Keep Your Eye on the Ball—The Evolutionary History and Physics of Vision

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"Keep your eye on the ball", my dad would tell me when I was playing softball. I tried, I really did, but it seemed as if that ball would just disappear as it crossed the plate after being fanned by my bat passing harmlessly by it. Why couldn't I follow the ball all the way in? Was it moving too fast for me to follow? Did it enter my blind spot? Was I focusing on it with the wrong eye, so that my brain was fooled as to its position as it crossed the plate? The same thing happened when I was fielding the ball. It would be coming right at me, and I would lose it for a second. (Closing your eyes doesn't help either, but what are you going to do about survival reflexes?) Even worse were high fly balls—I could never judge where they were going to come down, and I counted myself lucky if I happened to be underneath the ball in the right spot when it did. Maybe if I had understood more about how vision works, I would have been a better ball player.

Introduction

This unit is designed to be used with my IB Biology students as they study the eye and vision as part of the neurobiology option. It could also be used for an AP Biology or Anatomy and Physiology class. The activities will be used in conjunction with a previous unit I've written, "Neurobiology: Using BOTH Sides of the Brain" which can be found online at the Yale website:
http://teachers.yale.edu/curriculum/search/viewer.php?skin=h&id=initiative_09.06.11_u.
In that unit I focused more on the brain, how action potentials are propagated and behavior. I mentioned the eye as being part of that unit, but this time I delve more deeply into the evolution of the vertebrate eye, and the effects of its structure on how we perceive our world. I anticipate this part of the unit requiring four to five class periods. In this unit students will learn about the components of the eye by exploring and identifying the structures in a sheep eye through dissection. Students will learn about the evolution of the eye, and how the direction that evolution took led to an inside-out retina that resulted in light having to pass through several layers of cells before reaching the actual photoreceptors. How the path of evolution led to shadows on the retina caused by blood vessels in the eye and a blind spot where the optic nerve leaves the retina to go to the brain. They will learn about how vision occurs as light passes through the structures of the eye and is absorbed by photoreceptors in the retina, and how the brain interprets the signals in order to respond to what it is seeing.

Previously, I have had students perform a variety of activities that demonstrate different aspects of vision-- near point, accommodation, the blind spot, and peripheral vision. While these activities are interesting, I think relating these aspects of vision to how they affect the playing of various sports will add emphasis to why they are important. Peripheral vision might be important in many sports, but especially so when playing basketball. Depth of field and visual acuity are important in archery. Identification of which eye is dominant is important when batting in baseball. Students will perform certain sports movements—hitting a ball, shooting an arrow, passing a basketball—under normal conditions, and then, using the information they have about the variables that affect our vision, try to improve their performance by using techniques to improve aspects of vision such as peripheral vision and dynamic visual acuity. Students will be divided into groups based on their interest or skills in certain sports, collect visual data specific to that sport, and report on their results to the class.

Background Information

Light and Vision

Visible light is the portion of electromagnetic radiation that we can see. The wavelengths of visible light fall between those of infrared and ultraviolet regions of the spectrum—from 780 nm to 390 nm.[1] It is these wavelengths that stimulate the photoreceptors in the retinas of our eyes. The colors of light we see--red, orange, yellow, green, blue and violet—are simply our perceptions of those wavelengths.[2] Other animals, such as some birds, fish and insects, can see into the ultraviolet range, and some fish and butterflies can detect wavelengths of 60 nm, into the infrared range.[3] To understand the interaction between our eyes and light, it is necessary to understand something about the nature of light.

Light is energy in the form of massless particles, called photons, which behave as both particles and waves. Photons of light will be absorbed by pigments in the photoreceptors of our eyes, but before that happens, the light must pass through the various structures and fluids of the eye. This will result in bending of the light, or refraction, if the light enters the medium at an angle other than perpendicular (normal) to the medium. As each part of the wave enters a new medium, the wavelength changes as the light interacts with the molecules of the medium, but it maintains the same frequency.[4] (See Figure 1.)

