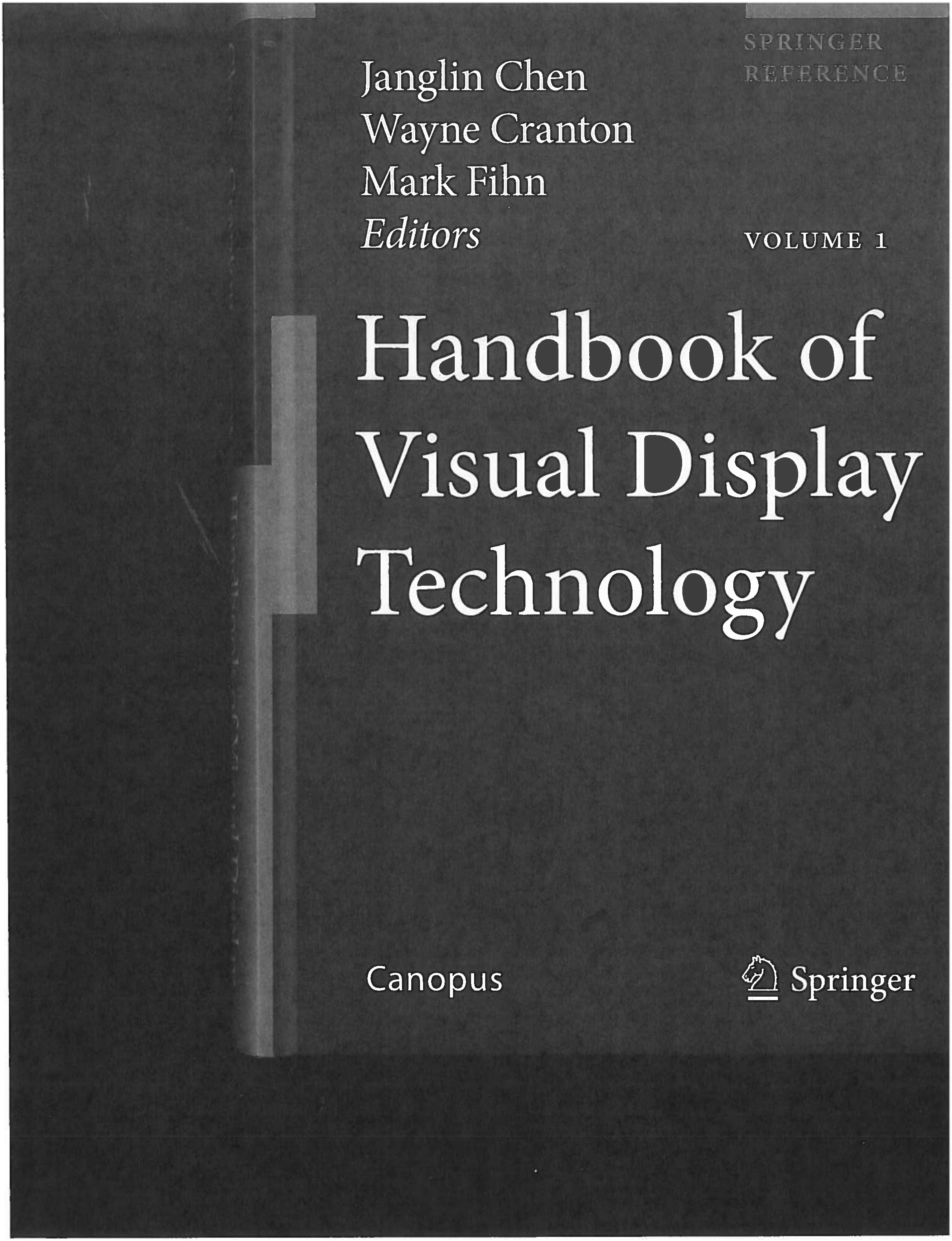

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# 2.1.2 Light Detection and Sensitivity

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**Abstract:** This chapter deals with the absolute threshold of vision, namely, the minimum amount of light necessary to elicit a visual response. The effect of intrinsic retinal noise which affects light detection is considered; this is followed by a discussion on intensity discrimination by both rods and cones.

