Evidence for a noise gain control mechanism in human vision

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Received 13 November 1996

Abstract

For small, brief targets incremental threshold is known to obey the de Vries–Rose law: threshold rises in direct proportion to the square-root of background intensity. We present data demonstrating a square-root law for brightness matching as well. The square-root law for brightness is obtained over the full range of scotopic vision, and the low intensity end of photopic vision. The classic theory of de Vries and Rose explains the square-root law on the basis of increased variability of the photon count as the background increases. Our brightness matching data instead indicates that the mean signal level is reduced by a factor which is inversely proportional to the standard deviation of the photon count. This result is consistent with the idea that in the retina there exists a gain control mechanism that is sensitive to the variance in the photon input, rather than to the mean illuminance. The importance of this idea to the modelling of retinal gain controls is discussed. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Light adaptation; Gain control; Quantal noise; Ganglion cell

1. Introduction

Recently, there has been increased interest in the subject of noise in the visual system, as evidenced by sessions devoted to the topic at major conferences. Researchers are examining the retina to discover which neurons demonstrate noise-limited performance and are proposing inherently stochastic models to explain them [1,2]. It has even been suggested that there are signal processing benefits of noise in visual circuits which overwhelm the obvious disadvantages [3]. Despite this recent interest in the role of noise in vision, it appears that many discussions of the role of noise in visual behavior still focus on data from a classic psychophysical threshold experiment and a half-century old interpretation of it. The experiment consists of a simple signal detection task in which the observer discriminates ‘target’ trials in which a test flash is presented on a uniform background from ‘blank’ trials, in which only the background is presented. The incremental threshold is defined as the luminance of the target required in order for the observer to achieve a criterion signal-to-noise ratio for discriminating targets from blanks.

In the 1940s, Rose and de Vries independently modelled the observer in the increment threshold experiment as a statistician who counts photons in order to make the target/blank discrimination [4–6]. Since the physics of light dictate that for an incandescent light source the number of photons absorbed within a small retinal area and small time interval is a Poisson random variable, the variance in the observed photon count will equal the mean. If \( N \) photons are absorbed on average, the root-mean-square fluctuations will be \( \sqrt{N} \). Letting \( I_B \) be the average illuminance of the uniform background field, \( \Delta I \) the average illuminance of the test flash, \( A \) the test area, and \( \tau \) the observer’s integration time, we may write—following Rose and de Vries—the \( d' \) statistic (or signal-to-noise ratio) of the ideal photon-counting observer as,

\[
d' = \frac{\Delta I A \tau - 0}{\sqrt{I_B A \tau + (I_B + \Delta I) A \tau}} \approx \frac{\Delta I (A \tau)^{1/2}}{\sqrt{2I_B}}.
\]
In the second step of this equation we have assumed that the variance contributed by the test flash is negligible, since at threshold $\Delta I \ll I_B$. With $I$ and $\tau$ fixed, the threshold flash luminance is related to the background luminance by the formula

$$\Delta I / \sqrt{I_B} = a \text{ constant.}$$

This equation is referred to in the literature as the square-root law, the de Vries–Rose Law, or the quantum fluctuation limit. On the basis of the Rose and de Vries argument, the experimental confirmation of this threshold law (usually in experiments with small, brief flashes) is often interpreted as evidence in favor of the hypothesis that detection under these conditions is limited by photon fluctuations.

Although the photon counting model can account for the square-root threshold behavior, the observer in an increment threshold experiment clearly does not literally count photons in order to make the discrimination. Presumably, the decision to respond ‘target’ or ‘blank’ is made somewhere in the cortex, and a more satisfactory model of the decision process would take into account the various stages of neural transduction and sensory coding that occur along the path from photon absorption to response selection.

An alternative explanation of how photon fluctuations produce the square-root law—one which takes physiological data explicitly into account—was recently proposed by Donner et al. [7] who recorded from red rods, horizontal cells, and ganglion cells in the retina of the toad *Bufo marinus*. Donner et al. demonstrated that there is a range of approximately one log unit of low background intensities over which the thresholds of the rods and horizontal cells are independent of the background level, but where ganglion cell sensitivity decreases substantially with increasing background level. In this range the ganglion cell threshold rises in direct proportion to the square-root of background intensity. Above this range, the thresholds of the rods, horizontal cells, and ganglion cells all follow Weber’s law.