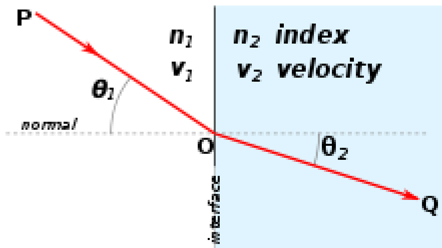

Figure 1: Refraction of light at the interface between two media of different refractive indices, with $n_2 > n_1$. Since the phase velocity is lower in the second medium ($v_2 < v_1$), the angle of refraction θ_2 is less than the angle of incidence θ_1; that is, the ray in the higher-index medium is closer to the normal. http://en.wikipedia.org/wiki/Refraction

Intensity of light is determined by the number of photons detected by the eye per second, and the environment in which a species evolved will have determined what adaptations an animal has for accommodating for various levels of light. Many nocturnal and deep sea animals have large eyes for collecting as many photons of light as possible. Humans use connections between photoreceptors to pool the information from the few photons that come in at low light intensities, and use the iris to control the amount of light that enters the eye when light is very intense. Therefore, the change in light intensity over the course of the day does not seem as great as what it actually is.[5]

The different wavelengths of visible light correspond to the different colors that we see. The color of an object is the result of the light reflected from that object back to our eyes, minus the wavelengths of light that the object absorbed. Therefore, green leaves are absorbing light in the red and blue ranges and reflecting green wavelengths. Our eyes contain two types of photoreceptors called rod and cone cells that detect these variations in wavelength. Rod cells are very sensitive to light and are used for detecting light and dark. There are three types of cone cells called red, green and blue cone cells, but actually, the "red" cone cells absorb light best at a wavelength of 564 nm—a yellow-green. We see red when there is a decrease in signals from the 564nm cones and even less, or no, signal from the 534 nm cone cells.[6] A similar summative effect can produce other colors. A combination of signals from green and red cone cells can result in perception of yellow light, and red and blue cone cells signaling together will result in seeing purple. Eyes absorb light best at wavelengths in the yellow-green range, which happens to be the range where photons are most abundant.[7]

The light absorbing pigments in photoreceptors contain two very important parts—an opsin protein enclosing a photon-absorbing chromophore. In rod cells this chromophore is called retinal, and is derived from vitamin A. There are three different types of cone cells with three different types of chromophores that absorb photons of 420nm, 534nm and 564nm. A chromophore changes shape when it reacts with a photon of light. This changes the shape of the opsin protein, starting a cascade of events in the photoreceptor that closes sodium channels, hyperpolarizing the cell, so that a signal is begun which sends a message to the brain[8]. This signal passes through bipolar neurons to ganglion cells whose axons come together to form the optic nerve which transmits the signal to the brain. Cones are linked individually to bipolar neurons, whereas several rod cells may be linked to one bipolar neuron, making the rod cells more sensitive to low levels of light.

To get to the retina, light has to pass through the cornea, which does most of the refracting of the light. Just behind the cornea is the aqueous humor which helps regulate pressure in the eye. Light then passes through the pupil, an opening whose diameter is controlled by the iris, a layer of muscle tissue that is part of the anterior choroid layer. Sitting just behind the iris is the lens, a transparent, slightly flexible biconvex disc of protein fibers, held in place by suspensory ligaments. The suspensory ligaments are connected to the ciliary body of the choroid layer, and as this muscle contracts and relaxes, the ligaments pull on the lens, causing it to change shape, becoming thicker or thinner to focus the light. The ability to make these changes in shape quickly is called accommodation. With age the lens becomes less flexible and it becomes more difficult to focus quickly from objects up close to objects far away. As light is refracted again as it passes through the lens, it then passes through the vitreous humor in the main part of the eye chamber. This fluid helps to maintain the shape of the eye cup. At the back of the vitreous humor is the retina with its layers of ganglion, bipolar and photoreceptors, backed by a pigmented layer of epithelial cells. (See Figure 2.)

