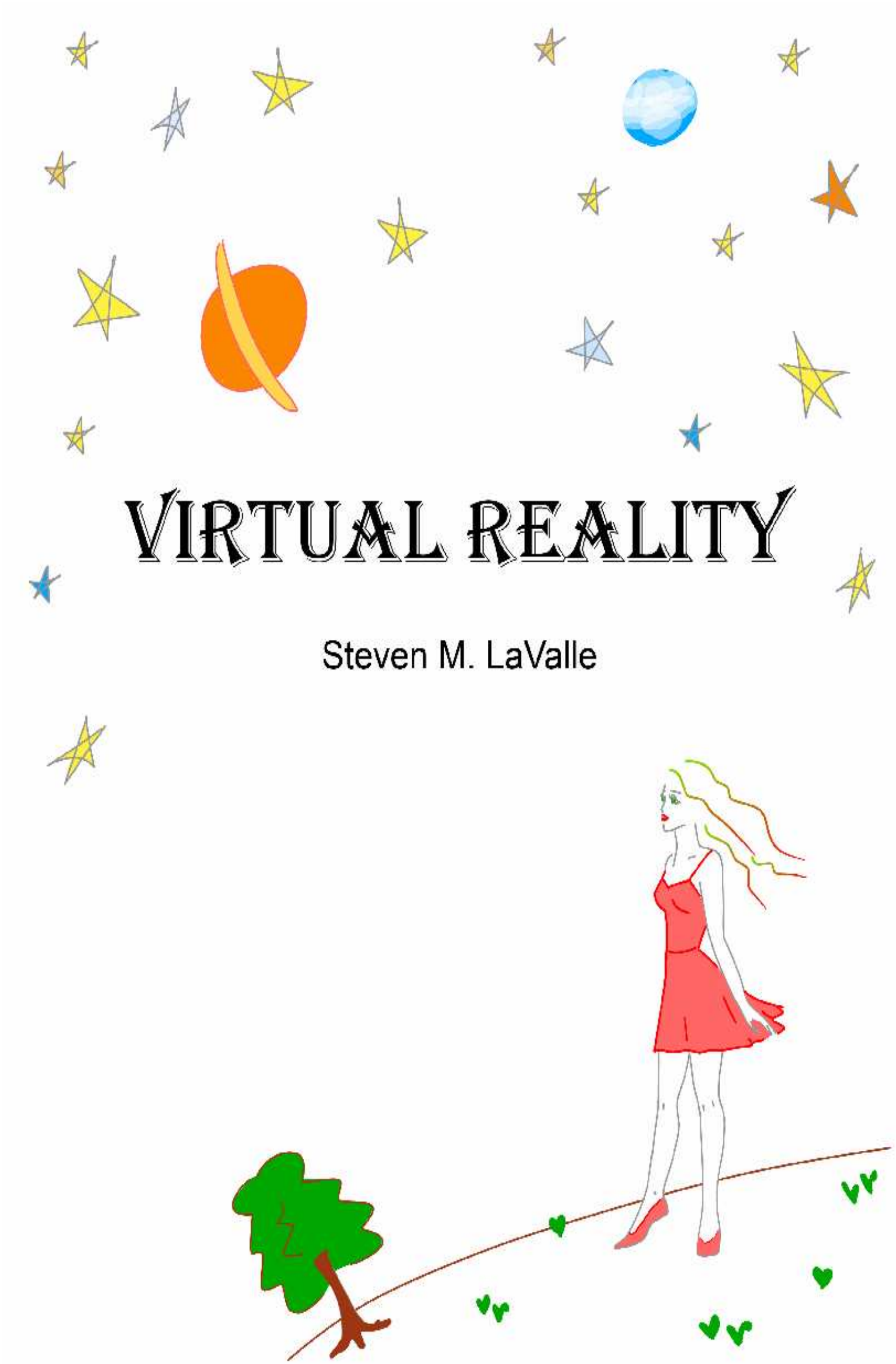

Chapter 5

The Physiology of Human Vision

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Chapter 5

The Physiology of Human Vision

What you perceive about the world around you is “all in your head”. After reading Chapter 4, especially Section 4.4, you should understand that the light around us forms images on our retinas that capture colors, motions, and spatial relationships in the physical world. For someone with normal vision, these captured images may appear to have perfect clarity, speed, accuracy, and resolution, while being distributed over a large field of view. However, we are being fooled. We will see in this chapter that this apparent perfection of our vision is mostly an illusion because neural structures are filling in plausible details to generate a coherent picture in our heads that is consistent with our life experiences. When building VR technology that co-opts these processes, it important to understand how they work. They were designed to do more with less, and fooling these processes with VR produces many unexpected side effects because the display technology is not a perfect replica of the surrounding world.

Section 5.1 continues where Section 4.4 left off by adding some anatomy of the human eye to the optical system. Most of the section is on photoreceptors, which are the “input pixels” that get paired with the “output pixels” of a digital display for VR. Section 5.2 offers a taste of neuroscience by explaining what is known about the visual information that hierarchically propagates from the photoreceptors up to the visual cortex. Section 5.3 explains how our eyes move, which serves a good purpose, but incessantly interferes with the images in our retinas. Section 5.4 concludes the chapter by applying the knowledge gained about visual physiology to determine VR display requirements, such as the screen resolution.

5.1 From the Cornea to Photoreceptors

Parts of the eye Figure 5.1 shows the physiology of a human eye. The shape is approximately spherical, with a diameter of around 24mm and only slight variation among people. The *cornea* is a hard, transparent surface through which light enters and provides the greatest optical power (recall from Section 4.4). The rest of the outer surface of the eye is protected by a hard, white layer called the

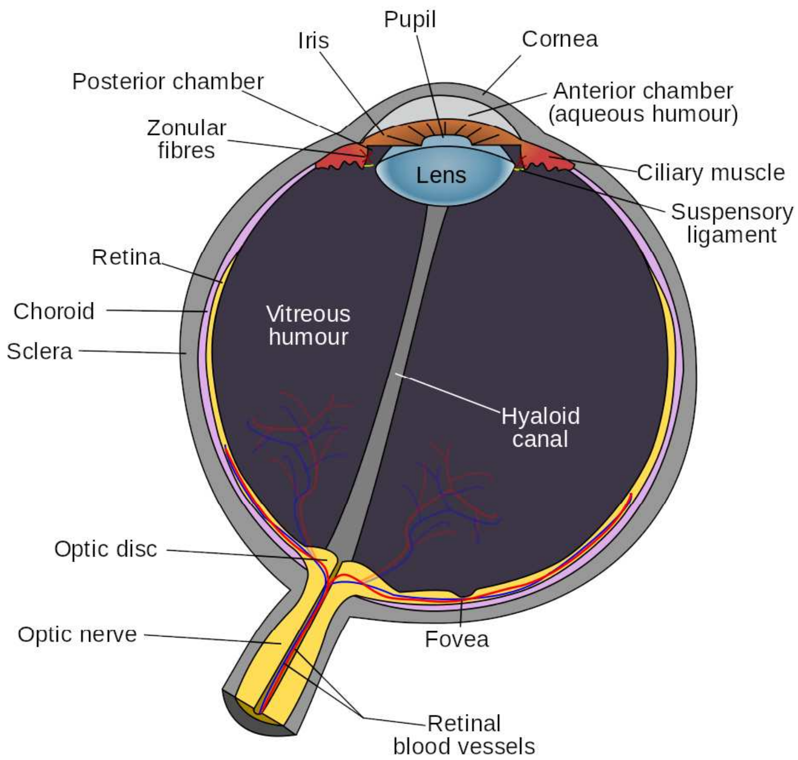


Figure 5.1: Physiology of the human eye. This viewpoint shows how the right eye would appear if sliced horizontally (the nose would be to the left). (From Wikipedia user Rhcastilhos.)

sclera. Most of the eye interior consists of *vitreous humor*, which is a transparent, gelatinous mass that allows light rays to penetrate with little distortion or attenuation.

As light rays cross the cornea, they pass through a small chamber containing *aqueous humour*, which is another transparent, gelatinous mass. After crossing this, rays enter the *lens* by passing through the *pupil*. The size of the pupil is controlled by a disc-shaped structure called the *iris*, which provides an aperture that regulates the amount of light that is allowed to pass. The optical power of the lens is altered by *ciliary muscles*. After passing through the lens, rays pass through the vitreous humor and strike the *retina*, which lines more than 180° of the inner eye boundary. Since Figure 5.1 shows a 2D cross section, the retina is shaped like an arc; however, keep in mind that it is a 2D surface. Imagine it as a curved counterpart to a visual display. To catch the light from the output pixels, it is lined with *photoreceptors*, which behave like "input pixels". The most important part of the retina is the *fovea*; the highest *visual acuity*, which is a measure of the sharpness or clarity of vision, is provided for rays that land on it. The *optic disc* is a small hole in the retina through which neural pulses are transmitted outside of the eye through the *optic nerve*. It is on the same side of the fovea as the nose.