To account for the cellular threshold data over the entire range of background levels investigated in their study, Donner et al. proposed a black box model of retinal light adaptation that included two sequential gain control stages: a Weber gain control stage located in the photoreceptors, and a ‘noise gain control’ stage located more proximally in the retina (Fig. 1). Over the

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Fig. 1. Schematic picture of the proposed two-level light adaptation involving a ‘Weber’ gain box in the photoreceptors, and a ‘noise’ gain box in the proximal retina. The passage of signal (continuous arrows) and that of noise (broken arrows) through the retina are drawn separately only for visual clarity; it should be noted that the arrows do not represent separate ‘channels’!

**Variables:**
- $G_w$: gain of Weber box
- $G_n$: gain of noise box
- $I_s$: stimulus intensity
- $I_w$: background intensity
- $\sigma_s$: standard deviation of noise component due to quantal fluctuations
- $\sigma_n$: standard deviation of neural noise in the frequency band of photoreponses
- $R$: response amplitude
- $k_1$ and $k_2$: proportionality constants
- $a$: stands for the spatio-temporal summation of the ganglion cell and may here be thought of as a constant, though strictly speaking it is not. The gain of the Weber box $G_w$ is constant for very dim backgrounds, but falls as $k_2/I_B$ when $I_B \gg I_0$. The gain of the noise box $G_n$ is set by the total retinal noise, measured by the standard deviation $\sqrt{\sigma_s^2 + \sigma_n^2}$. For dim backgrounds $G_n$ is essentially determined by $k_2/I_B \approx k_2/\sqrt{I_B}$. For bright backgrounds, $G_w$ and consequently $\sigma_n$ become very small; then $G_n$ approaches the constant value $k_2/\sigma_n$ and the ganglion cell response $R = G_nG_w(aI_s)$ will be governed by the Weber gain $G_w$ alone. [Figure from Donner et al., [7]. Copyright 1990 by the Rockefeller University Press. Reprinted with permission.]

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1 This assumption is common. Leaving $\Delta I$ in simply makes the algebra a bit more involved but the results are the same; the theory predicts a square-root law threshold-versus-intensity (t. v. i.) curve which may be shifted vertically (but not horizontally) by choosing different values for the observer’s $d'$. 
range of background intensities that produce square-root threshold behavior in the ganglion cells, the Weber gain stage is assumed to be inoperative, and the properties of the noise gain mechanism completely determine the ganglion cell gain factor.

The noise gain control stage in the Donner, Copenhagen and Reuter model (hereafter referred to as the DCR model) is assumed to act upon a measure of the incremental flash intensity $\Delta I$ that is computed by applying the spatial filter corresponding to the center-surround bipolar or ganglion cell receptive field structure to the stimulus. To the resulting incremental signal, the noise gain mechanism applies a gain factor which is inversely proportional to the root-mean-square magnitude of the noise in a spatiotemporal pool of quantal electrical rod signals. These quantal rod signals are assumed to arise from an additive combination of photon-induced and thermal isomerizations. Thus, the gain of the ganglion cell output (spike/quantum ratio) is given by the formula

$$O(t) = G_N \Delta I = \frac{\Delta I}{\sqrt{k(I_B + I_D) + \sigma_0^2}}$$  \hspace{1cm} (3)

where $G_N$ is the noise gain factor, $I_D$ is the rate of thermal isomerizations per rod, $k$ is a constant that depends on the retinal area and time over which the rod outputs are summed by the ganglion cell, and $\sigma_0^2$ is the noise variance contributed by neural processes that occur beyond the point of rod output summation, but prior to ganglion cell spike generation.

Over the range of background levels in which the ganglion cell threshold follows the square-root law it is assumed that $I_B \gg I_D$, and that $kI_B \gg \sigma_0^2$, so that

$$O(t) \approx \frac{\Delta I}{\sqrt{I_B}}$$  \hspace{1cm} (4)

The noise gain factor is applied to the noise fluctuations in the pooled rod output as well as to the signal. Since (in the absence of gain control) the fluctuation noise would grow like the square-root of the background level over this range, while the gain factor in fact decreases in inverse proportion to the square-root of the background, the noise in the ganglion cell output is kept constant over the square-root law region by the noise gain mechanism. Thus, according to the model, in order to keep the signal-to-noise ratio fixed within the background range for which the noise gain mechanism dominates, the signal must be increased in proportion to the square-root of the background level.

