repeating those which are to be found in the former of these works.”*



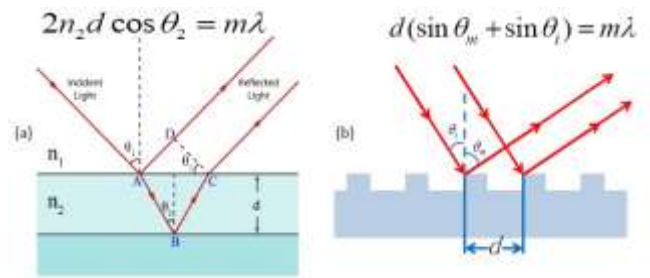
While Thomas Young is buried in St. Giles the Abbot Churchyard in Farnborough, London, England, a tablet was erected in his honor in Westminster Abbey. It reads, *“Sacred to the memory of Thomas Young M.D. Fellow and Foreign Secretary of the Royal Society Member of the National Institute of France. A man alike eminent in almost every department of human learning. Who, equally distinguished in the most abstruse investigations of*



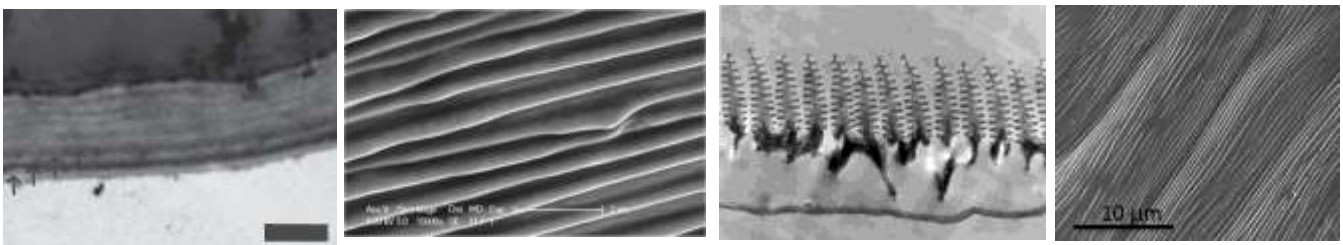
*letters and of science, first established the **undulatory theory of light** and first penetrated the obscurity which had veiled for ages the hieroglyphicks of Egypt. Endeared to his friends by his domestic virtues, honoured by the World for his unrivalled acquirements, he died in the hopes of the Resurrection of the just. Born at Milverton in Somersetshire June 13th 1773, died in Park Square London May 10th 1829, in the 56th year of his age.”*



Approximately a half century after Young espoused his wave theory of light, his theory was shown to be so useful that it was finally accepted. We will use Thomas Young’s wave theory of light to understand coloration in nature. **Structural colors** can result from the interference of light produced by both closely-spaced striated structures and thin layered lamellar structures.



The structures that give rise to structural colors have dimensions close to the wavelength of light. Electron microscopy is typically used to determine the spacing of transparent striated structures and the thicknesses of transparent lamella



structures that give rise to the colors. The alternating layers of cellulose gives *Selaginella willdenowii* its blue color, alternating layers of chitin and air that look like a tree from the side give the Morpho butterfly its blue color, and striations in

the cuticle of the Queen of the Night tulip give its purple color. Many structural colors also depend on melanin layers to give a **black background** so that the color is even **more vibrant**. Remember that the blue of the sky can be so vibrant and **saturated** because it set against the blackness of space.

While the **differential absorption of pigments** is the most prevalent cause of coloration in plants and animals, coloration can result from the **differential interference of the spectral colors of sunlight that result from lamellar or striated structural specializations**. The structures are **inherently transparent** and the colors result from differences in the **refractive indices** of the layers, or of the striations. The brilliant colored light produced by structural specializations is known as **iridescence**. Robert Hooke (1665) called colors that were due to structural elements and not to pigments, **fantastical colors** and he could distinguish these colors from those produced by pigments with the following test: *“Now, that these colours are only fantastical ones, that is, such as arise immediately from the refractions of the light, I found by this, that water wetting these colour'd parts, destroy'd their colours, which seem'd to proceed from the alteration of the reflection and refraction.”* Now we will apply the concept of interference to understand the colors of thin plates.

When light strikes a thin film some of it is reflected and some of it is refracted. The reflected light follows the **law of reflection** and the refracted light follows the **Snel-Descartes Law**. Some of the refracted light will reflect off the next surface and some of it will be refracted. The splitting between the reflected light and the refracted light occurs at each interface. The phase of the light that is reflected from the second interface will be retarded relative to the phase of the light that is reflected from the first interface. The amount of retardation will depend on two things—the length of the path in the refractive layer and the refractive index of

this layer. Remember from our discussion of geometrical optics, the greater the refractive index of a transparent medium, the slower the light will propagate through that medium. The product of the geometric length and the refractive index is known as the **optical path length**.

As long as the film is thin enough, the wave that is reflected from the top surface will be close enough to the wave that is reflected from the bottom surface and they will interfere with each other. If the two waves are in phase, the waves will constructively interfere and the reflection will be bright. If the two waves are one-half wavelength out of phase, the two waves will destructively interfere and the reflection will be black. The distance each wave travels through the thin film is independent of wavelength. However, the distance in proportion to the wavelength of light of each spectral color will be different. When sunlight impinges on the thin film, the **color of the reflected light is most similar to the color of the wavelength that undergoes complete constructive interference and the complementary color of the color of the wavelength that undergoes complete destructive interference**. The wavelength that undergoes complete destructive interference depends on the **thickness** and **refractive index** of the film which determine the **optical path length**. Since the optical path length increases as the angle of viewing increases, the color of the reflected light changes with the viewing angle. The color of the reflected light stabilizes with respect to color as the number of thin layers gets large.