Photoreceptors The retina contains two kinds of photoreceptors for vision: 1) *rods*, which are triggered by very low levels of light, and 2) *cones*, which require more light and are designed to distinguish between colors. See Figure 5.2. To understand the scale, the width of the smallest cones is around 1000nm. This is quite close to the wavelength of visible light, implying that photoreceptors need not be much smaller. Each human retina contains about 120 million rods and 6 million cones that are densely packed along the retina. Figure 5.3 shows the detection capabilities of each photoreceptor type. Rod sensitivity peaks at 498nm, between blue and green in the spectrum. Three categories of cones exist, based on whether they are designed to sense blue, green, or red light.

Photoreceptors respond to light levels over a large dynamic range. Figure 5.4 shows several familiar examples. The luminance is measured in SI units of candelas per square meter, which corresponds directly to the amount of light power per area. The range spans seven orders of magnitude, from 1 photon hitting a photoreceptor every 100 seconds up to $100,000$ photons per receptor per second. At low light levels, only rods are triggered. Our inability to distinguish colors at night is caused by the inability of rods to distinguish colors. Our eyes may take up to 35 minutes to fully adapt to low light, resulting in a monochromatic mode called *scotopic vision*. By contrast, our cones become active in brighter light. Adaptation to this trichromatic mode, called *photopic vision*, may take up to ten minutes (you have undoubtedly noticed the adjustment period when someone unexpectedly turns on lights while you are lying in bed at night).

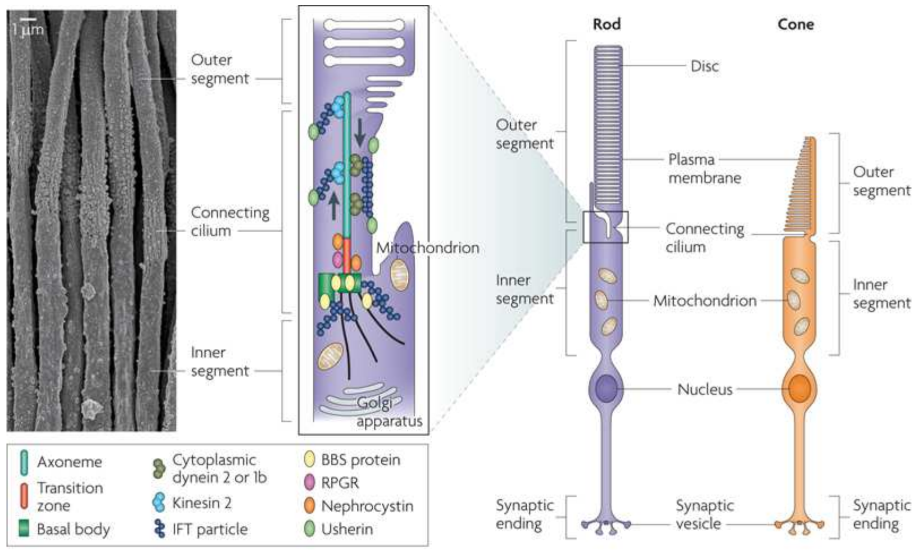


Figure 5.2: On the left is an electron micrograph image of photoreceptors. The right shows the structure and components of rods and cones. The outer segments contain photopigments that electrochemically respond when bombarded by photons. (Figure from [34].)

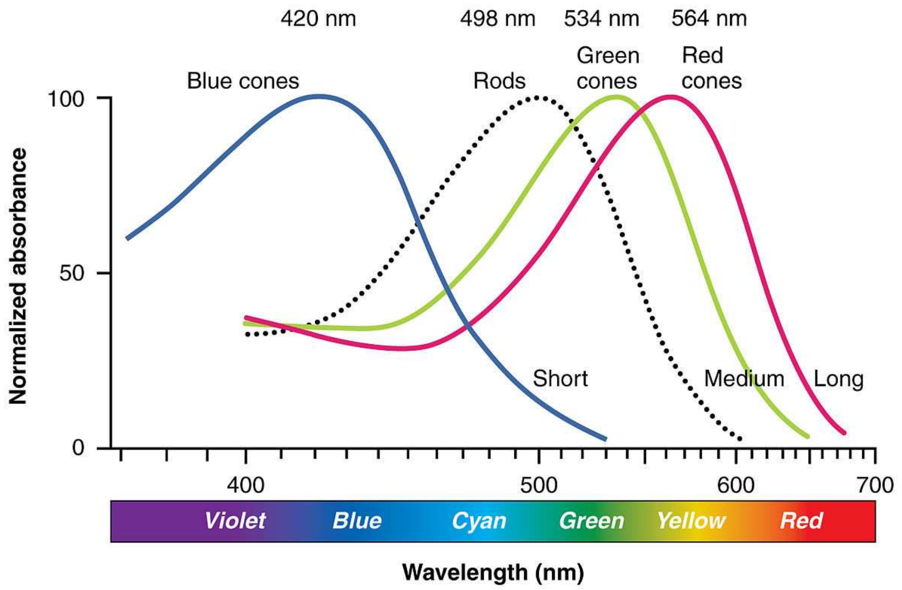


Figure 5.3: The sensitivity of rods and cones as a function of wavelength [4]. (Figure adapted by OpenStax College.)

Light source	**Luminance** (cd/m^2)	**Photons per receptor**
Paper in starlight	0.0003	0.01
Paper in moonlight	0.2	1
Computer monitor	63	100
Room light	316	1000
Blue sky	2500	10,000
Paper in sunlight	40,000	100,000

Figure 5.4: Several familiar settings and the approximate number of photons per second hitting a photoreceptor. (Figure adapted from [17, 22].)

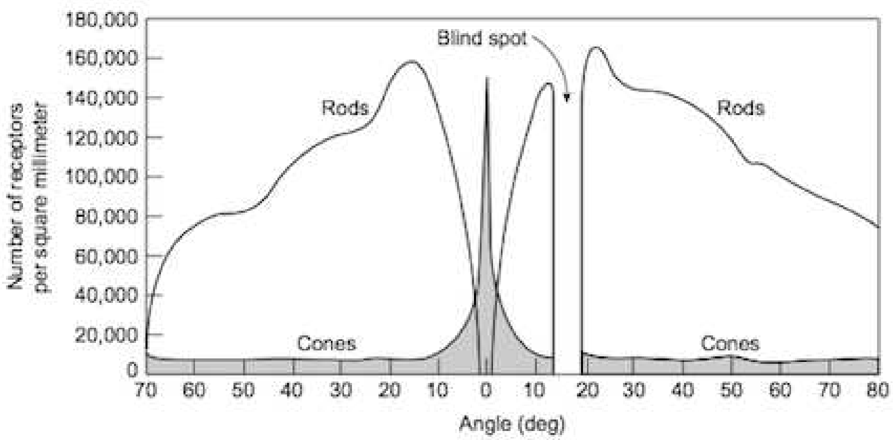


Figure 5.5: Photoreceptor density as a function of angle. The right of the plot is the nasal side (which corresponds to rays entering from the opposite, temporal side). (Figure based on [25])

Photoreceptor density The density of photoreceptors across the retina varies greatly, as plotted in Figure 5.5. The most interesting region is the *fovea*, which has the greatest concentration of photoreceptors. The innermost part of the fovea has a diameter of only 0.5mm or an angular range of ± 0.85 degrees, and contains almost entirely cones. This implies that the eye must be pointed straight at a target to perceive a sharp, colored image. The entire fovea has diameter 1.5mm (± 2.6 degrees angular range), with the outer ring having a dominant concentration of rods. Rays that enter the cornea from the sides land on parts of the retina with lower rod density and very low cone density. This corresponds to the case of *peripheral vision*. We are much better at detecting movement in our periphery, but cannot distinguish colors effectively. Peripheral movement detection may have helped our ancestors from being eaten by predators. Finally, the most intriguing part of the plot is the *blind spot*, where there are no photoreceptors. This is due to our retinas being inside-out and having no other way to route the neural signals to the brain; see Section 5.2.