**List of Abbreviations:** *tvi*, Threshold Versus Intensity

## 1 Introduction

Of all our sensory systems, the visual sense dominates – about 60% of all nerve fibers from a sensory organ to the brain come from the eyes. The visual cortex contains about 500 million nerve cells (the corresponding number for the auditory cortex is about 800,000 nerve cells; from the ear 30,000 nerve fibers convey acoustic information to the brain, while from the eye 1–3 million nerve fibers convey visual information to the brain). The eye operates over an amazing range of light levels, covering an intensity range of approximately 12 log units and possesses exquisite sensitivity. A good review is given by Rodieck [1].

## 2 Nature of Vision at (or Near) Absolute Threshold

Absolute threshold implies that the rod photoreceptors signal the absorption of single photons. The question of the sensitivity of the eye is not simply one of physics but also of the criterion used by the observer, thus bringing in the behavioral response of the observer. Hence, the question of the absolute threshold of human vision can only be answered in terms of a response probability. Lorentz in 1901 hypothesized that a just detectable flash of light delivered approximately 100 photons to the cornea (quoted in [2]). Identifying the minimum number of photons required for seeing from this number is difficult because of uncertainties in determining the number of photons absorbed by the retinal photoreceptors. This quantum efficiency has been estimated to be in the range of about 0.1–0.3. The best values of thresholds are obtained after prolonged dark adaptation of about 30–45 min. It is found that completely dark adapted rod photoreceptors approach the sensitivity limit imposed by the quantization of light and the Poisson fluctuations of photon absorption. In fact, isolated single photoreceptors signal the absorption of a single photon [2]. The number of photons required to give a psychophysical response (behavioral) was established by Van der Velden [3] and by Hecht, Schlaer, and Pirenne [4].

## 3 Behavioral Results

In their classic experiment, Hecht et al. measured the fraction of trials in which a flash was seen as a function of the number of photons incident on the cornea. This curve, a psychometric function, showed a broad transition from flashes that were rarely seen to those frequently seen, and from this curve the threshold and quantum efficiency can be derived based on the assumption that the variability in a subject's response was due to Poisson statistics of the photon absorption. Implicit in this analysis are two other basic ideas: only those instances wherein the number of photons which exceed a threshold number were seen and that the average number of photons contributing to "seeing" was directly proportional to the number of photons incident on the cornea and the constant of proportionality being the quantum efficiency. From these beautifully conducted and analyzed experiments, they concluded a quantum efficiency of about 0.06, which is much lower than that derived from light scattering and ocular media properties. The authors conclude that in order for a visual effect to be produced, one quantum must be absorbed by each of 5–8 or so rods in the retina (at a 65% probability of correct response). To give the reader a sense of how sensitive human observers can be, Pirenne [5] used a white light test stimulus spread out over many degrees on the retina, and the threshold was determined to be $0.75 \times 10^{-6}$ Cd/m$^2$. This is of the order of 5–30% of the luminance of the darkest night sky measured by the National Physical Laboratory.

There is a big discrepancy between the in vitro result that individual photoreceptors can detect and signal a single photon while psychophysically 5–8 photons absorptions are required. The reason for this discrepancy is the presence of biological noise in the visual system. However, it should be emphasized that the human eye sensitivity approaches the limit set by quantization of light, Poisson fluctuations in absorption, and the internal noise.

## 4 The Effect of Noise on Detection of Light

Visual sensitivity is hampered by background noise occurring along the visual retina–cortex pathway. There have been many studies to describe and show physiologically and mathematically the events occurring in the retina in response to stimuli and when no stimuli are present (see for example [6, 7]). The physiology and biochemistry is discussed in detail by Rodieck [1] and Wickehart [8].

What is retinal background noise? Spectral absorptions that occur in the photoreceptors cause a neural cascade which is encoded as sight in the occipital cortex, however, there are ever-present visual stimulations occurring randomly without photon absorption by the photoreceptors.

Barlow and others [9, 10] advocated the concept of "dark light" – a name given to internal events such as spontaneous decomposition of photopigment. It was shown by these and other researchers that additive Poisson noise can account for the discrepancy. In fact, it has been estimated based on spatial and temporal summation characteristics of the rod array, rod density, assumed quantum efficiency, etc., that the equivalent rate of photon-like noise events in rod photoreceptors, the dark light ranges from 0.002 to 0.03 per second [11].

Spontaneous background noise in the retina is usually described as having two components. Baylor et al. described discrete thermal activations in photoreceptors, which accounts partly for background noise [12, 13]. The rest of the noise is thought to be due to fluctuations of the concentrations of certain chemicals in the process of phototransduction.