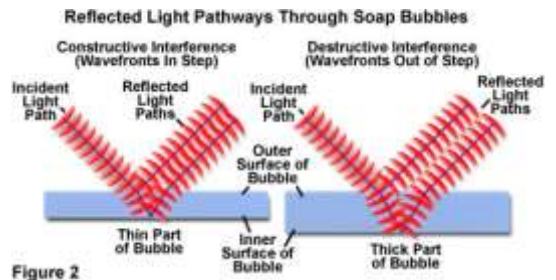
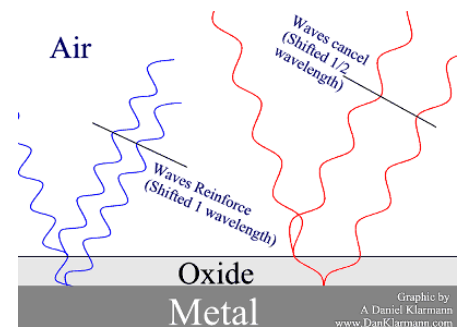
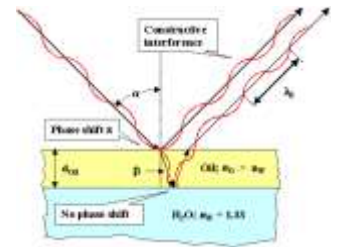


Figure 2



Optional: There is an added phase shift of one half wavelength when the reflection occurs at an interface where the light goes from a medium of lower refractive index to a medium of higher refractive index. There is no added phase shift of one half wavelength when the reflection occurs at an interface where the light goes from a medium of higher refractive index to a medium of lower refractive index. These properties are important for determining the effectiveness of anti-reflection coats for lenses and the colors of jewelry made from metal oxides.



Demonstration: Look at the **male blue *Morpho* butterfly**. Describe the colors you see. How does the angle you view the butterfly wings affect the colors that you see?



Demonstration: Look at the peacock feather. Describe the colors you see. How does the angle you view the feather affect the colors that you see?



Isaac Newton (1730) wrote, “*The finely colour’d Feathers of some Birds, and particularly those of Peacocks Tails, do, in the very same part of the Feather, appear of several Colours in several Positions of the Eye, after the very same manner that thin Plates were found to do....*” Indeed, **thin layer interference** is responsible for the **iridescent blue and green colors of the tail feathers of male peacock**.



Thin layer interference is responsible for the **iridescent blue color** of the feathers of the **blue jay** and **indigo bunting males**. It is also responsible for the **iridescent blue color** of the fruit of the marble berry (*Pollia*).



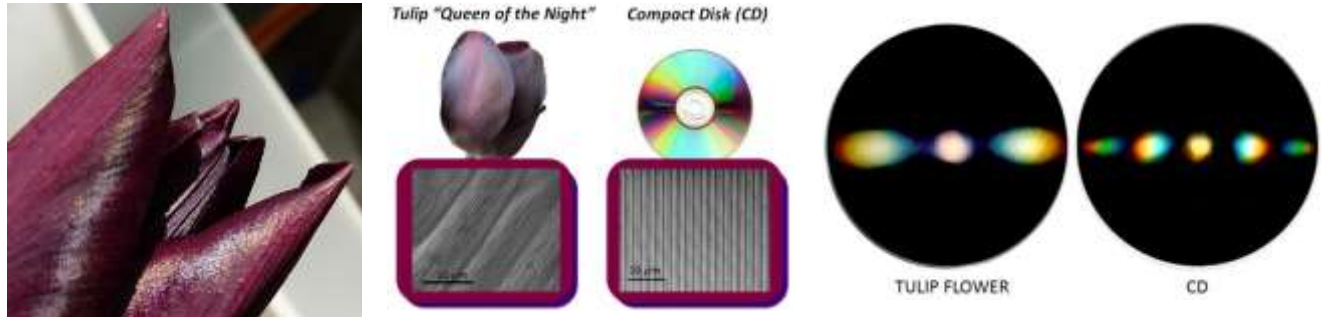
Thin layer interference is responsible for the **iridescent green color** of the feathers of the hummingbirds and exoskeleton of insects, including tiger beetles and chrysomelids.



Thin layer interference is responsible for the **iridescent blue color** of *Selaginella willdenowii*. The function of iridescence in this plant is unknown.



Interference of **diffracted waves** gives the Queen of the Night tulip its purple color (<http://www.colours.phy.cam.ac.uk/ferns-and-butterflies/>).

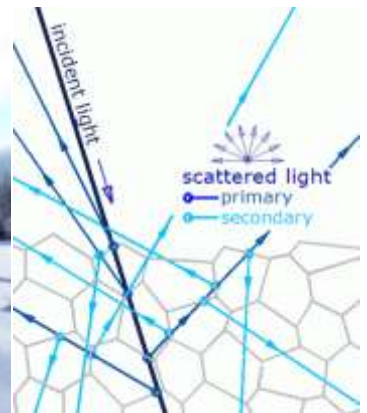


Iridescent blue feathers in **male parrots** and **parakeets** are due to **thin layer interference**. The **green** color of parrots and parakeets results from the combination of **blue** structural colors and **yellow carotenoid pigments**. The carotenoids produce many colors of bird feathers depending on the dietary source and the protein attachment. Deep red feathers are due to rhodoxanthin, golden-yellow feathers are due to zeaxanthin, lemon-yellow feathers are due to lutein, scarlet red feathers are due to canthaxanthin, orange-red feathers are due to phoenicoxanthin, pale yellow to pale orange feathers are due to beta carotene, and salmon pink feathers are due to astaxanthin. The **white** is due to reflection from numerous air pockets.