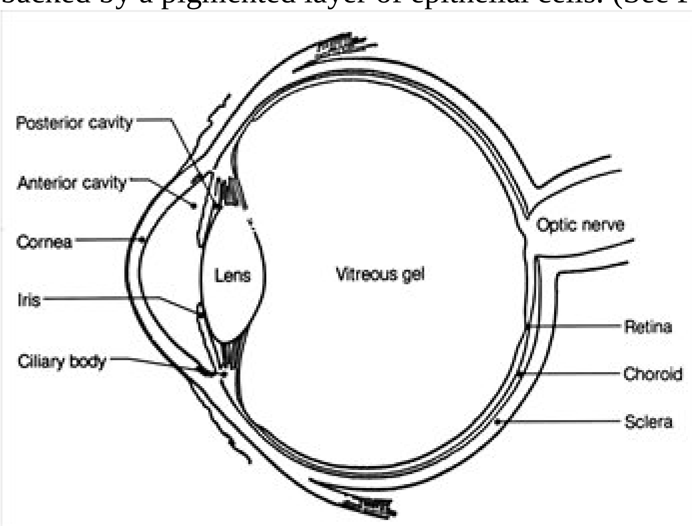

Figure 2. Cross-section of the human eye.
http://www.freeclipartnow.com/science/medicine/anatomy/Anatomy-Eye.jpg.html

Evolution of Vertebrate Eyes

Much of our understanding of how organisms have evolved has come from study of fossil evidence. However, when it comes to the evolution of the eye, fossil evidence is especially rare. Soft tissues do not fossilize easily, and even where we do see indications of what are possibly eyes, there is very little detail preserved. What we do have from the fossil record, and from recent analysis of DNA evidence, is a pretty good understanding of the phylogeny of animals—which groups arose first, when different groups branched off, and how closely related various phyla are to each other. Clues to the evolution of the eye can be found by comparing the eyes found in different phyla still existing today, as well as the clues available in the embryological development of the eye.

There is evidence of simple light sensing structures in organisms existing around 600 million years ago. These would not have been true eyes, in some unicellular organisms there would have been just some light sensitive pigments, such as we see in the "eyespots" of *Euglena* today. These unidirectional photoreceptors would be useful for regulation of circadian rhythms, detecting the presence of light for phototaxis, or determining depth in the water[9]. But 100 million years later, 25 million years after the beginning of the Cambrian explosion, the fossil record reveals the presence of chordates with relatively complete eyes[10].

Eyes evolved at different times in different ways. In order to go from simple detection of light to detecting light from different directions, there had to be multiple photoreceptor cells that would receive light from different directions—which was accomplished by blocking the light on one side of each photoreceptor with a pigmented cell or layer of cells. A pigmented cup shape allowed even better directionality of light detection. Some animals evolved one pigment cup with many receptors, and some evolved the pattern of many pigment cups with one photoreceptor each—which became compound eyes[11]. Most invertebrate animals have compound eyes, with the exception of cephalopods which have a camera-like eye like vertebrates, but with photoreceptors like those found in compound eyes.

The retina of vertebrates forms from the frontal part of the brain tissue during development, and the lens forms from epidermal tissue. (See Figure 3.) The eye cup and lens of cephalopods both form from skin tissue, an indication of different evolutionary pathways. During development of the central nervous system of vertebrates, the neural plate folds inward, separates from the epidermis, and then, as it grows, parts of it start to bulge out to the sides to form the optic vesicles and forward to form the forebrain. As the optic vesicles expand and come in contact with the epidermis, the reaction between the layers causes the vesicle to fold inward, forming the retina, while the epidermis is stimulated to form the lens.(See Figure 4.) Because the neural plate folded inwards, the receiving ends of the photoreceptors end up facing away from the direction light enters the eye[12]. These steps could have evolved if there was selection for lateral expansion of a light sensitive region to increase light exposure and selection for the interactions between the primitive eye vesicle and the ectoderm, leading to the development of a lens-like structure. The retina also goes through a two layer stage before finally ending up with the three layers we find in the mature retina. The hagfish, one of the most primitive vertebrates has a two layer retina, the lamprey and other vertebrates have three layers—more evidence from development about the evolutionary history of the eye[13].