The DCR model and the de Vries–Rose ideal observer model both account for the square-root law on the basis of the Poisson nature of photon fluctuations. However, the two theories differ in that the DCR model explains the sensitivity loss on the basis of a gain reduction, whereas, the ideal observer model explains it on the basis of an increased variability in the observer’s criterion variable (i.e. the photon count).

While the two models make similar predictions concerning the slope of the incremental threshold function, the DCR model additionally predicts that a superthreshold stimulus should also be subject to gain regulation by the noise gain mechanism. That is, the mean optic nerve signal should be given by Eq. (3), regardless of whether the test flash is at threshold or well above the threshold level. On the other hand, the logic of the ideal observer model applies only to near-threshold stimuli, for which the observer may reasonably be expected to confuse dim flashes with random fluctuations in the quantal absorption rate. There is no reason to expect photon fluctuations to affect the appearance of superthreshold stimuli in a photon counting model. The experiments reported here use a brightness matching technique in order to test the hypothesis that a square-root gain control influences the apparent intensity of stimuli that are well above threshold.

In the brightness matching paradigm, an observer adjusts the intensity $\Delta I$ of an incremental stimulus presented on a background of luminance $I_B$ until the brightness of the increment matches that of a comparison standard [8–10]. Experiments of this type measure what has come to be known as contrast brightness [11], because the subjective intensity of the increment depends on the physical intensity of the background as well as on $\Delta I$. From previous work it is known that contrast brightness is mediated by a monocular (probably retinal) mechanism [9,12]. Hence, if we make the assumption that perceived brightness is directly related to ganglion cell firing rate—the idea of a firing rate code for stimulus intensity going back to Adrian [13]—then the noise gain model predicts that (under conditions where the square-root law is obtained at threshold) photon fluctuations will set the level of the psychological variable ‘brightness’.

While various researchers have recorded brightness matching curves under photopic and scotopic conditions [14,10], none appear to have performed brightness matching under conditions where the square-root law is obtained at threshold (with small, brief flashes). We have thus performed the experiment, under separate scotopic and photopic conditions.

2. Methods

2.1. Apparatus and stimuli: general description

Our experiments were performed with a multi-channel Maxwellian view optical system [15,16]. There were three channels for the right eye: one for the background field, one for the test flash, and one for the fixation cross. There were two channels for the left eye: one for a standard flash and another for a fixation cross. Incre-
ment thresholds were measured in the right eye. Brightness matches were made dichoptically: the right eye saw a display consisting of a fixation cross, the target, and the background; the left eye saw a display consisting of a fixation cross and a standard comparison flash of the same size and duration as the test flash (no background presented to left eye; test and comparison flashes presented simultaneously). The optics were aligned for each subject to make fusion of the left and right eye images trivial, resulting in a unified percept of a single fixation cross and two small flashes superimposed on a large background. The display was very similar to brightness matching displays described in detail in previous reports [9,10].

Background fields for all conditions were provided by tungsten-halogen projector bulbs run off of a conditioned DC power supply (the voltage to the lamps was nonetheless monitored during the course of the experiment). Calibration was performed immediately before each experimental session by placing an International Light research radiometer in place of the observer's pupil. Overall retinal illuminance was controlled with precision-calibrated metallic neutral density filters (Melles Griot).

2.2. Scotopic condition stimuli

Our experimental conditions for the scotopic condition were chosen to favor rod detection [17–19]. A schematic of the stimulus arrangement is shown in Fig. 2A. The target was 39 in. diameter, 10 ms in duration, centered 10° from the fovea in the temporal field of view and presented in the center of an adapting field or background 11° in diameter. The target and background both had a peak wavelength of 509 nm produced by narrow band interference filters (Earing, FWHM bandwidth 7.7 nm). The fixation cross was white and kept as dim as the task allowed. A 3 mm artificial pupil was used for scotopic work and the eye was not dilated. It is important that the background was not of long wavelength composition because this leads to corruption of the rod data by cone input as demonstrated in the work by Sharpe and his collaborators—contrary to what Aguilar and Stiles [20] assumed in their classic paper. Sharpe and coworkers have provided multiple demonstrations that the conditions used here produce responses in normal observers similar to those of a complete rod monochromat.

For the scotopic experiments, test flashes were provided by custom made fluorescent flash lamps. These lamps were T5 bulbs manufactured by Osram Sylvania and filled with a green phosphor with a narrow emission spectrum centered at 509 nm, and an extremely fast decay time (5.1 μs). The lamps were controlled by custom electronics which allow them to be flashed on for any duration between 1 ms and 99 s, in 1 ms steps.