As long as I am talking about white as a color, the white color of snow comes from the reflections of all wavelengths of sunlight **from air sandwiched between the layers of transparent snowflakes.** This **random sandwich-like structure** reflects all the wavelengths of sunlight because none of the wavelengths are differentially scattered or absorbed. Ice and water are not white because they are homogeneous and transmit all the wavelengths almost equally. While a snowball is white, it becomes transparent as it melts and loses its sandwich-like structure. When you crush or shave ice, it forms air pockets and appears white.



<http://www.weather.com/storms/winter/video/why-is-snow-white>

Likewise, the white color of hair comes from the reflections of sunlight from air sandwiched between the keratin layers of hair. I do not know any more details than this.



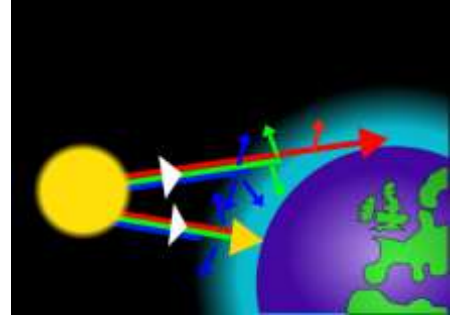
Likewise reflection of sunlight from air trapped between cells is also responsible for the silver white color of the aluminum plant.



Structural colors can also be caused by **Rayleigh scattering (also known as Tyndall scattering)**. The grayish to bluish appearance of some leaves, including **blue spruce**, and **Atlas blue cedar**, probably results from the scattering of sunlight from the wax molecules that coat the epidermal surface of the leaves.



The **blue-eared glossy starling** provides one example in birds where the blue color of the feathers is generated by **Rayleigh or Tyndall scattering** in the same way that the **blue color of the eye** and the **blue color of the sky** are generated.



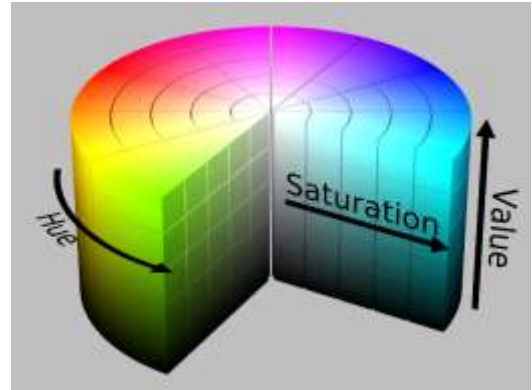
Structural colors may be a means to an end. What are the functions of the vibrant structural colors? It is possible that some animals use vibrant colors to **warn predators** that they are **poisonous** and do not taste good so that they will not be eaten and will be able to leave more offspring. Another function may be for **sexual selection**, since the males but not the females are typically brightly colored. The bright coloration of the males may make them more attractive to females making it possible for them to leave more offspring. I will discuss **warning coloration** first.



Poison frogs are brightly colored to warn their predators to leave them alone. The colors result from a combination of the **differential absorption of the spectral colors of sunlight by pigments** and the **differential interference of the spectral colors of sunlight that result from lamellar structural specializations**. In general the bright skin colors



result from three color influencing layers. The top layer contains **chromatophores** that contain **carotenoids or pteridine**. The middle layer contains **iridophores** containing thin plates of crystallized **guanine** that produce **structural blue**, and the bottom layer contains **melanin**-containing chromatophores to ensure that the colors are **not unsaturated because of reflected light** but saturated.



The poison dart frogs in Panama are very brightly colored and there seems to be a slight correlation ($r^2 = 0.61$) between color brightness and toxicity, especially considering the color brightness that the predatory birds see (Maan and Cummings, 2012).



Figure 1: Sampled populations of *Dendrobates pumilio* in the Bocas del Toro Archipelago, Panama. From Isla Baslmeritos, two *D. pumilio* color morphs were collected (green and orange), as well as four individuals of the closely related but nontoxic control species *Albolete talamanca*.

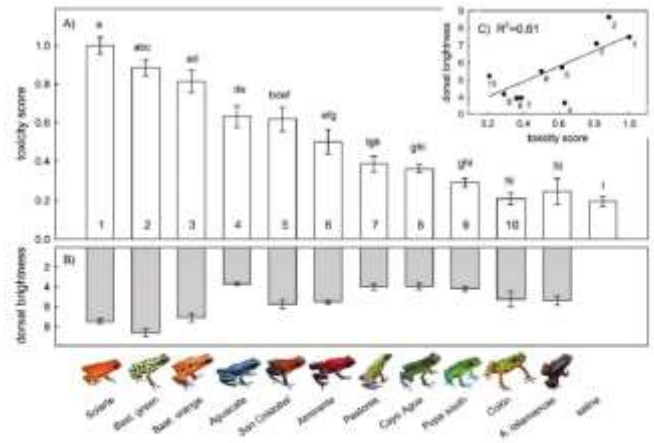


Figure 2: Toxicity scores and coloration brightness in *Dendrobates pumilio*. A. Open bars indicate toxicity scores with standard error. Different letters above the bars indicate statistically significant differences; numbers are population numbers referred to in C and in subsequent figures. *Albolete talamanca* (a closely related *Dendrobates* frog) and *Salix solitaria* served as toxicity measure controls. B. Gray bars indicate the overall brightness of dorsal coloration (total reflectance flux, LR, in arbitrary units) for the 11 frog taxa. C. The inset gives the correlation between toxicity and dorsal brightness for the 16 *D. pumilio* populations. Numbers refer to the population labels in A.

From 1849 to 1860, **Henry Bates** wandered through the Amazon collecting butterflies. Bates grouped together the butterflies that looked similar but on close inspection he saw that many of the similarly looking butterflies were only distantly related.



Bates (1862) realized that the **Heliconiidae** butterflies resembled each other as would be expected of closely related species. The typical Heliconiidae are vibrantly colored with a **pattern of warning coloration** that communicates to their predators to leave them alone, because they are poisonous.