The photoreceptor densities shown in Figure 5.5 leave us with a conundrum. With 20/20 vision, we perceive the world as if our eyes are capturing a sharp, colorful image over a huge angular range. This seems impossible, however, because we can only sense sharp, colored images in a narrow range. Furthermore, the blind spot should place a black hole in our image. Surprisingly, our *perceptual* processes produce an illusion that a complete image is being captured. This is accomplished by filling in the missing details using contextual information, which is described in Section 5.2, and by frequent eye movements, the subject of Section 5.3. If you are still not convinced that your brain is fooling you into seeing a complete image,

Figure 5.6: An experiment that reveals your blind spot. Close your right eye and look directly at the "X". Vary the distance of the paper (or screen) from your eye. Over some range, the dot should appear to vanish. You can carry this experiment one step further by writing an "X" and dot on a textured surface, such as graph paper. In that case, the dot disappears and you might notice the surface texture perfectly repeating in the place where the dot once existed. This is caused by your brain filling in the expected texture over the blind spot!

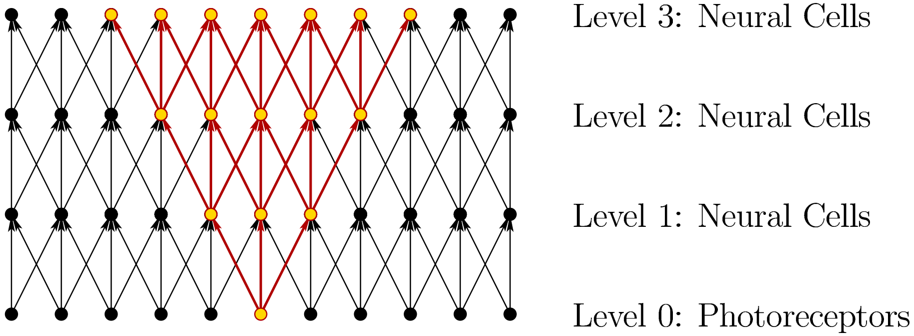


Figure 5.7: Four levels in a simple hierarchy are shown. Each disk corresponds to a neural cell or photoreceptor, and the arrows indicate the flow of information. Photoreceptors generate information at Level 0. In this extremely simplified and idealized view, each photoreceptor and neuron connects to exactly three others at the next level. The red and gold part highlights the growing zone of influence that a single photoreceptor can have as the levels increase.

then try the blind spot experiment shown in Figure 5.6.

5.2 From Photoreceptors to the Visual Cortex

Photoreceptors are transducers that convert the light-energy stimulus into an electrical signal called a neural impulse, thereby inserting information about the outside world into our neural structures. Recall from Section 2.3 that signals are propagated upward in a hierarchical manner, from photoreceptors to the visual cortex (Figure 2.19). Think about the influence that each photoreceptor has on the network of neurons. Figure 5.7 shows a simplified model. As the levels increase, the number of influenced neurons grows rapidly. Figure 5.8 shows the same diagram, but highlighted in a different way by showing how the number of photoreceptors that influence a single neuron increases with level. Neurons at

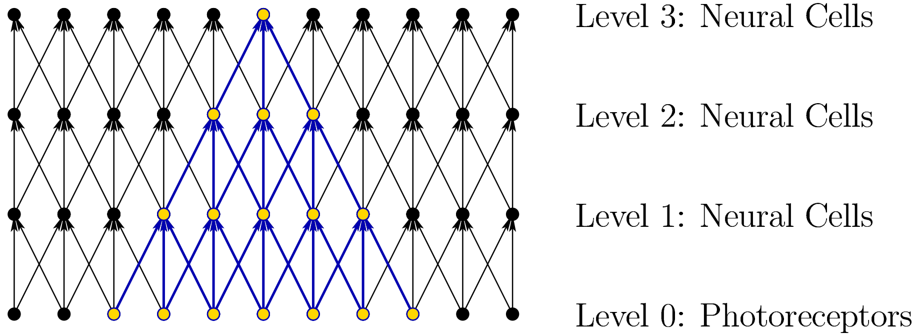


Figure 5.8: This diagram is the same as Figure 5.7 except that the information feeding into a single neuron is highlighted. Consider the set of photoreceptors involved in the reaction of a single neural cell. This is called the *receptive field*. As the level increases, the receptive field size grows dramatically. Due to the spatial arrangement of the photoreceptors, this will imply that each neuron responds to a growing patch in the image on the retina. The patch increases in size at higher levels.

the lowest levels are able to make simple comparisons of signals from neighboring photoreceptors. As the levels increase, the neurons may respond to a larger patch of the retinal image. This principle will become clear when seeing more neural structures in this section. Eventually, when signals reach the highest levels (beyond these figures), information from the memory of a lifetime of experiences is fused with the information that propagated up from photoreceptors. As the brain performs significant processing, a perceptual phenomenon results, such as recognizing a face or judging the size of a tree. It takes the brain over 100ms to produce a result that enters our consciousness.

Now consider the first layers of neurons in more detail, as shown in Figure 5.9. The information is sent from right to left, passing from the rods and cones to the bipolar, amacrine, and horizontal cells. These three types of cells are in the *inner nuclear layer*. From there, the signals reach the ganglion cells, which form the *ganglion cell layer*. Note that the light appears to be entering from the wrong direction: It passes over these neural cells before reaching the photoreceptors. This is due to the fact that the human retina is inside-out, as shown in Figure 5.10. Evolution got it right with octopuses and other cephalopods, for which the light directly reaches the photoreceptors. One consequence of an inside-out retina is that the axons of the ganglion cells cannot be directly connected to the *optic nerve* (item 3 in Figure 5.10), which sends the signals outside of the eye. Therefore, a hole has been punctured in our retinas so that the "cables" from the ganglion cells can be routed outside of the eye (item 4 in Figure 5.10). This causes the blind spot that was illustrated in Figure 5.6.

Upon studying Figure 5.9 closely, it becomes clear that the neural cells are not

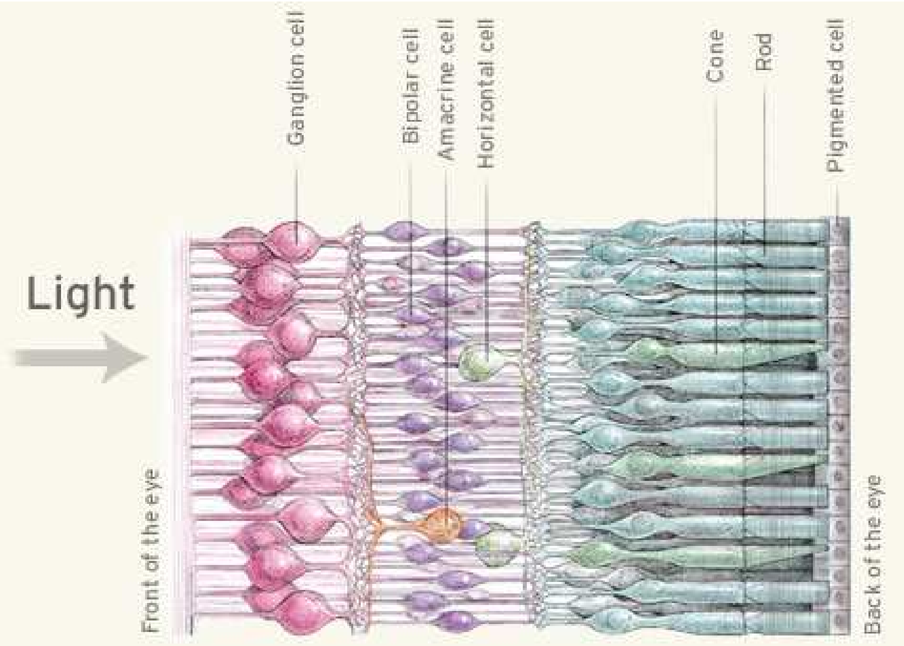


Figure 5.9: Light passes through a few neural layers before hitting the rods and cones. (Figure by the Institute for Dynamic Educational Advancement.)

