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INTRODUCTION TO THE DUPLEX RETINA

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THIS CHAPTER WILL INCLUDE A REVIEW OF:

- Duplex nature of the retina
- Comparison of rods and cones
- Rhodopsin
- Spectral sensitivity of the scotopic system

DUPLEX NATURE OF THE RETINA

At the end of Chapter 6, we discussed retinal illuminance, which is the amount of light falling on the retina in a retinal image. The unit for **retinal illuminance** is the **troland**, and the computation of retinal illuminance is simple (Schwartz, 2004 Ch. 3):

Retinal illuminance (in trolands) = object luminance (in nits) x pupil area (in mm^2)

In the example in the previous lecture, we found that when viewing a piece of paper in bright sunlight (10 000 nits, 2-mm diameter pupil), the retinal illuminance is equal to 31 400 trolands. When viewing a piece of paper in starlight (0.0001 nits, 8-mm diameter pupil), the retinal illuminance is 0.005 trolands.

How much greater is the retinal illuminance in this example of a bright condition, compared with the dim?

Ratio = 31 400/0.005 = 6 280 000

We have no difficulty seeing a piece of paper under either bright sunlight or starlight, in spite of the fact that retinal illuminance for a piece of paper in bright sunlight is approximately 6.3 million times brighter (31 400/.005 times; 6.8 log units) than the paper seen in star light.

The human visual system is capable of operating across an amazingly large range of illumination levels – more than 10 log units (100 dB) of illumination change! That is a 10 000 000 000 (ten billion)-fold change in light level! Man-made cameras using either film, digital or video electronics have difficulty matching the **dynamic range** of the human eye. Quoting from an online article about a wide dynamic range image sensor:

DUPLEX NATURE OF THE RETINA (CONT.)

Dynamic range is the ratio of the brightest image that can be captured by the imaging system to the darkest image that can be captured. Light intensity greater than the brightest possible image will cause the sensor to saturate, while light intensity less than the darkest possible image will not register on the sensor. Both of these conditions distort the image, hiding potentially vital information that lies outside the dynamic range of the sensor. (http://www.videsignline.com/showArticle.jhtml?articleID=181502565)

Another online article dated on February 5, 2008 described how an engineer at Panasonic was trying to improve the dynamic range of digital cameras by combining multiple photos, each of which was taken at a different exposure level. By doing this, they were able to achieve a dynamic range of 140 decibels compared with ordinary sensors with a 60dB range. Despite efforts such as Fujifilm's Super CCD sensors, camera buffs are often frustrated by the image sensors dynamic range that are significantly weaker than what the human eye can detect. Although the Panasonic research shows some promise, the research showed only black-and-white images so far and was suited "for automotive and security cameras," according to the researchers' paper. (http://news.cnet.com/8301-13580_3-9864843-39.html)

Computer displays also have the same problem. How can they display a wide range of brightness levels with a dynamic range that is far less than that of the human eye?

Also, quoting from Wikipedia's article on dynamic range:

In practice, it is difficult to achieve the full dynamic range seen by human beings using electronic equipment, since most electronic reproduction equipment is essentially linear rather than logarithmic like human perception. Electronically reproduced audio and video often uses some trickery to fit original material with a wide dynamic range into a narrower recorded dynamic range that can more easily be reproduced: this is dynamic compression. For example, a good quality LCD display has a dynamic range of around 1,000 or 30 dB

(http://en.wikipedia.org/wiki/Dynamic_range#Photography)

Film cameras have only about a 3-log unit dynamic range (30 dB) and electronic sensors such as a digital or video camera have about a 6-log range (60 dB). How can you maximize the dynamic range of a camera? This can be accomplished by the following methods:

1. Changing the camera aperture.
2. Changing shutter speed (exposure time).
3. Change the camera's sensitivity. For example in film cameras, ISO 400 film is more sensitive and useful for taking photographs in low illumination. ISO 100 film, on the other hand, is useful for taking photographs in bright conditions.

How does the visual system adapt to such an extreme (10 billion fold) range of light levels? How much can a change in pupil size achieve? Can this explain the eye's ability to operate across such a range of illumination? By changing pupil size, can the eye adjust retinal illuminance by this great a range? We can investigate this by computing retinal illuminance for the extremes of pupil size, given an object with fixed luminance.