2.3. Photopic condition stimuli

For the photopic measurements, a dim green fixation cross was presented slightly above the center of a large white (opal flashed glass) background. The targets appeared slightly below and to each side of the cross (~0.75° away). Fig. 2B shows a schematic of the display. Targets were of long wavelength composition, produced with a long-pass filter which only passes wavelengths ≥ 600 nm. The targets were also smaller.
and briefer, 3.5’ in diameter, 8 ms in duration. For photopic measurements the test flash was created by shuttering the beam from the stabilized tungsten-halogen source, and the artificial pupil was reduced to 1.5 mm.

2.4. Procedures

Subjects were dark adapted for 35 min before the start of each scotopic experiment, and 25 min for photopic measurements. The subject was adapted to each successive background level for at least 3 min. Thresholds were found using an unbiased staircase procedure [21,22] run by a computer which recorded responses and determined whether the next trial was a target present or absent trial (each with 50% probability). The staircase ran for 12 reversals, the first two of which were discarded and the last ten averaged for the threshold estimate. For brightness matching, the experimenter set the left eye ‘standard’ flash to a suitably chosen intensity level which then remained constant. The observer then adjusted the intensity of the right-eye incremental flash, as a function of background luminance, to match the standard flash. Settings were made three times at each background level and averaged. We stopped recording scotopic data around 1 log scot. td. of background intensity because it was apparent that at backgrounds above 0 log scot. td. cones began to contribute to perception: observers usually reported the background appearing green above 0 log scot. td. and the test flash began to appear to colored at about 1 log scot. td. of incremental intensity.

Note that the primary methodological concern was achieving fine sampling of the t.v.i. curve—that is, taking small steps in background level between threshold or brightness determinations. Previous reports on dichoptic brightness matching (e.g. [9,14]) which might have addressed the issues we are concerned with here (such as the existence of a square-root law segment in the low photopic range), do not allow for definitive conclusions because of coarse sampling of the t.v.i. curve. Of course, much finer sampling requires much more time and effort. Our approach was to record the absolute threshold, then take a large step (or two) in background level until it appeared we were on the rising portion of the t.v.i. curve, at which point we began taking finer steps. This allowed us to spend most of our time finely sampling the rising portion of the t.v.i. curve for an accurate determination of its slope.

Although we were primarily interested in sampling the square-root law portion of the t.v.i. curve, we did not collect many points near the toe of the curve (where it is transitioning from absolute threshold to the steadily rising portion), making accurate determination of the ‘dark light’ value difficult.

2.5. Subjects

Three normal observers participated in the experiments, the author LGB and naive subjects HSL and EY. Subjects LGB (male, age 29) and HSL (female, 17) had natural 20/20 vision and wore no corrective lenses. Subject EY (female, 29) wore her glasses (which correct a moderate myopia) during the experiment. The observers were fully informed about the nature of the experiments and any possible hazards (none). The scotopic brightness matching condition was somewhat difficult and required careful concentration on the part of the subject. The task amounted to comparing two small, brief flashes, 10° off in the periphery; not easy when resolution itself is so poor in the periphery. Though the subjects felt the task to be difficult, their judgements were in fact very reliable: often two of the three settings would turn out to be the same.

3. Results

The scotopic data are shown in Fig. 3. The curve fit through the threshold points (‘+’ symbols) is composed of two segments: a segment with slope zero at low backgrounds (absolute threshold), and a segment with slope 0.5 (square-root law). Subject LGB made brightness matches to two different standards: one that subjectively appeared just barely brighter than threshold (diamonds), and another that appeared many times brighter (squares). Subject HSL made matches to a standard that appeared much brighter than threshold. The threshold data replicate other modern data with respect to the square-root performance and absolute threshold values obtained (see Refs. under Sharpe et al.). That the brightness matching data follows the square-root law over the same range of background levels that produces the square-root threshold law is evidence for the operation of a scotopic gain control mechanism that reduces the gain of the visual system in inverse proportion to the square-root of the background level.