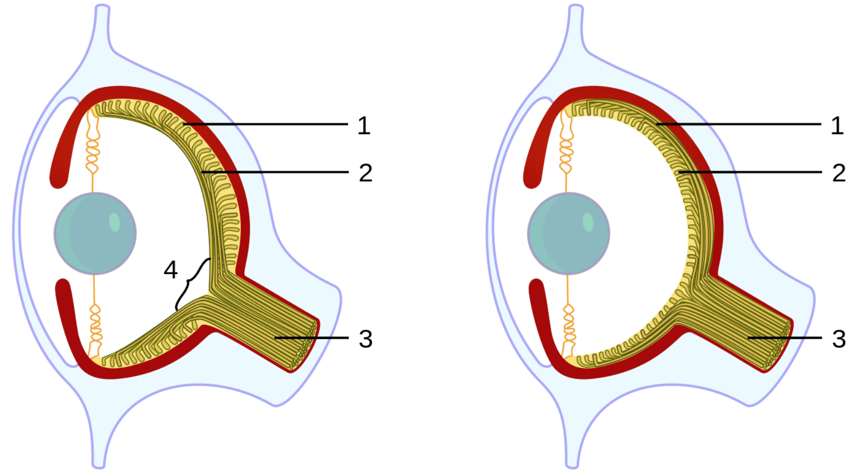


Figure 5.10: Vertebrates (including humans) have inside-out retinas, which lead to a blind spot and photoreceptors aimed away from the incoming light. The left shows a vertebrate eye, and the right shows a cephalopod eye, for which nature got it right: The photoreceptors face the light and there is no blind spot. (Figure by Jerry Crimson Mann.)

arranged in the ideal way of Figure 5.8. The *bipolar cells* transmit signals from the photoreceptors to the ganglion cells. Some bipolars connect only to cones, with the number being between cones 1 and 10 per bipolar. Others connect only to rods, with about 30 to 50 rods per bipolar. There are two types of bipolar cells based on their function. An *ON bipolar* activates when the rate of photon absorption in its connected photoreceptors *increases*. An *OFF bipolar* activates for *decreasing* photon absorption. The bipolars connected to cones have both kinds; however, the bipolars for rods have only ON bipolars. The bipolar connections are considered to be *vertical* because they connect directly from photoreceptors to the ganglion cells This is in contrast to the remaining two cell types in the inner nuclear layer. The *horizontal cells* are connected by inputs (dendrites) to photoreceptors and bipolar cells within a radius of up to 1mm. Their output (axon) is fed into photoreceptors, causing *lateral inhibition*, which means that the activation of one photoreceptor tends to decrease the activation of its neighbors. Finally, *amacrine cells* connect horizontally between bipolar cells, other amacrine cells, and vertically to ganglion cells. There are dozens of types, and their function is not well understood. Thus, scientists do not have a complete understanding of human vision, even at the lowest layers. Nevertheless, the well understood parts contribute greatly to our ability to design effective VR systems and predict other human responses to visual stimuli.

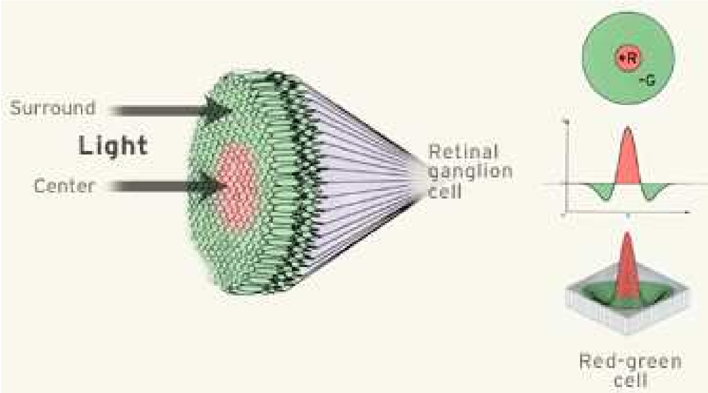


Figure 5.11: The receptive field of an ON-center ganglion cell. (Figure by the Institute for Dynamic Educational Advancement.)

At the ganglion cell layer, several kinds of cells process portions of the retinal image. Each ganglion cell has a large receptive field, which corresponds to the photoreceptors that contribute to its activation as shown in Figure 5.8. The three most common and well understood types of ganglion cells are called *midget*, *parasol*, and *bistratified*. They perform simple filtering operations over their receptive fields based on spatial, temporal, and spectral (color) variations in the stimulus across the photoreceptors. Figure 5.11 shows one example. In this case, a ganglion cell is triggered when red is detected in the center but not green in the surrounding area. This condition is an example of *spatial opponency*, for which neural structures are designed to detect local image variations. Thus, consider ganglion cells as tiny image processing units that can pick out local changes in time, space, and/or color. They can detect and emphasize simple image features such as edges. Once the ganglion axons leave the eye through the optic nerve, a significant amount of image processing has already been performed to aid in visual perception. The raw image based purely on photons hitting the photoreceptor never leaves the eye.

The optic nerve connects to a part of the *thalamus* called the *lateral geniculate nucleus* (*LGN*); see Figure 5.12. The LGN mainly serves as a router that sends signals from the senses to the brain, but also performs some processing. The LGN sends image information to the *primary visual cortex* (V1), which is located at the back of the brain. The *visual cortex*, highlighted in Figure 5.13, contains several interconnected areas that each perform specialized functions. Figure 5.14 shows one well-studied operation performed by the visual cortex. Chapter 6 will describe visual perception, which is the conscious result of processing in the visual cortex, based on neural circuitry, stimulation of the retinas, information from other senses, and expectations based on prior experiences. Characterizing how all of these processes function and integrate together remains an active field of

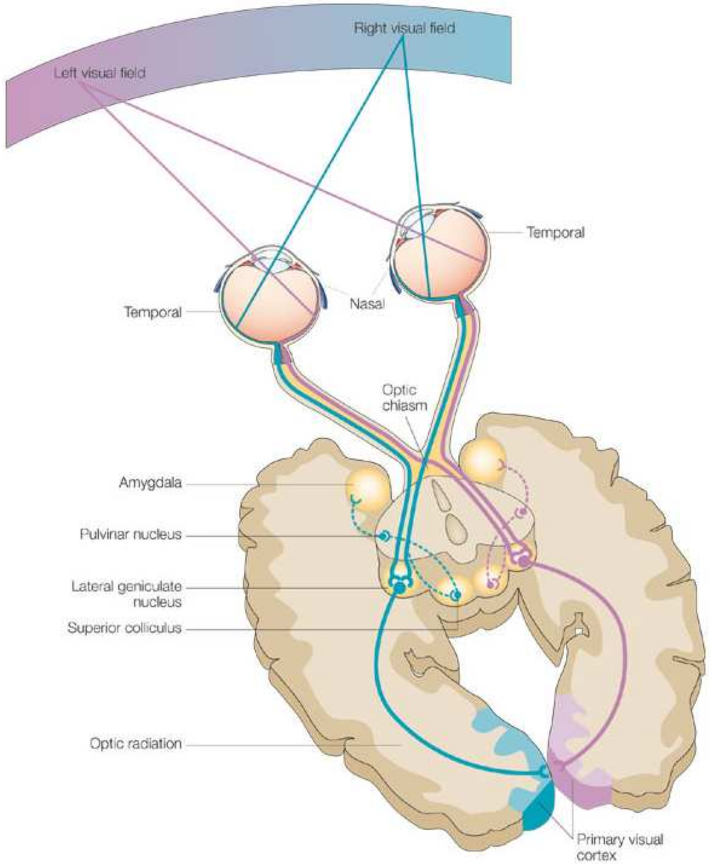


Figure 5.12: The visual pathway from the eyes to the LGN to the visual cortex. Note that information from the right and left sides of the visual field becomes swapped in the cortex. (Figure from Nature Reviews: Neuroscience)

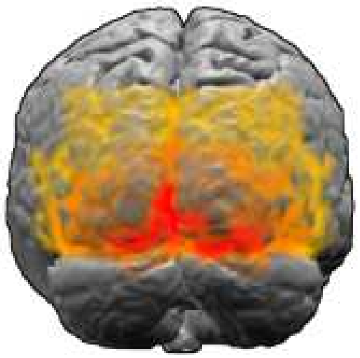


Figure 5.13: The visual cortex is located in the back of the head (Figure by Washington Irving).

research.

5.3 Eye Movements

Eye rotations are a complicated and integral part of human vision. They occur both voluntarily and involuntarily, and allow a person to fixate on features in the world, even as his head or target features are moving. One of the main reasons for eye movement is to position the feature of interest on the fovea. Recall from Section 5.2 that only the fovea can sense dense, color images, and it unfortunately spans a very narrow field of view. To gain a coherent, detailed view of a large object, the eyes rapidly scan over it while fixating on points of interest. Figure 5.15 shows an example. Another reason for eye movement is that our photoreceptors are slow to respond to stimuli due to their chemical nature. They take up to 10ms to fully respond to stimuli and produce a response for up to 100ms. Eye movements help keep the image fixed on the same set of photoreceptors so that they can fully charge. This is similar to the image blurring problem that occurs in cameras at low light levels and slow shutter speeds. Additional reasons for eye movement are to maintain a stereoscopic view and to prevent adaptation to a constant stimulation. To support the last claim, it has been shown experimentally that when eye motions are completely suppressed, visual perception disappears completely [14]. As movements combine to build a coherent view, it is difficult for scientists to predict and explain how people interpret some stimuli. For example, the optical illusion in Figure 5.16 appears to be moving when our eyes scan over it.