Background retinal noise is generated among both the rod and the cone photoreceptors. Cones have been shown to be noisier than rods, possibly hampering our vision when we fixate on important stimuli in our environment, but presumably have less of an effect on our sensitivity at absolute visual threshold levels. This would make sense because we know rods function as low light detectors, and would therefore necessitate quieter biological conditions. In addition, it is also found that the power spectrum of dark noise had the same shape as the spectrum of a dim flash of light, evidence that retinal noise consists of random events with an average shape of the single photon response. There are a number of unanswered questions such as the effect of continuous noise, false-positives due to the noise in setting threshold, etc., and these are beyond the scope of this chapter.

In summary, physiological noise is indistinguishable from signals generated by light stimuli, and it is hypothesized to be the main neural limit to our visual acuity. A more detailed description of the problem of noise in photoreceptor can be found in the articles by Lakshminarayanan [14], Reike and Baylor [15], and Field et al. [16].

## 5 Intensity Discrimination

Up to this point, we have been discussing the detection of light at (or near) absolute threshold values. Here, we discuss the important issue of intensity discrimination – that is, how does the visual system determine if one luminous stimulus differs in intensity from another. It should be obvious from the above discussion that the quantum fluctuations provide a theoretical lower limit for intensity discrimination by an ideal observer. How about at values of stimuli well above threshold? In an increment threshold measurement, a test stimulus of luminance Lt is compared to an adjacent stimulus of luminance L, which is a reference stimulus. The psychophysical task is to determine how different Lt must be from L (above or below) for it to be seen as different (at some preassigned probability value, say 50% of the time). Let this difference be given by $\Delta L$. If we determine $\Delta L$ for a number of different values of the reference $L$, we get a curve called a threshold versus intensity function (tvi function). A typical tvi curve is shown in ➋ *Fig. 1*; typically there are two branches showing the duplex nature of the retina.

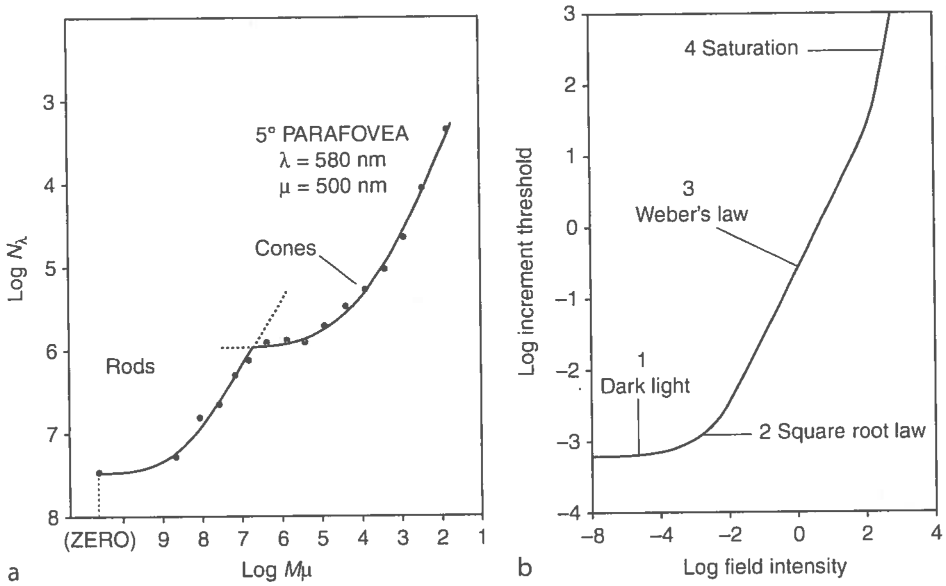

**Fig. 1**

**(a) Light adaptation curve plotted as increment threshold versus background luminance (or a threshold versus intensity: tvi curve). The above plot shows increment threshold ($N_\lambda$) and background luminance ($M_\mu$). Light of two different wavelengths are used in this case (580 nm for the test and 500 nm for the background) (Adapted from Stiles' data from [17]). (b) Schematic of the increment threshold curve (Adapted from Aguilar and Stiles' data from [17])**

If we start from near absolute threshold, the threshold in the flat horizontal portion of the curve is determined by the dark light level or the internal noise (portion 1); Increases in luminance does not change $\Delta L$ very much; this implies that an imposer would not be able to always detect an intensity difference between two flashed stimuli that on average differ in intensity only be a few quanta. As the background luminance is further increased, we pass on to region 2 of the curve, the "square root" law region. Quantum fluctuations increase with number of quanta in the stimulus, and as stimulus luminance increases, the minimum discriminable threshold increases in proportion to the square root of the intensity level. This is known as the deVries Rose law or the square root law and is expressed as:

$$\frac{\Delta L}{\sqrt{L}} = K$$

In this portion, the slope of the curve is ½. For the rod pathway, a slope of 0.6 is often found. At low reference luminance levels, humans behave as ideal detectors and follow the deVries Rose law.