Bates noticed that the Heliconiidae butterflies flew around at a leisurely pace and were not eaten by birds, dragonflies, lizards or robber-flies. He surmised that they could be so leisurely because they were care-free because they were **unpalatable**. The butterflies are poisonous as a result of eating and accumulating the chemicals produced by plants that are poisonous to most organisms but not to the butterflies. Bates then guessed that the nearby palatable Pieridae butterflies **evolved by natural selection** to look like or **mimic** the Heliconiidae butterflies.

The typical Pieridae butterflies are not very vibrant and do not have much of a pattern. In fact the name butterfly may have come from the name of a yellow member of this group (*Gonepteryx rhamni*) that was known as the **butter-coloured fly** by British Lepidopterists.

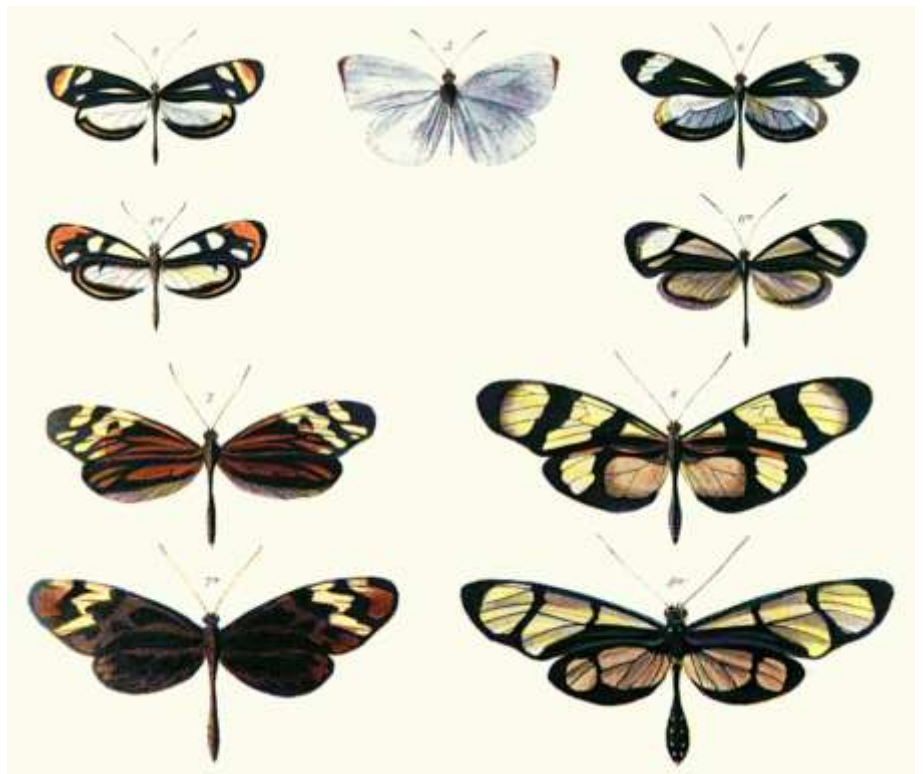


However, Bates noticed that the **Pieridae** butterflies that lived near the Heliconiidae butterflies did not look very much like the typical Pieridae but looked like the Heliconiidae. These Pieridae were vibrantly colored with a warning coloration pattern that communicated to their predators to leave them alone, even though they were not poisonous. According to Bates, they “played a part” or mimicked like a mine the poisonous Heliconiidae.

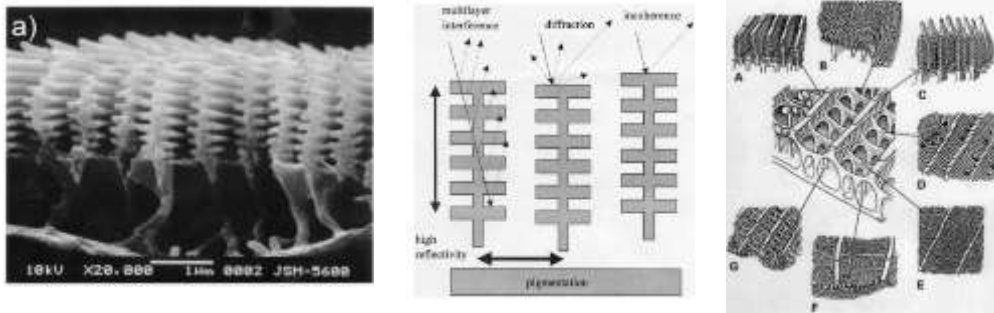


A palatable species that comes to look like an unpalatable and unrelated species is called a **Batesian mimic** and the strategy is known as **Batesian mimicry**. According to Bates, the variants of a palatable species that come to look like an unrelated unpalatable species have a selective advantage in that the predators learn not to eat the palatable butterflies that look most like the unpalatable butterflies. In this way, a palatable species develops a similar pattern of warning coloration as a poisonous species and the best mimics avoid predation and produce the most offspring. **It is a case of evolution by natural selection.** I do not know if there is or isn't direct evidence for speciation by natural selection.

Here is a plate of **Batesian mimicry** from an 1862 publication of Bates himself. The butterflies (*Ithomiini*) in the second and fourth row are poisonous and unpalatable members of the Nymphalidae. The butterflies (*Dismorphia*) in the top and third row are the palatable mimics from the Pieridae.



The vibrant **iridescent** colors of butterfly wings are **structural colors**. The forms of the transparent structures, which are on the scale of the wavelengths of light, are both simple and complicated. Thus the spectral colors of butterfly wings are caused by a combination of **thin film interference** and **diffraction**.