Example

Consider a white page with a luminance of 100 nits. Compute the retinal illuminance for a 9-mm diameter pupil.

trolands = (luminance in nits) × (pupil area in mm)

pupil area = $\pi r^2 = (3.14)(4.5)_2 = 63.62$ mm^2

trolands = (100)(63.62) = 6,362 trolands

Repeat the computation for the same object, but with a pupil diameter of 2 mm.

trolands = (luminance in nits) × (pupil area in mm)

pupil area is, $\pi r^2 = (3.14)\ (1)2 = 3.14$ mm^2

trolands = (100)(3.14) = 314 trolands

DUPLEX NATURE OF THE RETINA (CONT.)

The ratio of these retinal illuminances caused by the extremes in pupil sizes is 6 362:314 = ~20:1. The pupil then can adjust retinal illuminance by a factor of only about 20, which is equal to about 1.3 log units (13 dB). How then, can the eye adjust to a 10-log unit (100 dB) range of retinal illuminance?

The rest of the adjustment to different light levels is accomplished in the retina itself. It is as if the retina has different kinds of film for different light levels, except that the retina's system for adapting to different light levels is far more complex than camera film.

Visual adaptation is so effective because we have two classes of photoreceptors that are designed to operate over different light levels. Each kind of photoreceptor is able to adapt or adjust to a wide range of light levels and together they give the human visual system a huge dynamic range:

- The **photopic system** is designed to operate in bright lighting conditions and it receives input from the cone photoreceptors.
- The **scotopic system** is designed to operate under low light conditions and it receives input from the rod photoreceptors.

Because we have two systems designed to operate across different ranges of retinal illuminances, scientists say that we have a **duplex retina**. The range of illumination over which the photopic and scotopic systems work overlaps slightly, so for intermediate light levels, both photopic and scotopic systems may be operating at the same time. Vision in this in-between light level is called **mesopic** vision (see Schwartz, 2004 Table 3-1).

COMPARISON OF RODS AND CONES

The retinal photoreceptor, the rods and cones, have similarities, as well as distinct features in terms of cellular structure and physiological function.

SIMILARITIES IN CELLULAR STRUCTURE BETWEEN RODS AND CONES

(See Schwartz, 2004 Ch. 3, Figs. 3-1, 3-2)

- Long tubular cells
- **Outer segment** (near RPE) contains stacks of disk-like components
- **Inner segment** (toward vitreous) contains cellular organelles such as the nucleus and mitochondria
- A ciliary process connects inner and outer segments
- Synapse with bipolar and other cells in the **outer plexiform layer**

OUTER SEGMENTS

We will focus our attention on the photoreceptor outer segment, because the disks within the outer segments contain the **photopigments** that start the physiological process of vision by capturing light. The outer segment of the cones is more tapered (cone-shaped), while the rod outer segments are more tubular (Schwartz Fig. 3-1). However this is not true of all cones; in the fovea, where cones are most densely packed, they are much more rod-like in their shape.

COMPARISON OF RODS AND CONES

Outer segments disks:

- Contain the photopigments that capture light and begin **phototransduction**. Phototransduction is the process by which light energy is converted to an electrical signal that is transmitted via neurons to the brain. We will learn more about this process later
- Formed by in-folding of outer segment cellular membrane near the ciliary process
- They are being continually produced and migrate outward towards the RPE forming a stack of disks
- In the rod outer segment, the disks separate from the cellular membrane and become free-floating structures. One rod has about 1 000 disks
- In cones, the disks remain connected with the cellular membrane
- At the outer end of the cell, spent disks are shed and phagocytized by the RPE
- Phagocytosis is critical to continuing normal health and metabolism of the photoreceptor. Without phagocytosis, metabolic wastes such as free radicals accumulate and damage the photoreceptors. This is a possible disease mechanism for retinal damage in *retinitis pigmentosa (RP).* We will discuss RP again when we learn about electrodiagnostic testing
- Rod disks are shed during the day at a rate of about 10% per day
- Cones disks are usually shed at night
- Rod synaptic endings are more sphere-like (spherule), cones synapses flatter (pedicle)

RETINAL DISTRIBUTION OF RODS AND CONES

Schwartz Fig. 3-7 shows the relative distribution of rods and cones in a cross section of the retina. This is similar to Figure 4-2 in Chapter 4. As we discussed before, the rods reach their maximum concentration at about 20° peripheral to the fovea. At that point there are about 150 000 rods per mm^2. At two locations in the retina there are no rods – the optic disk and the fovea.