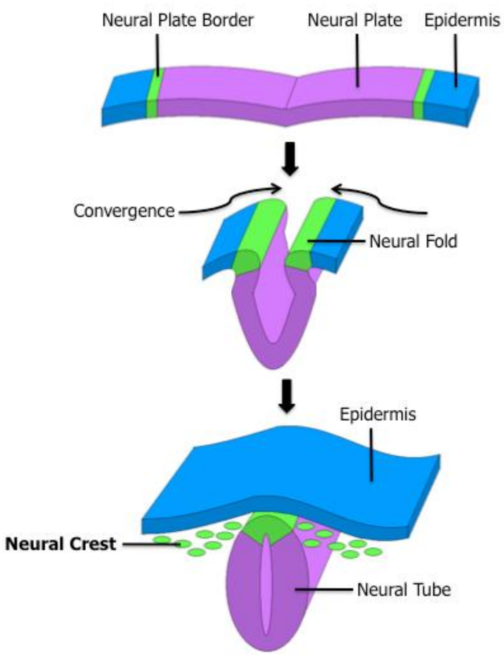

Figure 3: Neural Plate. http://en.wikipedia.org/wiki/Neural_plate

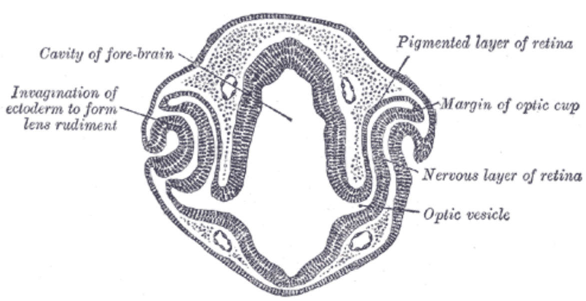

Figure 4: Transverse section of head of chick embryo of forty-eight hours' incubation. (Optic vesicle labeled at lower right.) http://en.wikipedia.org/wiki/File:Gray863.png

The fact that the retina is inside out creates the problem of light having to pass through all three layers of cells in the retina before being absorbed by the photoreceptors. Blood vessels also form to supply the retina and grow on the inner surface and cast shadows on it. Since all the ganglia cells of the retina, which provide output of the signal to the brain, are now facing outwards, their axons have to all come together at one spot on the retina forming the optic nerve. This creates a small spot on the retina where there are no photoreceptors—a blind spot. These problems are the result of how the steps in the formation of the retina evolved[14].

The formation of a lens made it possible to receive better images and to focus on objects. There would have been selection for lenses that produce better images. In the aquatic environment of the first animals, the cornea was only a protective covering. The fluid on both sides of the cornea has about the same refractive index. The lens does most of the job of refracting the light so that it focuses on the retina. Fish have a spherical lens with a refractive index gradient which varies from the middle of the lens to the outer edges, which keeps the light from being bent as much as it passed through the edges of the lens as it would if the lens was homogenous[15]. But when the first vertebrates emerged from the water and began life on land, suddenly it was the cornea that became the important focusing structure. The refractive index difference between the air and the cornea is much greater than between the water and the cornea. So those first land animals must have been very near sighted. Over time selection occurred so that the cornea became less curved and the lens flatter. The result was a 2 to 1 ratio of optical power between the cornea and the lens. Selection could have resulted in the disappearance of the lens or the cornea, but there are fewer optical defects as light is refracted through several curved surfaces rather than one surface with more curvature, so most vertebrates retained both in a modified form[16].