Snakes also exhibit **warning coloration**. Poisonous snakes, like the coral snakes of North America, may have **vibrant red, black and yellow warning colors** that let their predators know that they are poisonous and do not taste good. **We can tell the poisonous snakes because the yellow band meets both the red and black bands in the poisonous snakes.**



The harmless milk snake may gain some protection by mimicking the red, black, and yellow warning coloration of the poisonous coral snake. We can tell that it is not poisonous because the yellow band only touches the black bands.



Vibrant coloration may also be a result of sexual selection. According to **Charles Darwin** (1871), in humans, the males choose the females with whom they want to mate. In other animals, by contrast, it is the females who choose their mates. Consequently, in animals, the males have developed either weapons such as the **antlers of deer** and **horns of beetles** to chase off their competition and/or ornate displays such as the plumage of the peacock to attract the females. Interestingly, longer horns on beetles may come at the expense of smaller testes. (<http://www.bu.edu/phpbin/news-cms/news/?dept=1127&id=41428&template=226>) Samuel Wilberforce would smile.



In *On the Origin of Species by Means of Natural Selection, Or the Preservation of Favoured Races in the Struggle for Life*, Charles Darwin (1859) wrote, “*Inasmuch as peculiarities often appear under domestication in one sex and become hereditarily attached to that sex, the same fact probably occurs under nature, and if so, natural selection will be able to modify one sex in its functional relations to the other sex, or in relation to wholly different habits of life in the two sexes, as is sometimes the case with insects. And this leads me to say a few words on what I call **Sexual Selection**. This depends, not on a struggle for existence, but on a **struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring**. Sexual selection is, therefore, less rigorous than natural selection. Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex. A **hornless stag or spurless cock** would have a poor chance of leaving offspring. Sexual selection by always allowing the victor to breed might surely give indomitable courage, length to the spur, and strength to*

*the wing to strike in the spurred leg, as well as the brutal cock-fighter, who knows well that he can improve his breed by careful selection of the best cocks. How low in the scale of nature this law of battle descends, I know not; male alligators have been described as fighting, bellowing, and whirling round, like Indians in a war-dance, for the possession of the females; male salmons have been seen fighting all day long; male stag-beetles often bear wounds from the huge mandibles of other males. The war is, perhaps, severest between the males of polygamous animals, and these seem oftenest provided with special weapons. The males of carnivorous animals are already well armed; though to them and to others, special means of defence may be given through means of sexual selection, as **the mane to the lion**, the shoulder-pad to the boar, and the hooked jaw to the male salmon; for the shield may be as important for victory, as the sword or spear.*

Amongst birds, the contest is often of a more peaceful character. All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract by singing the females.

*The rock-thrush of Guiana, birds of Paradise, and some others, congregate; and **successive males display their gorgeous plumage and perform strange antics before the females, which standing by as spectators, at last choose the most attractive partner.***

Those who have closely attended to birds in confinement well know that they often take individual preferences and dislikes: thus Sir R. Heron has described how one pied peacock was eminently attractive to all his hen birds. It may appear childish to attribute any effect to such apparently weak means: I cannot here enter on the details necessary to support this view; but if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see



*no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect. I strongly suspect that some **well-known laws** with respect to the plumage of male and female birds, in comparison with the plumage of the young, can be explained on the view of **plumage having been chiefly modified by sexual selection**, acting when the birds have come to the breeding age or during the breeding season; the modifications thus produced being inherited at corresponding ages or seasons, either by the males alone, or by the males and females; but I have not space here to enter on this subject.*

Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring. Yet, I would not wish to attribute all such sexual differences to this agency: for we see peculiarities arising and becoming attached to the male sex in our domestic animals (as the wattle in male carriers, horn-like protuberances in the cocks of certain fowls, &c.), which we cannot believe to be either useful to the males in battle, or attractive to the females. We see analogous cases under nature, for instance, the tuft of hair on the breast of the turkey-cock, which can hardly be either useful or ornamental to this bird;—indeed, had the tuft appeared under domestication, it would have been called a monstrosity.”

In his *The Descent of Man, and Selection in Relation to Sex*, Charles Darwin (1871) expanded on his ideas concerning sexual selection. He notes the sexual dimorphism in the amount of adornment—the males being more lavishly adorned

than the females.



Charles Darwin discussed the “*care male birds display their various charms, and this they do with the utmost skill. Whilst preening their feathers, they have frequent opportunities for admiring themselves and of studying how best to exhibit their beauty. But as all the males of the same species display themselves in exactly the same manner, it appears that actions, at first perhaps intentional, have become instinctive. If so, we ought not to accuse birds of conscious vanity; yet when we see a peacock strutting about, with expanded and quivering tail-feathers, he seems the very emblem of pride and vanity.*”

Charles Darwin then discussed the cost and benefits of the adornment: “*The various ornaments possessed by the males are certainly of the highest importance to them, for they have been acquired in some cases at the expense of greatly impeded powers of flight or of running..... Nor can we doubt that the long train of the peacock and the long tail and wing-feathers of the Argus pheasant must render them a more easy prey to any prowling tiger-cat than would otherwise be the case. Even the bright colours of many male birds cannot fail to make them conspicuous to their enemies of all kinds.... What then are we to conclude from these facts and considerations? Does the male parade his charms with so much pomp and rivalry for no purpose? Are we not justified in believing that the female exerts a choice, and that she receives the addresses of the male who pleases her most? It is not probable that she consciously deliberates; but she is most excited or attracted by*

the most beautiful, or melodious, or gallant males. Nor need it be supposed that the female studies each stripe or spot of colour; that the peahen, for instance, admires each detail in the gorgeous train of the peacock—she is probably struck only by the general effect.”