The cones have maximum density in the fovea (150 000 cones per mm2), but note that **cones are still present in the periphery**, though their concentration is smaller. That is why we have color vision in the periphery. If you consider the total number of cones in the entire retina*, only 4% of all cones are in the fovea and 96% are in the periphery*.

RHODOPSIN

When light falls on the retina, the physiological process of vision begins when a photopigment molecule in the outer segment captures a photon. This sets off the biochemical chain reaction known as phototransduction. The photopigment that captures photons in the rods is called rhodopsin.

In its unexposed state, that is, prior to absorbing light, rhodopsin is purple, and has been referred to as visual purple. When exposed to light, rhodopsin absorbs light, then undergoes a chemical change and bleaches to a transparent yellow color. One rhodopsin molecule is capable of capturing only one photon and once bleached, it is no longer available to capture another photon. Since the bleached rhodopsin is transparent, light can pass through it and be captured by the next available rhodopsin molecule.
With time, rhodopsin regenerates back to its unbleached (purple) state and is then again ready to absorb light. The half-life for rhodopsin recovery is about 5 minutes, therefore about half of the bleached rhodopsin will return to its unbleached state in five minutes.

One eye contains about 120 million rods. Each rod contains about 1000 disks, and each disk contains about 10 000 rhodopsin molecules. Each eye therefore contains a tremendous number (10^{15}) of rhodopsin molecules and they are continually regenerating. The eye has been designed with a tremendous capacity to absorb light.

RHODOPSIN (CONT.)

The efficiency with which rhodopsin absorbs light varies with wavelength. Rhodopsin is most effective at absorbing light with a wavelength of 507 nm, and its absorption efficiency decreases at shorter and longer wavelengths. The relative absorption spectrum of rhodopsin can be determined by the following experiment illustrated in Schwartz Fig. 3-3.

- Shine a fixed, known quantity of monochromatic (one wavelength) light onto a jar of rhodopsin.
- Measure with a radiometer the amount of light transmitted
- Light that has not been transmitted is absorbed. High transmission corresponds with low absorption and vice versa. Schwartz Fig. 3-3 A shows the rhodopsin transmission curve. The transmission curve for rhodopsin looks similar to the left hand graph in Figure 7-2
- The reciprocal of the transmission curve is the absorption curve, which for rhodopsin is similar to the right hand graph in Figure 7-2. (Schwartz Fig. 3-3 B)
- The peak absorption for rhodopsin is at ~507 nm

No matter what the wavelength, once a photon has been absorbed by rhodopsin, there is only one response – the rhodopsin bleaches and the process of phototransduction begins. After the molecule bleaches, regardless of the wavelength, the subsequent physiological process is the same. Therefore, the process of phototransduction, once started, preserves no information about the wavelength of light that started the process.

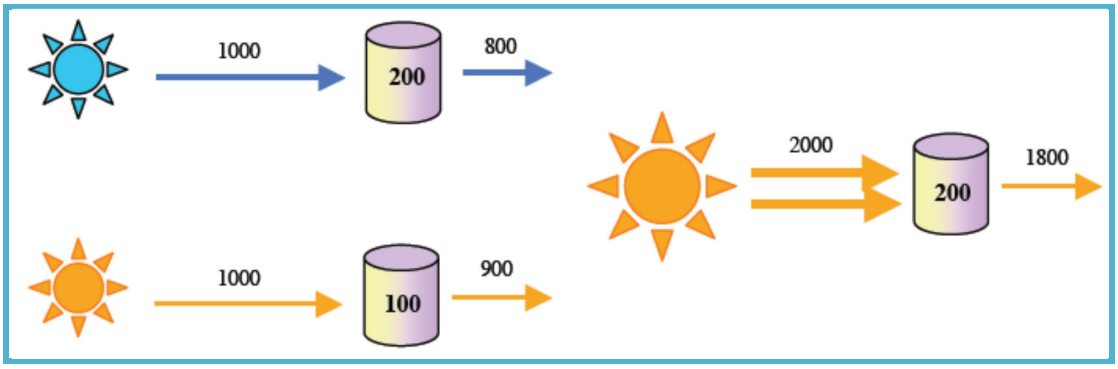

Figure 7-1: *Principle of univariance. Rhodopsin can absorb photons more efficiently at some wavelengths (Upper left; blue, representing 507 nm) than others (Lower left; orange, representing 580 nm), but the response of a rod to an efficient wavelength (507 nm) can be matched by increasing the radiance of a less efficient wavelength (right; orange with more radiance)*