The photoreceptors of invertebrates are rhabdomeric—the membranes that contain the light absorbing pigments are formed from apical microvilli of the cells. Rhabdomeric receptors evolved solely for vision. The receptors of vertebrates are ciliary—the membranes are formed by a cilium in the cell[17]. (A cilium is a structure made of microtubules, like external cilia, but single and internal.) This type of receptor evolved first for regulating circadian rhythms and other non-visual purposes. Vertebrates adapted some ciliary receptors for vision, and retained the rhabdomeric receptors in a modified form that became the ganglion cells sending signals to the brain[18]. The two types of receptors have different responses to light—rhabdomeric photoreceptors response pathways result in depolarization and ciliary photoreceptor response pathways result in hyperpolarization[19].

The opsin pigments in these cells that absorb light have even more ancient origins, and were probably used for other functions before being adapted for light detection. Likewise, the genes that control development of the eye in the embryological stages also evolved early on, as they are common to most animals with eyes of any kind[20].

The simplest of the chordate animals, the amphioxus, has ciliary photoreceptors in a frontal eye as well as rhabdomeric photoreceptors in dorsal ocelli. Another simple chordate, the sea squirts have two ocelli with just a few ciliary photoreceptors surrounded by a pigmented cell[21]. If sea squirts evolved after amphioxus, as it is now believed, then the rhabdomeric photoreceptors may have been adapted to receive input from the ciliary receptors[22].

The earliest of the true vertebrates, the hagfish, have eyes with no lens, iris, or cornea. The retina has only two layers—photoreceptor cells, directly connected to the ganglion cells which send signals to the hypothalamus. The retina is covered by a translucent layer of skin. This "eye" is probably more functional for circadian rhythm regulation than vision, therefore functioning more like pineal gland photoreceptors in non-mammalian vertebrates[23].

The lampreys are another group of jawless fish like the hagfish.. These fish go through a larval stage that lasts for five years. During that time they are essentially blind with eyes much like that of the hagfish. Most of the retinal cells are undifferentiated, with only a small area around the optic nerve that has three retinal layers of cells—photoreceptors, bipolar cells, and ganglion cells. As development proceeds, cells are appear gradually in the order of ganglion cells, amacrine cells, horizontal cells, photoreceptors and bipolar cells—the same order they appear in jawed vertebrates. The photoreceptors of the jawless fishes are cone cells, they do not have rod cells. Jawed vertebrates contain both cone and rod cells, indicating the later evolution of rod cells[24]. (The function of rods and cones are discussed later in this paper.) During metamorphosis, the lens and cornea develop, as well as muscles to move the eye. This can be interpreted in two ways. Either the lampreys evolved from hagfish, or the hagfish is a neotenous form of the lamprey and its eye development was arrested at the larval stage[25].

Most higher vertebrates have similar eye structures with minor variations in the size of the eyes and the shape and size of the lens. Nocturnal animals tend to have large eyes and diurnal animals have smaller eyes. The larger the eye, the greater the focal length, and the smaller the angle between receptors, resulting in greater resolution if there is a large lens to go with the large eye[26]. Large eyes also allow for increased sensitivity to low levels of light since a large eye allows for a greater pupil opening letting in more light. Aquatic mammals which have returned to the sea have eyes with round lenses for greater focusing power in the water. But that creates a problem when they are on land, so to offset the round lens, the cornea is flattened to reduce its focusing power[27].

So why haven't the eyes of all animals evolved into the complex structures that we see in vertebrates? If the cost of increased resolution outweighs the benefits to the organism, then selection pressure decreases. For many organisms, having eyes with better resolution would not bring them any additional advantage because of the environment they live in[28]. So we continue to see what amounts to intermediate versions of the vertebrate eyes in species in existence today. And the eyes that humans have inherited are the result of millions of years of evolution and the flaws in its design are the result of how that evolution occurred.