After noting that in various species of peacocks there are gradations in the degree of adornments of the tail, he suggested a mechanism as to how the peacock obtained his magnificent train gradually through sexual selection: “*As far, then, as the principle of gradation throws light on the steps by which the magnificent train of the peacock has been acquired, hardly anything more is needed. We may picture to ourselves a progenitor of the peacock in an almost exactly intermediate condition between the existing peacock, with his enormously elongated tail-coverts, ornamented with single ocelli, and an ordinary gallinaceous bird with short tail-coverts, merely spotted with some colour; and we shall then see in our mind's eye, a bird possessing tail-coverts, capable of erection and expansion, ornamented with two partially confluent ocelli, and long enough almost to conceal the tail-feathers,—the latter having already partially lost their ocelli; we shall see in short, a Polyplectron. The indentation of the central disc and surrounding zones of the ocellus in both species of peacock, seems to me to speak plainly in favour of this view; and this structure is otherwise inexplicable. The males of Polyplectron are no doubt very beautiful birds, but their beauty, when viewed from a little distance, cannot be compared, as I formerly saw in the Zoological Gardens, with that of the peacock. Many female progenitors of the peacock must, during a long line of descent, have appreciated this superiority; for they have unconsciously, by the continued preference of the most beautiful males, rendered the peacock the most splendid of living birds.”*

Sexual selection can be experimentally tested by mechanically reducing the number of eyespots in the peacock feathers and counting the number of copulations. When the eyespots are removed, the males have fewer copulations, indicating that the females may favor males with greater adornments with more eyespots. Ornate plumage gives the male an advantage in attracting females which supports Charles Darwin's theory of sexual selection (Dakin and Montgomerie, 2011). This experiment may have been flawed in that the peacocks may have been mangy and less attractive due to the cutting.

When the tail feathers remained intact, but the colored eyespots were covered with white or black stickers, the copulations per hour decreased. Ornate plumage gives the male an advantage in attracting females which supports Charles Darwin's theory of sexual selection (Dakin and Montgomerie, 2013).

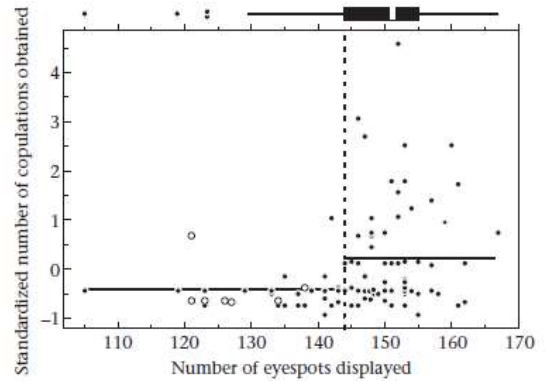
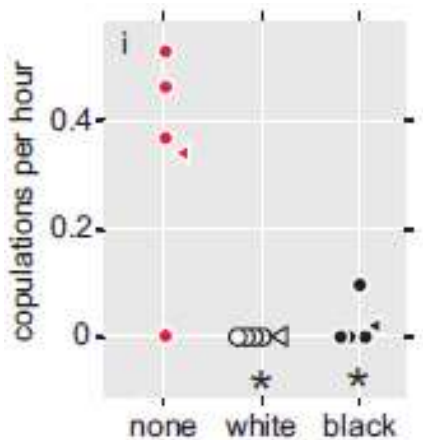


Figure 4. Relation between the number of copulations obtained (standardized by population-year) and the number of eyespots displayed on a peacock's train ($N = 102$). Data are from four studies (Petrie et al. 1991; Petrie & Halliday 1994; Loyau et al. 2005a; this study). The seven open circles are from the removal experiment in this study. Vertical dotted line is at the 25th percentile of displayed eyespot number shown in the main graph; horizontal solid lines are mean values for trains below and above that 25th percentile. Tukey box plot above graph shows the distribution of total number of eyespots displayed per train.

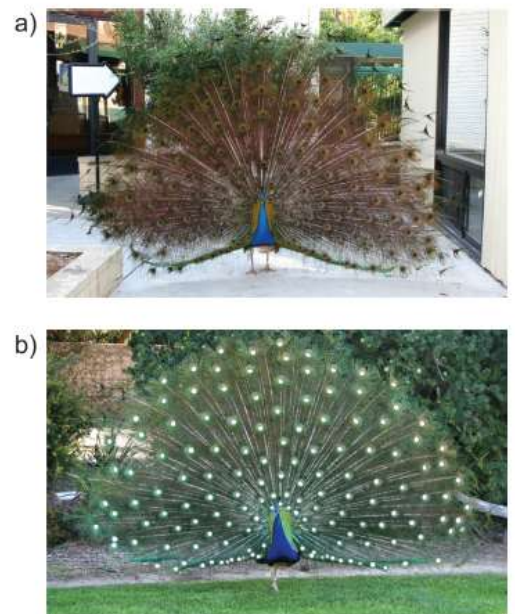


Figure 3
Experimental manipulation of peacock eyespot colors. Experimental males had either (a) black or (b) white stickers masking the purple-black and blue-green patches on all of the eyespot feathers in their train ornament.

By the way, we have been talking about males and females as if those were the only two choices. Indeed **gyandromorph** cardinals, in which one half is male and one half is female, exist.