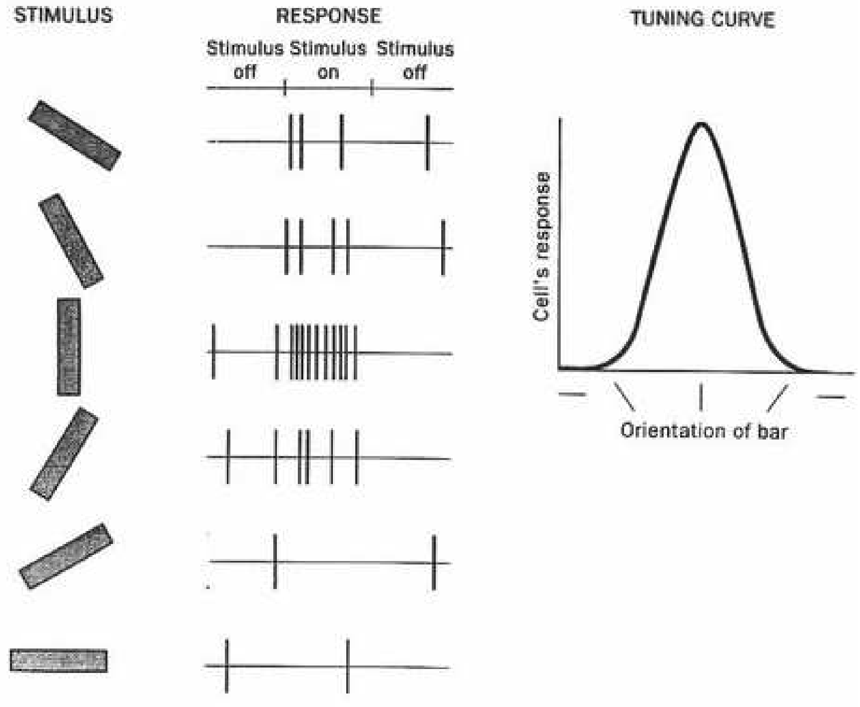


Figure 5.14: A popular example of visual cortex function is *orientation tuning*, in which a single-unit recording is made of a single neuron in the cortex. As the bar is rotated in front of the eye, the response of the neuron varies. It strongly favors one particular orientation.

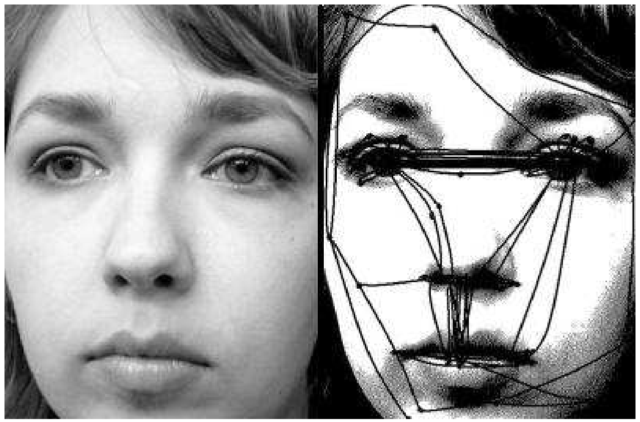


Figure 5.15: The trace of scanning a face using saccades.

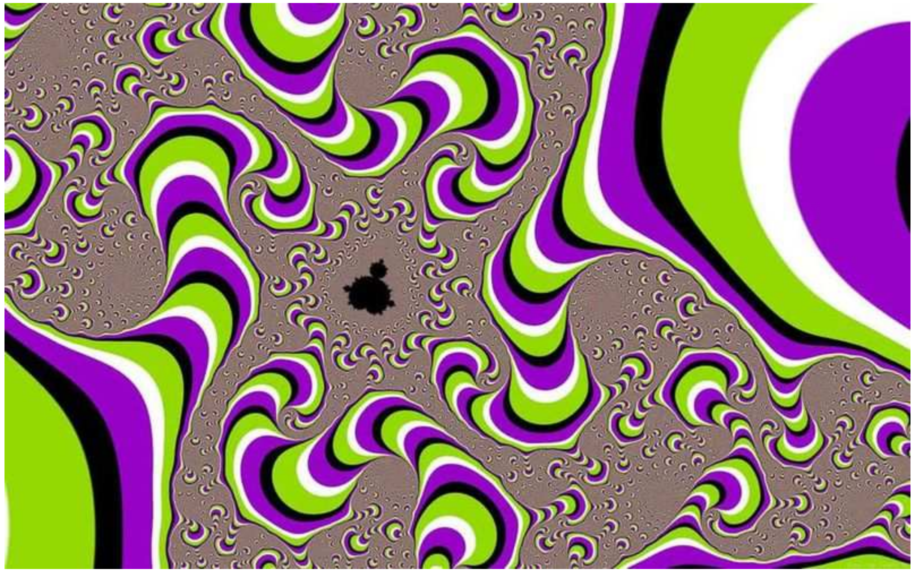


Figure 5.16: The fractal appears to be moving until you carefully fixate on a single part to verify that it is not.

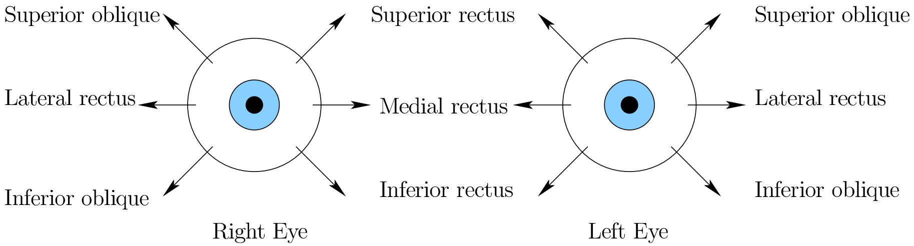


Figure 5.17: There are six muscles per eye, each of which is capable of pulling the pupil toward its location.

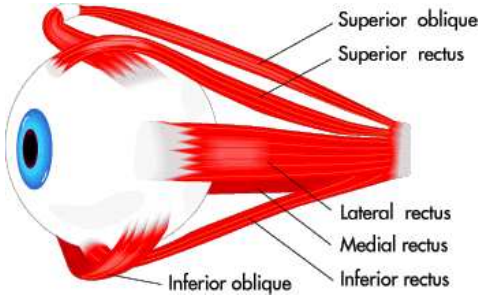


Figure 5.18: The six muscle tendons attach to the eye so that yaw, pitch, and a small amount of roll become possible.

Eye muscles The rotation of each eye is controlled by six muscles that are each attached to the sclera (outer eyeball surface) by a tendon. Figures 5.17 and 5.18 show their names and arrangement. The tendons pull on the eye in opposite pairs. For example, to perform a yaw (side-to-side) rotation, the tensions on the medial rectus and lateral rectus are varied while the other muscles are largely unaffected. To cause a pitch motion, four muscles per eye become involved. All six are involved to perform both a pitch and yaw, for example, looking upward and to the right. A small amount of roll can be generated; however, our eyes are generally not designed for much roll motion. Imagine if you could turn your eyeballs upside-down inside of their sockets! Thus, it is reasonable in most cases to approximate eye rotations as a 2D set that includes only yaw and pitch, rather than the full 3 DOFs obtained for rigid body rotations in Section 3.2.

Types of movements We now consider movements based on their purpose, resulting in six categories: 1) saccades, 2) smooth pursuit, 3) vestibulo-ocular reflex, 4) optokinetic reflex, 5) vergence, and 6) microsaccades. All of these motions cause both eyes to rotate approximately the same way, except for vergence, which causes the eyes to rotate in opposite directions. We will skip a seventh category of motion, called *rapid eye movements* (REMs), because they only occur while we are sleeping and therefore do not contribute to a VR experience. The remaining six categories will now be discussed in detail.

Saccades The eye can move in a rapid motion called a *saccade*, which lasts less than 45ms with rotations of about 900° per second. The purpose is to quickly relocate the fovea so that important features in a scene are sensed with highest visual acuity. Figure 5.15 showed an example in which a face is scanned by *fixating* on various features in rapid succession. Each transition between features is accomplished by a saccade. Interestingly, our brains use *saccadic masking* to hide the intervals of time over which saccades occur from our memory. This results in distorted time perception, as in the case when second hands click into position on an analog clock. The result of saccades is that we obtain the illusion of high acuity over a large angular range. Although saccades frequently occur while we have little or no awareness of them, we have the ability to consciously control them as we choose features for fixation.