Example

If you irradiate the retina with 1000 quanta of light at 507nm, you might successfully bleach 200 rhodopsin molecules (absorb 200, transmit 800). If you irradiate the same part of the retina with 1000 quanta of light at 580 nm, you might bleach 100 rhodopsin molecules, since the longer wavelength is absorbed less effectively. If you double the irradiance of 580 nm light to 2000 quanta, you would bleach approximately double the number (200) of rhodopsin molecules. This is equal to the result of bleaching the retina with 1000 quanta of 507nm light. Therefore, once absorbed, the physiological response of the visual system to 1000 quanta of 507nm light and 2000 quanta of 580nm light is the same. This is referred to as the **principle of univariance** (Fig. 7-1).

Since the scotopic (rod) system produces one physiological response irrespective of the wavelength, and it is possible to match the output signal for all wavelengths by adjusting the brightness of the light, the scotopic system transmits no wavelength information and is colorblind.

SPECTRAL SENSITIVITY OF THE SCOTOPIC SYSTEM

The spectral absorption of rods (that is, rhodopsin) is closely related to the spectral sensitivity of the scotopic system. Our ability to see very dim lights using the scotopic system varies as a function of wavelength. If you perform an experiment to determine the dimmest light of one wavelength that a person can detect, you will be measuring his/her *detection threshold* for that wavelength. Figure 7-2 - left (similar to Schwartz Fig. 3-4 A) illustrates how the **threshold** varies as a function of wavelength. The inverse of *threshold* is *sensitivity*, and the spectral **sensitivity** of the scotopic system is shown in Figure 7-2 - right (similar to Schwartz Fig. 3-4 B).

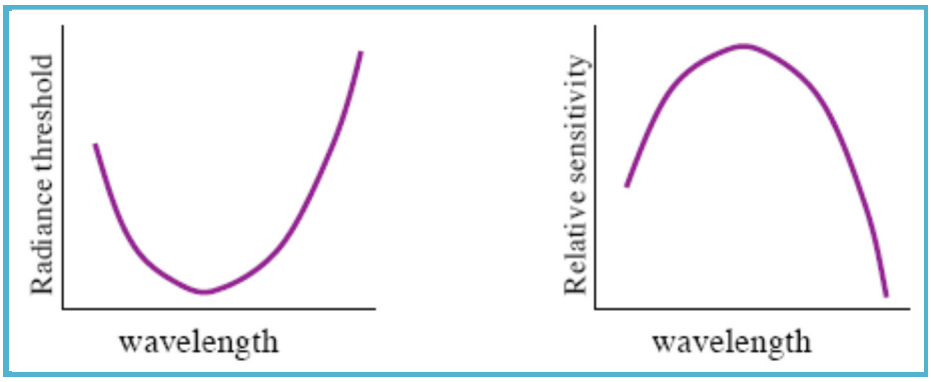

Figure 7-2: *Derivation of the scotopic spectral sensitivity function*

Many psychophysical vision experiments measure a visual threshold, but convert the data to sensitivity for display. It is important to remember that **threshold and sensitivity have a reciprocal relationship**. We discussed the same concept when we studied visual field testing. In a visual field test, you measure the patient's threshold for detecting a small spot of light, but what you really want to know the sensitivity of the visual system across the field.

Another clinical example is a test called **contrast sensitivity**, which we will study in detail later in the course. Contrast sensitivity provides more detailed information about visual performance than **visual acuity**. You determine a person's contrast sensitivity by measuring the minimum contrast that he/she can see; that is, the *contrast threshold*. The (Michelson) contrast threshold will be some small number such as 0.01, and the inverse of this value is the contrast sensitivity.

The spectral threshold and spectral transmission functions are similar; also the spectral sensitivity and spectral absorption spectra are similar. This is because rhodopsin absorption is a major (but not the only) factor that determines sensitivity of the scotopic system.

SELECTED READING/REFERENCES

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