How often do we even consider the colors of nature? Eighteenth and nineteenth century naturalists, including Christian Konrad Sprengel, Charles Darwin, Henry Bates and Alfred Russel Wallace have helped us to notice, think about, and appreciate the colors of nature, and the color of color in the life of plants and animals. The role of these naturalists in developing our appreciation and understanding is clear from reading the

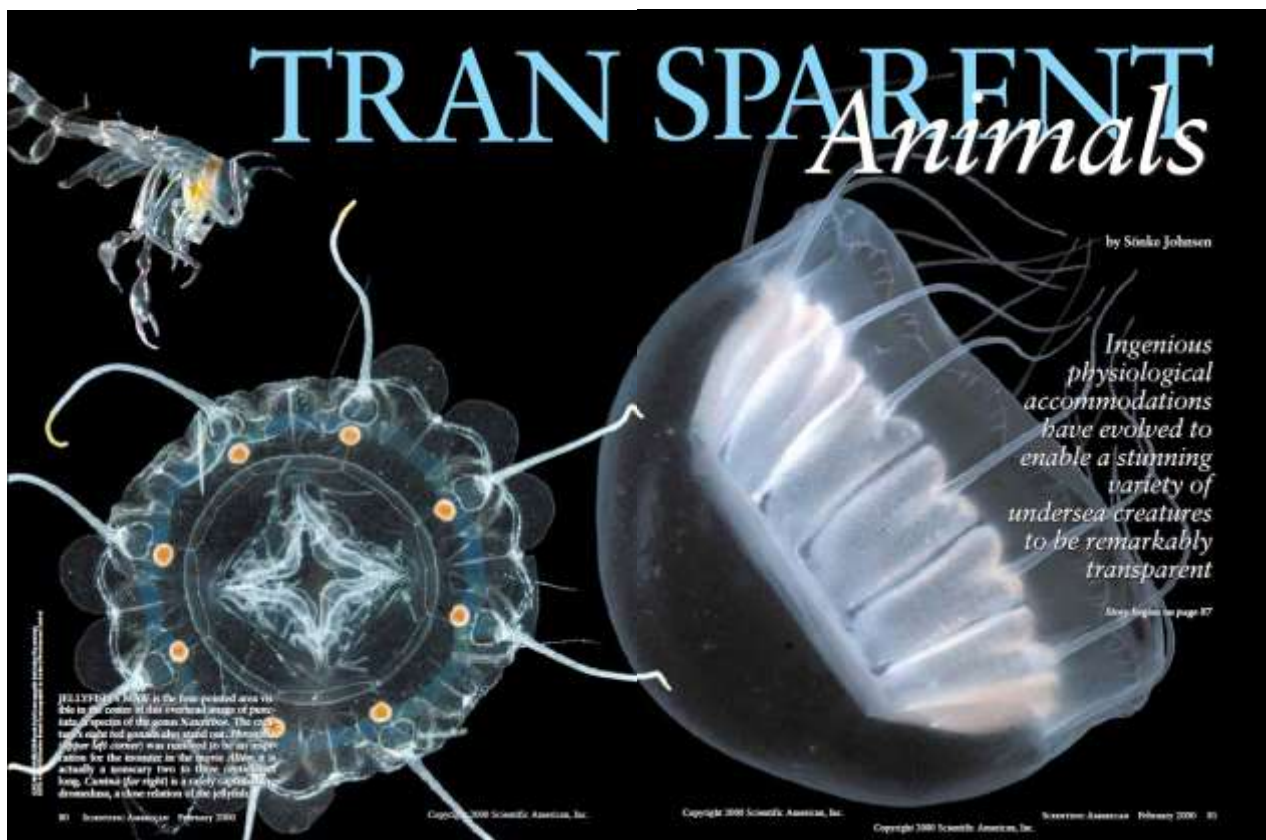
following two paragraphs. Alfred Russel Wallace (1879) began his essay on *The Protective Colours of Animals* like so: “To the ordinary observer the colours of the various



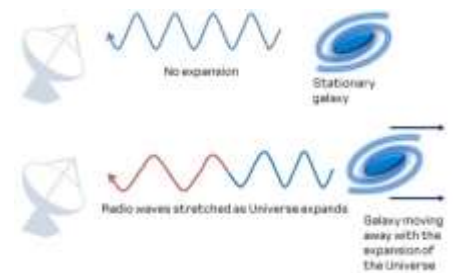
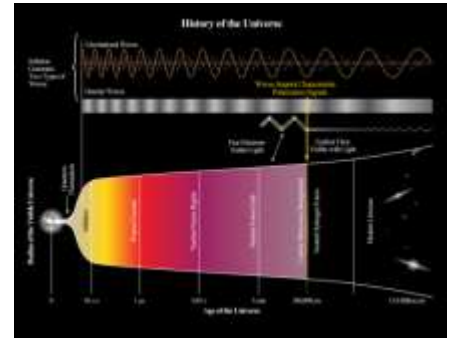
kinds of molluscs, insects, reptiles, birds, and mammals, appear to have no use, and to be distributed pretty much at random. There is a general notion that in the tropics everything—insects, birds, and flowers especially—is much more brilliantly coloured than with us; but the idea that we should ever be able to give a satisfactory reason why one creature is white and another black, why this caterpillar is green and that one brown, and a third adorned with stripes and spots of the most gaudy colours, would seem to most persons both presumptuous and absurd. We propose to show, however, that in a large number of cases the colours of animals are of the greatest importance to them, and that sometimes even their very existence depends upon their peculiar tints.” Alfred Russel Wallace ended the essay like so: “*We must now conclude this very brief outline of one of the most*

curious chapters in natural history. We have shown how varied and how widespread are protective colours among animals; and, if we add to these the cases in which conspicuous colours are useful, sometimes to warn enemies from such as are distasteful or are possessed of dangerous weapons, at other times to aid wandering species to recognise their companions or to find their mates, we shall become satisfied that we have a clue to much of the varied coloration and singular markings throughout the animal kingdom, which at first sight seem to have no purpose but variety and beauty.”

Some animals are **transparent**. For example jellyfish are made out gelatinous materials that have a **refractive index** so close to that of sea water that they are invisible—like the Pyrex glass rod in Wesson (soybean) oil.