Smooth pursuit In the case of *smooth pursuit*, the eye slowly rotates to track a moving target feature. Examples are a car, a tennis ball, or a person walking by. The rate of rotation is usually less than 30° per second, which is much slower than for saccades. The main function of smooth pursuit is to reduce motion blur on the retina; this is also known as *image stabilization*. The blur is due to the slow response time of photoreceptors, as discussed in Section 5.1. If the target is moving too fast, then saccades may be intermittently inserted into the pursuit motions to catch up to it.

Vestibulo-ocular reflex One of the most important motions to understand for VR is the *vestibulo-ocular reflex* or *VOR*. Hold your finger at a comfortable distance in front of your face and fixate on it. Next, yaw your head back and forth (like you are nodding "no"), turning about 20 or 30 degrees to the left and right sides each time. You may notice that your eyes are effortlessly rotating to counteract the rotation of your head so that your finger remains in view. The eye motion is involuntary. If you do not believe it, then try to avoid rotating your eyes while paying attention to your finger and rotating your head. It is called a reflex because the motion control bypasses higher brain functions. Figure 5.19 shows how this circuitry works. Based on angular accelerations sensed by vestibular organs, signals are sent to the eye muscles to provide the appropriate counter motion. The main purpose of the VOR is to provide image stabilization, as in the case of smooth pursuit. For more details about the vestibular organ, see Section 8.2.

Optokinetic reflex The next category is called the *optokinetic reflex*, which occurs when a fast object speeds along. This occurs when watching a fast-moving train while standing nearby on fixed ground. The eyes rapidly and involuntarily choose features for tracking on the object, while alternating between smooth pursuit and saccade motions.

Vergence *Stereopsis* refers to the case in which both eyes are fixated on the same object, resulting in a single perceived image. Two kinds of *vergence* motions occur to align the eyes with an object. See Figure 5.20. If the object is closer than a previous fixation, then a *convergence* motion occurs. This means that the eyes are rotating so that the pupils are becoming closer. If the object is further, then *divergence* motion occurs, which causes the pupils to move further apart. The eye orientations resulting from vergence motions provide important information about the distance of objects.

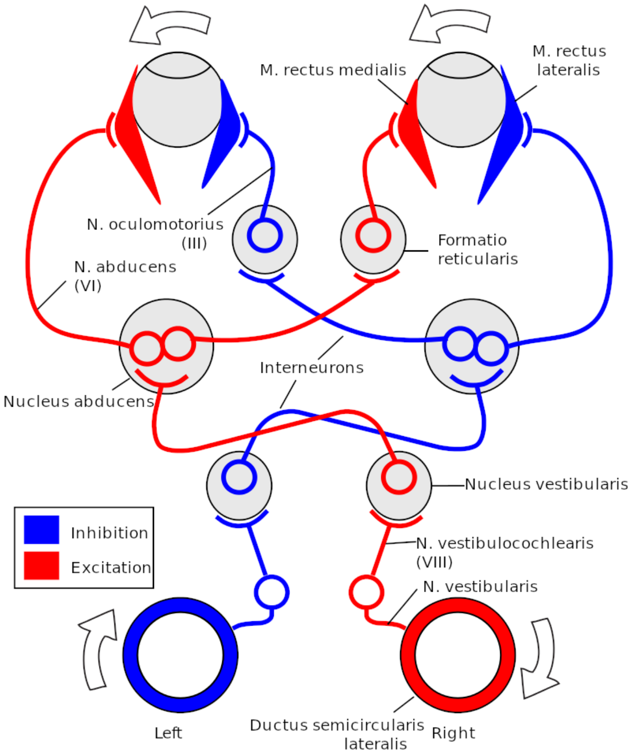


Figure 5.19: The vestibulo-ocular reflex (VOR). The eye muscles are wired to angular accelerometers in the vestibular organ to counter head movement with the opposite eye movement with less than 10ms of latency. The connection between the eyes and the vestibular organ is provided by specialized vestibular and extraocular motor nuclei, thereby bypassing higher brain functions.

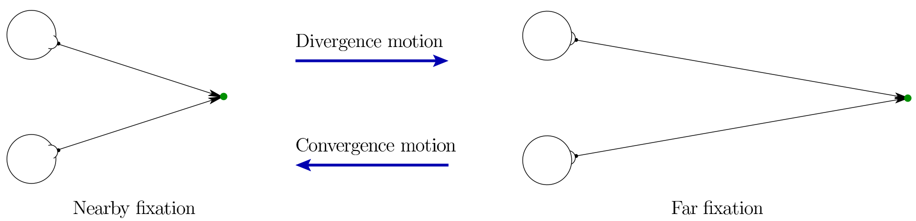


Figure 5.20: In the process of stereopsis, both eyes are fixated on the same feature in the world. To transition from a close to far feature, a divergence motion occurs. A convergence motion happens for the opposite transition.

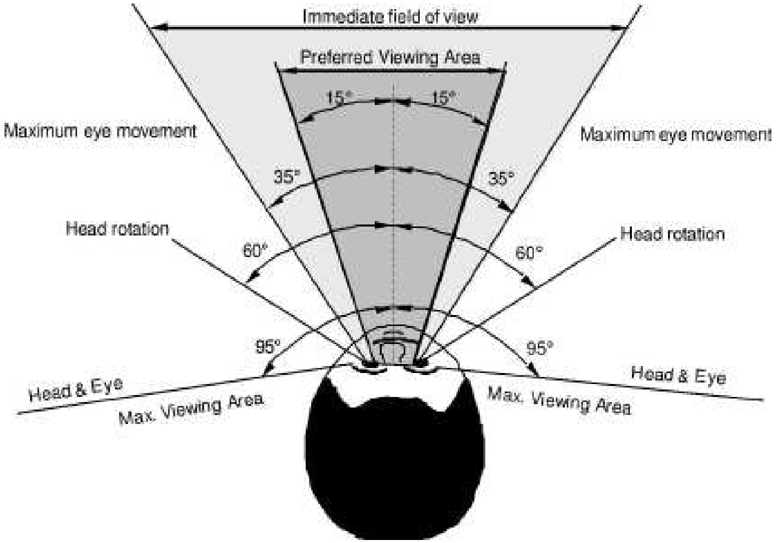


Figure 5.21: The head and eyes rotate together to fixate on new or moving targets. (Figure from MSC/Circ.982 20 December 2000.)

Microsaccades The sixth category of movements is called *microsaccades*, which are small, involuntary jerks of less than one degree that trace out an erratic path. They are believed to augment many other processes, including control of fixations, reduction of perceptual fading due to adaptation, improvement of visual acuity, and resolving perceptual ambiguities [28]. Although these motions have been known since the 18th century [7], their behavior is extremely complex and not fully understood. Microsaccades are an active topic of research in perceptual psychology, biology, and neuroscience.

Eye and head movements together Although this section has focused on eye movement, it is important to understand that most of the time the eyes and head are moving together. Figure 5.21 shows the angular range for yaw rotations of the head and eyes. Although eye yaw is symmetric by allowing 35° to the left or right, pitching of the eyes is not. Human eyes can pitch 20° upward and 25° downward, which suggests that it might be optimal to center a VR display slightly below the pupils when the eyes are looking directly forward. In the case of VOR, eye rotation is controlled to counteract head motion. In the case of smooth pursuit, the head and eyes may move together to keep a moving target in the preferred viewing area.

5.4 Implications for VR

This chapter has so far covered the human hardware for vision. Basic physiological properties, such as photoreceptor density or VOR circuitry directly impact the engineering requirements for visual display hardware. The engineered systems must be good enough to adequately fool our senses, but they need not have levels of quality that are well beyond the limits of our receptors. Thus, the VR display should ideally be designed to perfectly match the performance of the sense it is trying to fool.

How good does the VR visual display need to be? Three crucial factors for the display are:

1. *Spatial resolution:* How many pixels per square area are needed?

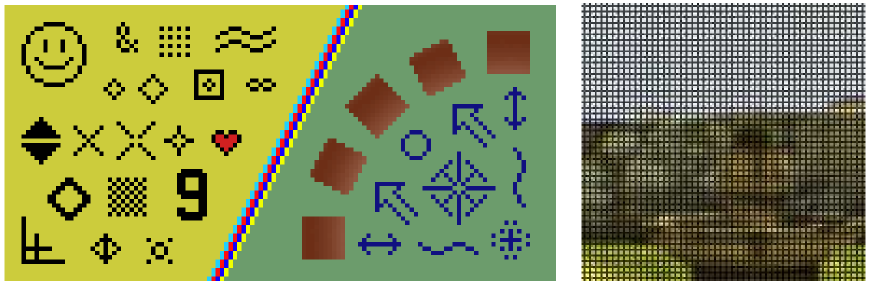
2. *Intensity resolution and range:* How many intensity values can be produced, and what are the minimum and maximum intensity values?