Lesson Plans and Activities

Day 1—Design an Eye. Students will have learned about the nervous system and how neurons send signals using action potentials and synaptic transmission of neurotransmitters. Using this information, students will be challenged to come up with a plan for a sensory organ that can detect visual images. I will lead the class in a brainstorming session where we identify some of the important aspects about vision that should be included in their designs— how will reflected light from objects be detected, how will the image be focused, how will the organ send the information about the image to the brain, and how will the brain be able to determine from which direction the light is coming from. I will use an overhead projector and a camera to show how an image can be focused on a screen to get them thinking about how that image is focused. Students will then work in teams of three to come up with a plan for an eye. The plans can include mechanical as well as biological components to accomplish the tasks that are required to create an image. Students may use the PhET simulation on Geometric Optics at http://phet.colorado.edu/en/simulation/geometric-optics to determine the size of their lens and the distance to their retina/sensors. The simulation does not allow for a round lens, but students can see how changing the refractive index of the lens and its shape can change the distance to the focal point.

Following this activity, students will draw, label and give the functions of the parts of a human eye. They will then identify any parts in the eye they designed that relate to the functions of the real structures of the eye. The idea is for them to see that the eye may have some flaws in its design as a result of the evolutionary pathway that it took that resulted in its present design. Students will then be presented with a brief summary of the evolution of the vertebrate eye—the advantage of an eye cup and a pigmented layer on one side of the retina; how the eye cup forms during development and why that leads to a retina that seems to be facing in the wrong direction, with a blind spot created by the optic nerve. The embryological origins of the lens will be discussed, and the importance of the cornea in focusing on land.

Day 2—Eye Dissection. With this functional and evolutionary background information about the eye, students will dissect a sheep eye on day 2 and compare the structures of the sheep eye to those found in a human eye. They will also remove the cornea and the lens of the sheep eye and record information on the size, thickness and shape of these structures—looking for the variation in the thickness of the cornea and the lens. Fresh eyes would be preferable to preserved eyes if available, as the preservative often used and storage of the eyes often alters their appearance.

Day 3and 4—Sports and Vision Lab. Students will go outside to practice various sports movements—hitting a baseball, shooting a bow, passing a basketball—and will then discuss how vision plays a role in using those skills. They will then come inside to conduct a series of tests on different aspects of their vision. Unless otherwise noted, the following tests are adapted from the Carolina Biological Supply Company publication, *What about Human Vision*, part of the Carolina *What About Science Series.* Following the tests, students will return to the field to try the various sports activities again, making adjustments to use what they have learned about their vision to improve their performance.

Peripheral Vision. Peripheral vision is important in sports such as basketball, where an opponent, teammate, or the ball may be coming up from behind a player's visual field. Are there gender differences in peripheral vision? Students will test this idea by measuring the visual fields of males and females. First students will map their visual fields using the Goldmann field exam. The student sits one meter away from a white poster mounted on the wall which has a "target" on it. While the student stares at the target, another student will move a basketball toward the test subject's field of view. The student will indicate when they see the ball come into view, and the position will be measured to create a map of the visual field[29].

Blind Spot Determination. The blind spot is caused by the interruption of the retina where the axons of all the ganglion cells come together to form the optic nerve. We don't usually notice it because our brain fills in the missing part of the image. A white sheet of paper with and X on the left side is hung on the wall. The student closes his left eye, stares at the X with his right eye while standing 30 cm from the wall. A partner then moves a pencil wrapped in white, except for the tip, into the field of view until the tip disappears. The position is marked on the paper and the process is repeated from various directions until the blind area is mapped. The actual size of the blind spot on the retina can be determined using the following formula:

A/B=C/D   A-width of the blind spot on paper
B—unknown width of blind spot on retina
C.--Distance from the paper to the eye (300mm)
D—Focal length of the eye (17mm)

Now, knowing it is there, students will be asked to hypothesize and will later test whether or not the blind spots could interfere with seeing something like a baseball as it comes toward a batter.