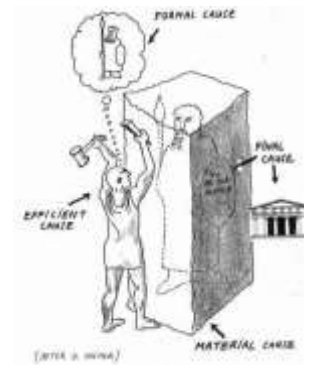
One last thing about the wave theory of light—the wave theory of light helps astrophysicists understand the wavelength of the cosmic background radiation and the **expansion of space**. (Since I am a minority of one who doesn't think that space itself expands but that the universe expands in space, I see the red shift of the galaxies as a result of the Doppler effect and not from the expansion of space. I also see the wavelength distribution of the cosmic microwave background as the result of light undergoing billions of years of collisions which dissipate energy must like the energy of the gamma ray photons produced by fusion in the core of the sun is dissipated as they collide with electrons over the 100,000 year journey they make to the surface of the sun.



Study Questions

Let's answer some questions taking into consideration the **four Aristotelean causes: the material, the formal, the efficient and the final**? We discussed Aristotles four causes when we talked about the **Ship of Theseus** in the luminescence lecture.

Why are leaves green? The material cause is chlorophyll. The formal cause is the arrangement of congugated double bonds around the magnesium ion in the porphorin group on chlorophyll. The efficient cause is the reflection and transmission of light that is not absorbed by the chlorophyll. And the final cause is that the red and blue portions of the spectrum that are not



reflected provide radiant energy that the plant transforms into the chemical energy of food.

Now you try—you may not be able to give all four causes in each case (at least I can't).

Why are forget-me-nots colored blue and yellow?

Why does foxfire glow in the dark?

Why do fireflies glow in the dark?

Why are peppered moths either light or dark?

Why are palatable butterflies patterned after unpalatable butterflies?

Why are tadpoles invisible sometimes?

Why are male peacocks so colorful?

Why is human skin tone lighter or darker?

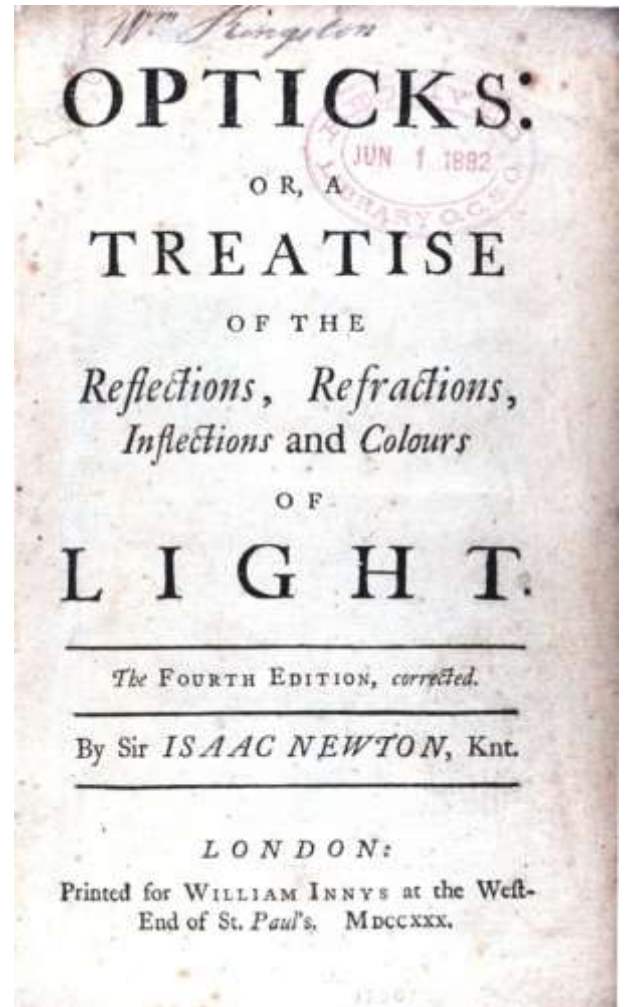
Why are human eyes the color they are?

Why do the endogenous clocks of humans synchronize with the daily rotation period of the earth?

Why do plants measure the lengths of the light and dark periods of a day?

Why is the snow white, the sky blue and the sun yellow-white?

What about a first cause? In Query 28 of his *Opticks: or, A Treatise of the Reflections, Refractions, Inflections and Colours of Light*, Isaac Newton (1730) reflected on the First Cause, when he wrote “*Whereas the main business of natural philosophy is to argue from phenomena without feigning hypotheses, and to deduce causes from effects, til we come to the very first cause, which certainly is not mechanical; and not only to unfold the mechanism of the world, but chiefly to resolve these and such like questions. What is there in places almost empty of matter, and whence is it that the sun and planets gravitate towards one another, without dense matter between them? Whence is it that nature doth nothing in vain; and whence arises all that order and beauty which we see in the world? To what end are comets, and when is it that planets move all one and the same way in orbs concentrick, while comets move all manner of ways in orbs very excentrick; and what hinders the fix’d stars from falling upon one another? How came the bodies of animals to be contrived with so much art, and for what ends were their several parts? Was the eye contrived without skill in opticks, and the ear without knowledge of sounds? How do the motions of the body follow from the will, and whence is the instinct in animals? Is not the sensory of animals that place to which the sensible species of things are carried through the nerves and brain, that there they may be perceived by their immediate presence to that substance? And these things being rightly dispatch’d, does it not appear from phanomena that there is a being incorporeal, living,*



intelligent, omnipresent, who in infinite space, as it were in his sensory, sees the things themselves intimately, and thoroughly perceives them, and comprehends them wholly by their immediate presence to himself: Of which things the images only carried through the organs of sense into our little sensoriums, are there seen and beheld by that which in us perceives and thinks. And though every true step made in this philosophy brings us not immediately to the knowledge of the first cause, yet it brings us nearer to it, and on that account it is to be highly valued.”