3. *Temporal resolution:* How fast do displays need to change their pixels?

The spatial resolution factor will be addressed in the next paragraph. The second factor could also be called *color resolution and range* because the intensity values of each red, green, or blue subpixel produce points in the space of colors; see Section 6.3. Recall the range of intensities from Figure 5.4 that trigger photoreceptors. Photoreceptors can span seven orders of magnitude of light intensity. However, displays have only 256 intensity levels per color to cover this range. Entering scotopic vision mode does not even seem possible using current display technology because of the high intensity resolution needed at extremely low light levels. Temporal resolution is extremely important, but is deferred until Section 6.2, in the context of motion perception.

How much pixel density is enough? We now address the spatial resolution. Insights into the required spatial resolution are obtained from the photoreceptor densities. As was shown in Figure 4.36, we see individual lights when a display is highly magnified. As it is zoomed out, we may still perceive sharp diagonal lines as being jagged, as shown in Figure 5.22(a); this phenomenon is known as *aliasing*. Another artifact is the *screen-door effect*, shown in Figure 5.22(b); this is commonly noticed in an image produced by a digital LCD projector. What does the display pixel density need to be so that we do not perceive individual pixels? In 2010, Steve Jobs of Apple Inc. claimed that 326 pixels per linear inch (*PPI*) is enough, achieving what they called a *retina display*.[1] Is this reasonable, and how does it relate to VR?

[1] This is equivalent to a density of 165 pixels per mm^2, but we will use linear inches because it is the international standard for display comparisons.



(a) (b)

Figure 5.22: (a) Due to pixels, we obtain a bad case of the *jaggies* (more formally known as *aliasing*) instead of sharp, straight lines. (Figure from Wikipedia user Jmf145.) (b) In the *screen-door effect*, a black grid is visible around the pixels.

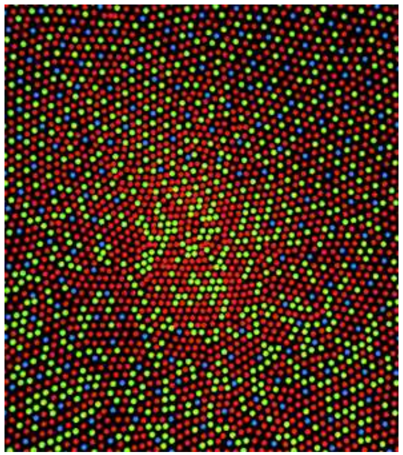
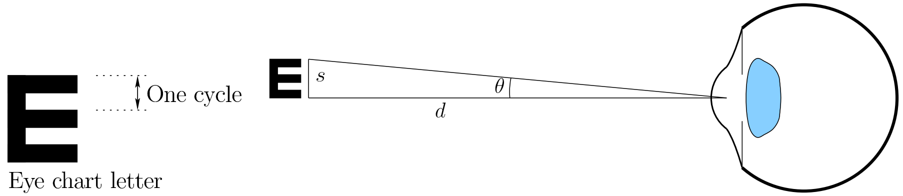


Figure 5.23: Red, green, and blue cone photoreceptors are distributed in a complicated mosaic in the center of the fovea. (Figure by Mark Fairchild.)



(a) (b)

Figure 5.24: (a) A single letter on an eye chart. (b) The size s of the letter (or other feature of interest), the distance d of the viewer, and the viewing angle θ are related as $s = d \tan\theta$.

Assume that the fovea is pointed directly at the display to provide the best sensing possible. The first issue is that red, green, and blue cones are arranged in a mosaic, as shown in Figure 5.23. The patterns are more erratic than the engineered versions in Figure 4.36. Vision scientists and neurobiologists have studied the effective or perceived input resolution through measures of *visual acuity* [15]. Subjects in a study are usually asked to indicate whether they can *detect* or *recognize* a particular target. In the case of detection, for example, scientists might like to know the smallest dot that can be perceived when printed onto a surface. In terms of displays, a similar question is: How small do pixels need to be so that a single white pixel against a black background is not detectable? In the case of recognition, a familiar example is attempting to read an eye chart, which displays arbitrary letters of various sizes. In terms of displays, this could correspond to trying to read text under various sizes, resolutions, and fonts. Many factors contribute to acuity tasks, such as brightness, contrast, eye movements, time exposure, and the part of the retina that is stimulated.

One of the most widely used concepts is *cycles per degree*, which roughly corresponds to the number of stripes (or sinusoidal peaks) that can be seen as separate along a viewing arc; see Figure 5.24. The *Snellen eye chart*, which is widely used by optometrists, is designed so that patients attempt to recognize printed letters from 20 feet away (or 6 meters). A person with "normal" 20/20 (or 6/6 in metric) vision is expected to barely make out the horizontal stripes in the letter "E" shown in Figure 5.24. This assumes he is looking directly at the letters, using the photoreceptors in the central fovea. The 20/20 line on the chart is designed so that letter height corresponds to 30 cycles per degree when the eye is 20 feet away. The total height of the "E" is 1/12 of a degree. Note that each stripe is half of a cycle. What happens if the subject stands only 10 feet away from the eye chart? The letters should roughly appear to twice as large.

Using simple trigonometry,

$$s = d \tan\theta, \tag{5.1}$$

we can determine what the size s of some feature should be for a viewing angle

θ at a distance d from the eye. For very small θ, $\tan\theta \approx \theta$ (in radians). For the example of the eye chart, s could correspond to the height of a letter. Doubling the distance d and the size s should keep θ roughly fixed, which corresponds to the size of the image on the retina.

We now return to the retina display concept. Suppose that a person with 20/20 vision is viewing a large screen that is 20 feet (6.096m) away. To generate 30 cycles per degree, it must have at least 60 pixels per degree. Using (5.1), the size would be $s = 20 * \tan 1° = 0.349$ft, which is equivalent to 4.189in. Thus, only $60/4.189 = 14.32$ PPI would be sufficient. Now suppose that a smartphone screen is placed 12 inches from the user's eye. In this case, $s = 12 * \tan 1° = 0.209$in. This requires that the screen have at least $60/0.209 = 286.4$ PPI, which was satisfied by the 326 PPI originally claimed by Apple.

In the case of VR, the user is not looking directly at the screen as in the case of smartphones. By inserting a lens for magnification, the display can be brought even closer to the eye. This is commonly done for VR headsets, as was shown in Figure 4.30. Suppose that the lens is positioned at its focal distance away from the screen, which for the sake of example is only 1.5in (this is comparable to current VR headsets). In this case, $s = 1 * \tan 1° = 0.0261$in, and the display must have at least 2291.6 PPI to achieve 60 cycles per degree! One of the highest-density smartphone displays available today is in the Sony Xperia Z5 Premium. It has only 801 PPI, which means that the PPI needs to increase by roughly a factor of three to obtain retina display resolution for VR headsets.

This is not the complete story because some people, particularly youths, have better than 20/20 vision. The limits of visual acuity have been established to be around 60 to 77 cycles per degree, based on photoreceptor density and neural processes [5, 6]; however, this is based on shining a laser directly onto the retina, which bypasses many optical aberration problems as the light passes through the eye. A small number of people (perhaps one percent) have acuity up to 60 cycles per degree. In this extreme case, the display density would need to be 4583 PPI. Thus, many factors are involved in determining a sufficient resolution for VR. It suffices to say that the resolutions that exist today in consumer VR headsets are inadequate, and retinal display resolution will not be achieved until the PPI is several times higher.

How much field of view is enough? What if the screen is brought even closer to the eye to fill more of the field of view? Based on the photoreceptor density plot in Figure 5.5 and the limits of eye rotations shown in Figure 5.21, the maximum field of view seems to be around 270°, which is larger than what could be provided by a flat screen (less than 180°). Increasing the field of view by bringing the screen closer would require even higher pixel density, but lens aberrations (Section 4.3) at the periphery may limit the effective field of view. Furthermore, if the lens is too thick and too close to the eye, then the eyelashes may scrape it; Fresnel lenses may provide a thin alternative, but introduce artifacts. Thus, the quest for a VR retina display may end with a balance between optical system quality and limitations of the human eye. Curved screens may help alleviate some of the problems.

Foveated rendering One of the frustrations with this analysis is that we have not been able to exploit that fact that photoreceptor density decreases away from the fovea. We had to keep the pixel density high everywhere because we have no control over which part of the display the user will be look at. If we could track where the eye is looking and have a tiny, movable display that is always positioned in front of the pupil, with zero delay, then much fewer pixels would be needed. This would greatly decrease computational burdens on graphical rendering systems (covered in Chapter 7). Instead of moving a tiny screen, the process can be simulated by keeping the fixed display but focusing the graphical rendering only in the spot where the eye is looking. This is called *foveated rendering*, which has been shown to work [13], but is currently too costly and there is too much delay and other discrepancies between the eye movements and the display updates. In the near future, it may become an effective approach for the mass market.