Dominant Eye Determination. Most people use one eye more than the other. To determine which eye is dominant, students will look through an empty paper towel tube at an object across the room, using both eyes. Then, keeping the tube steady, they open and close one eye at a time. The eye which stays lined up with the tube best, is the dominant eye. Knowing which eye is dominant can help an athlete make adjustments to the positioning of the head and eyes. For example, when batting, if one is right eye dominant, then they should shift the body to better line up the dominant eye with the incoming pitch. In sports like archery or shooting, having the dominant eye and dominant hand on the same side of the body is an advantage. If a student learns she is cross-dominant, with the dominant eye and dominant hand on opposite sides of the body, then adjustments might need to be made to improve performance, and on returning to the field the students can use this knowledge to try to improve their skills.

Dynamic Visual Acuity. Students can test their visual acuity with a Snellen chart. But being able to see letters on a stabilized chart is very different from trying to see a baseball moving toward you at high speeds. In order to hit the ball, or catch it, the eyes have to collect a lot of information very quickly and the brain has to process it even more quickly. Part of the problem may be keeping the eyes focused on the ball. An activity to improve this skill is to put colored dots on baseballs, each with a different color of dots. One person then randomly throws the balls to be hit or caught, and the person batting or catching has to call out the color of the dots before they hit or catch the ball. This forces the person to watch the ball all the way in[30]. More eye speed exercises can be found at http://www.livestrong.com/article/133380-baseball-eye-exercises/.

Notes

[1]"Visible Light and the Eye's Response." The Physics Classroom. http://www.physicsclassroom.com/Class/light/U12L2b.cfm (accessed October 2, 2011).
[2]Ibid.
[3]Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 25.
[4]Conceptual Physics Alive! with Paul G. Hewitt, Volume 9. DVD.
[5]Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 20-21.
[6] Ibid, p26.
[7] Conceptual Physics Alive! with Paul G. Hewitt, Volume 9. DVD.
[8] Lamb, Trevor D.. "Evolution of the Eye." Scientific American 305,64.
[9] Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 6.
[10] Ibid.
[11] Ibid.7.
[12] Lamb, Trevor D., Shaun P. Collin, and Edward N. Pugh, Jr.. "Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup." 968.
[13] Lamb, Trevor D.. "Evolution of the Eye." Scientific American 305,68.
[14] Ibid. 69.
[15] Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 60.
[16] Ibid. 81.
[17] Lamb, Trevor D., Shaun P. Collin, and Edward N. Pugh, Jr.. "Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup." 964.
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[20] Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 60.

[21] Lamb, Trevor D., Shaun P. Collin, and Edward N. Pugh, Jr.. "Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup."963.
[22] Ibid.
[23] Ibid.
[24] Lamb, Trevor D.. "Evolution of the Eye." Scientific American 305, 66.
[25] Lamb, Trevor D., Shaun P. Collin, and Edward N. Pugh, Jr.. "Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup."963.
[26] Land, Michael F., and Dan-Eric Nilsson. *Animal Eyes*, 83.
[27] Ibid. 84.
[28] Ibid. 10.

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Lamb, Trevor D., Shaun P. Collin, and Edward N. Pugh, Jr.. "Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup." *Nature* 8, no. December (2007): 960-975. This review article presented a lot of information about eye evolution in a very organized manner, laying out the evidence clearly.

Lamb, Trevor D.. "Evolution of the Eye." *Scientific American* 305, no. July (2011): 64-69. Trevor Lamb seems to be an authority on eye evolution, and here he writes an article for Scientific American that is very readable and could be used with high school students.

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LIVESTRONG.COM. http://www.livestrong.com/article/133380-baseball-eye-exercises/ (accessed November 29, 2011). This is a very good site for teachers to find activities and experiments to do with students involving sports and science.

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"The Electromagnetic and Visible Spectra." The Physics Classroom. http://www.physicsclassroom.com/Class/light/u12l2a.cfm (accessed October 2, 2011). The Physics Classroom website was recommended to me as a good online textbook on physics that even a biology teacher could handle. Would be a good resource for students as well.

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