As we further increase background levels, Weber's law holds and the intensity discrimination threshold is higher than expected from an ideal detector. In this region, also called Weber's law region, we get a straight line portion of the curve, where the slope is a constant. The constant proportional relationship between increment threshold ($\Delta L$) and reference luminance ($L$) is called Weber's law, $\Delta L / L$ = constant.

This proportional change in threshold $\Delta L$ with $L$ implies that the visual system is not detecting luminance differences at the theoretical limit. It should be noted that the Weber constant is affected by stimulus size, duration, wavelength, and retinal location [18–21]. Weber's law implies that there is a limitation on intensity discrimination due to loss of information.

At higher luminance levels, the Weber fraction becomes large – that is $\Delta L$ increases faster than $L$ and the visual system saturates.

## 6 Visual Adaptation

As noted before, the visual system operates over a huge range of retinal illuminances. One of the reasons that the visual system can move its "operating curve" over such a wide range of illuminances is the fact that we have different photoreceptor subsystems – the rods and cones (see ➋ Chap. 2.1.1). This adjustment of the operating level to the existent light level is known as adaptation. In this section, we will discuss the dark and light adaptation characteristics of the visual system.

Light adaptation refers to the process that increases/decreases threshold luminance/sensitivity (recall that threshold is the inverse of sensitivity) in response to an increased level of illumination. Dark adaptation is the reverse of this change in sensitivity. Dark adaptation can be easily measured in the laboratory (and routinely tested in the clinic) using standard psychophysical methodology. The eyes are exposed to a suprathreshold adapting light (monochromatic or multichromatic) of large spatial dimension. Then, the adaptation light is turned off (time 0) and a test flash of a certain wavelength(s) and size is presented at a specific retinal location, and the $\Delta L$ is measured at specific times. The classic dark adaptation curve is shown in ➋ *Fig. 2.*

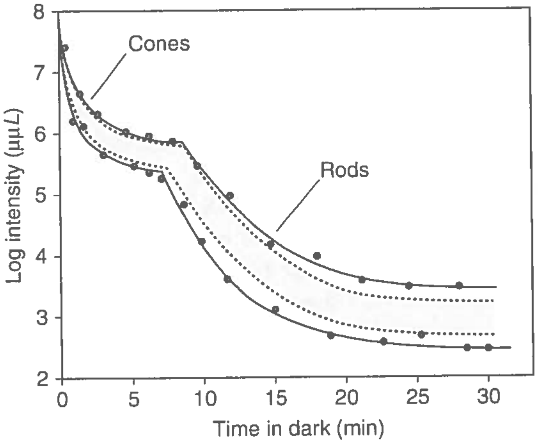

**Fig. 2**
**Dark adaptation curve. The shaded area represents 80% of the group of subjects (Adapted from Hecht and Mandelbaum's data from [22])**

The dark adaptation curve has certain specific features. There are two main branches – the cone branch and the rod branch. Initially, there is a rather large decrease in threshold luminance (about 3 min mark or so), followed by a rather slow change until about 8–12 min or so. Here, the cones approach their lowest threshold level and are fully dark adapted. The curve is pretty much flat during this portion. After about this time period, the cones saturate, and the rod system takes over, and the curve drops again as the rods become more sensitive. This point of transition is called the cone–rod break. Within about 30 min or so, the rod portion becomes flat and rods have adapted. Rods begin to dark adapt at the same time as the cones, but initially they are less sensitive than cones and have a larger time constant. The reader is referred to the chapter by Birch [23] for a detailed description of the physiology and mechanism of dark adaptation.

## 7 Summary

In this chapter, we have discussed the fact that luminance detection under certain conditions is limited only by internal noise in the visual system. We have also examined intensity discrimination by the eye and the basic laws of psychophysics, namely, the DeVries Rose square root law and Weber's law. Finally, we have examined the response of the photoreceptors to dark adaptation.

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