VOR gain adaptation The *VOR gain* is a ratio that compares the eye rotation rate (numerator) to counter the rotation and translation rate of the head (denominator). Because head motion has six DOFs, it is appropriate to break the gain into six components. In the case of head pitch and yaw, the VOR gain is close to 1.0. For example, if you yaw your head to the left at 10° per second, then your eyes yaw at 10° per second in the opposite direction. The VOR roll gain is very small because the eyes have a tiny roll range. The VOR translational gain depends on the distance to the features.

Recall from Section 2.3 that adaptation is a universal feature of our sensory systems. VOR gain is no exception. For those who wear eyeglasses, the VOR gain must adapt due to the optical transformations described in Section 4.2. Lenses affect the field of view and perceived size and distance of objects. The VOR comfortably adapts to this problem by changing the gain. Now suppose that you are wearing a VR headset that may suffer from flaws such as an imperfect optical system, tracking latency, and incorrectly rendered objects on the screen. In this case, adaptation may occur as the brain attempts to adapt its perception of stationarity to compensate for the flaws. In this case, your visual system could convince your brain that the headset is functioning correctly, and then your perception of stationarity in the real world would become distorted until you readapt. For example, after a flawed VR experience, you might yaw your head in the real world and have the sensation that truly stationary objects are sliding back and forth![2]

[2] This frequently happened to the author while developing and testing the Oculus Rift.

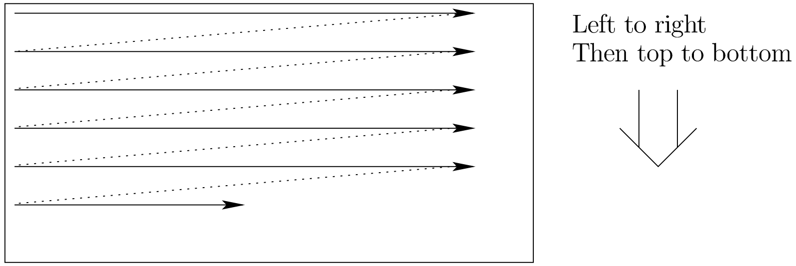


Figure 5.25: Most displays still work in the way as old TV sets and CRT monitors: By updating pixels line-by-line. For a display that has 60 FPS (frames per second), this could take up to 16.67ms.

Display scanout Recall from Section 4.5 that cameras have either a rolling or global shutter based on whether the sensing elements are scanned line-by-line or in parallel. Displays work the same way, but whereas cameras are an *input* device, displays are the *output* analog. Most displays today have a *rolling scanout* (called *raster scan*), rather than *global scanout*. This implies that the pixels are updated line by line, as shown in Figure 5.25. This procedure is an artifact of old TV sets and monitors, which each had a cathode ray tube (CRT) with phosphor elements on the screen. An electron beam was bent by electromagnets so that it would repeatedly strike and refresh the glowing phosphors.

Due to the slow charge and response time of photoreceptors, we do not perceive the scanout pattern during normal use. However, when our eyes, features in the scene, or both are moving, then side effects of the rolling scanout may become perceptible. Think about the operation of a line-by-line printer, as in the case of a receipt printer on a cash register. If we pull on the tape while it is printing, then the lines would become stretched apart. If it is unable to print a single line at once, then the lines themselves would become slanted. If we could pull the tape to the side while it is printing, then the entire page would become slanted. You can also achieve this effect by repeatedly drawing a horizontal line with a pencil while using the other hand to gently pull the paper in a particular direction. The paper in this analogy is the retina and the pencil corresponds to light rays attempting to charge photoreceptors. Figure 5.26 shows how a rectangle would distort under cases of smooth pursuit and VOR. One possibility is to fix this by rendering a distorted image that will be corrected by the distortion due to the line-by-line scanout [23] (this was later suggested in [1]). Constructing these images requires precise calculations of the scanout timings. Yet another problem with displays is that the pixels could take so long to switch (up to 20ms) that sharp edges appear to be blurred. We will continue discussing these problems in Section 6.2 in the context of motion perception, and Section 7.4 in the context of rendering.

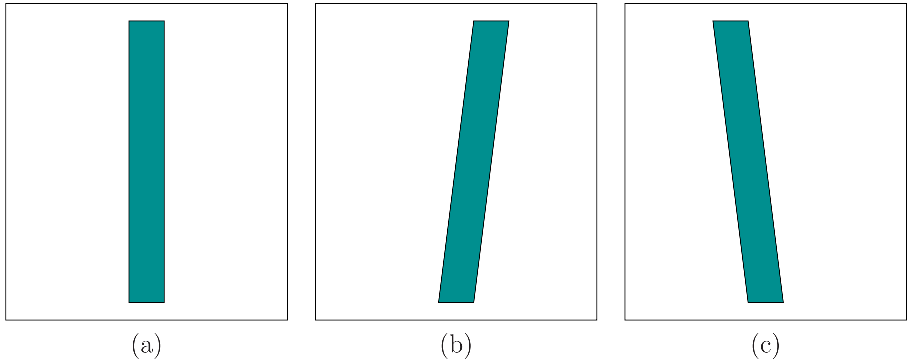


Figure 5.26: Artifacts due to display scanout: (a) A vertical rectangle in the scene. (b) How it may distort during smooth pursuit while the rectangle moves to the right in the virtual world. (c) How a stationary rectangle may distort when rotating the head to the right while using the VOR to compensate. The cases of (b) are (c) are swapped if the direction of motion is reversed in each case.

Retinal image slip Recall that eye movements contribute both to maintaining a target in a fixed location on the retina (smooth pursuit, VOR) and also to changing its location slightly to reduce perceptual fading (microsaccades). During ordinary activities (not VR), the eyes move and the image of a feature may move slightly on the retina due to motions and optical distortions. This is called *retinal image slip*. Once a VR headset is used, the motions of image features on the retina might not match what would happen in the real world. This is due to many factors already mentioned, such as optical distortions, tracking latency, and display scanout. Thus, the retinal image slip due to VR artifacts does not match the retinal image slip encountered in the real world. The consequences of this have barely been identified, much less characterized scientifically. They are likely to contribute to fatigue, and possibly VR sickness. As an example of the problem, there is evidence that microsaccades are triggered by the lack of retinal image slip [9]. This implies that differences in retinal image slip due to VR usage could interfere with microsaccade motions, which are already not fully understood.

Vergence-accommodation mismatch Recall from Section 4.4 that accommodation is the process of changing the eye lens' optical power so that close objects can be brought into focus. This normally occurs with both eyes fixated on the same object, resulting in a stereoscopic view that is brought into focus. In the real world, the vergence motion of the eyes and the accommodation of the lens are tightly coupled. For example, if you place your finger 10cm in front of your face, then your eyes will try to increase the lens power while the eyes are strongly converging. If a lens is placed at a distance of its focal length from a screen, then with normal eyes it will always be in focus while the eye is relaxed (recall Figure 4.30). What if an object is rendered to the screen so that it appears to be only 10cm away? In this case, the eyes strongly converge, but they do not need to change the optical power of the eye lens. The eyes may nevertheless try to accommodate, which would have the effect of blurring the perceived image. The result is called *vergence-accommodation mismatch* because the stimulus provided by VR is inconsistent with the real world. Even if the eyes become accustomed to the mismatch, the user may feel extra strain or fatigue after prolonged use [26, 30]. The eyes are essentially being trained to allow a new degree of freedom: Separating vergence from accommodation, rather than coupling them. New display technologies may provide some relief from this problem, but they are currently too costly and imprecise. For example, the mismatch can be greatly reduced by using eye tracking to estimate the amount of vergence and then altering the power of the optical system [2, 21].

Further Reading

Most of the concepts from Sections 5.1 to 5.1 appear in standard textbooks on sensation and perception [12, 22, 33]. Chapter 7 of [22] contains substantially more neuroscience than covered in this chapter. More details on photoreceptor structure appear in [6, 24, 32]. The interface between eyes and engineered optical systems is covered in [31], of which digital optical systems are also related [16].

Sweeping coverage of eye movements is provided in [20]. For eye movements from a neuroscience perspective, see [19]. VOR gain adaptation is studied in [8, 11, 29]. Theories of microsaccade function are discussed in [28]. Coordination between smooth pursuit and saccades is explained in [10]. Coordination of head and eye movements is studied in [18, 27]. See [3, 26, 30] regarding comfort issues with vergence-accommodation mismatch.

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