Our photopic data are presented in Fig. 4. The data replicates the classic finding [23,24] that at low photopic levels for small targets there is a clear range over which the square-root law holds (~1.5–2 log units of the background intensity), followed by a transition to near-Weber performance (slopes near one on the log–log graph) at high background levels. As with the scotopic data, dichoptic brightness matches follow the square-root law over approximately the same range of background intensities as the threshold measurements. We stopped recording photopic data once it was clear that the observer was in a near-Weber region: Weber behavior at high photopic backgrounds is well documented [14,24,25] removing any motivation for approaching the
highest backgrounds. The exact slopes of the various segments of the threshold functions for each observer were found by linear regression and are given in the figure captions.

The following well-known equation is often fit to t.v.i. data ([10]; [14]):

\[ \Delta I = k(I_B + I_D)^n. \]  

The reader may wonder if the curve composed of three straight-line segments that we have fit to the data is as good a fit as the more commonly used Eq. (5), for this bears on the issue of whether or not the square-root region in our data could be called simply a transition region between absolute threshold and Weber performance. We performed \( \chi^2 \) minimization on both curves to address this issue. In the case of Eq. (5), \( n \) was fixed at 1, and \( k \) and \( I_D \) were varied during the minimization. For the ‘3-segment’ curve, we fixed the length of the square-root region and slid the entire curve up-down and left-right by manipulating the coordinates of the point where the absolute threshold and square-root line intersect. By fixing the standard deviation of the measurement error at 0.1 log units (the importance of this value will be discussed shortly), we found that the minimal \( \chi^2 \) for Eq. (5) was 3.1 (the optimal parameters were \( k = 3.9 \) and \( I_D = 36.4 \)), while the minimal \( \chi^2 \) for the 3-segment curve was 0.69. Recalling that we have 10 degrees-of-freedom (d.f.) and the rule that a typical value of \( \chi^2 \) for a ‘moderately’ good fit is approximately equal to the d.f., one realizes that both curves are capable of producing good fits to the data. In order for Eq. (5) to produce a \( \chi^2 \) large enough for us to question its validity, the standard deviation of the measurement error must be < 0.04 log units—in our experience, probably much too low for this type of data. Finally, we directly compared the fits of the two models by computing the \( F \)-ratio corresponding to the \( \chi^2 \) for Eq. (5) divided by the \( \chi^2 \) for the 3-segment curve. The resulting \( F(10, 10) = 4.49 \), which is significant at the 0.025 level. Hence, both curves provide statistically good fits to the data with the 3-segment curve being significantly better when compared to Eq. (5).

4. Discussion

Our scotopic data are the first that we are aware of to demonstrate a square-root law for brightness matching over an extended range of backgrounds (~ 5 log units in our data). The data provides compelling evidence that in the rod-driven visual system there exists a mechanism which adjusts the gain in inverse proportion to the square-root of background intensity.

The photopic results are not as clear because the curves switch into near-Weber performance just above 2 log td., leaving little room to tease out a square-root law at the lower backgrounds. In contrast to the scotopic condition, we are not the first to present photopic threshold and brightness matching data and suggest that the data may be well described by a ‘3-segment’ t.v.i. curve (that is, a t.v.i. curve composed of 3 segments with slopes 0, 0.5 and 1). Whittle [26] measured threshold and brightness matches with red and green targets presented on either red or green backgrounds.
In one of his experimental conditions, the test and background were the same color (homochromatic condition), and in the other condition the test and background were of different color (heterochromatic condition). The main goal of his study was to attempt to replicate Stiles threshold work [27] in the brightness domain.

Whittle’s homochromatic t.v.i. and brightness curves are very similar to those that we have presented in Fig. 4. He analyzed his data both in terms of Stiles \( \pi \)-mechanisms, and in terms of 3-segment curves. Whittle decided that one could interpret the curves in either scheme, and that ‘surely both should be considered in our present state of ignorance.’ However, he favored the Stiles interpretation, primarily because in his data the points in the potential square-root law region did not lie along a straight line, but rather along a gradual curve. The 4–5 data points that we recorded in the range 1–2 log td. do appear to lie on a straight line that follows the square-root law. That our photopic t.v.i. curves exhibit a more pronounced square-root law segment than Whittle’s is likely due to the fact that we used significantly smaller and briefer flashes than Whittle (who used 30’, 40 ms targets).

One possible advantage of the 3-segment scheme over the classic Stiles description (which was pointed out by Whittle) is that the shift in slope of the curves (from 0.5 to 1) corresponds with a break between Whittle’s homo- and heterochromatic conditions. Specifically, the homo- and heterochromatic data sets were perfectly superimposed on each other on the absolute threshold and square-root law segments of the t.v.i. curve; the two sets clearly branched apart at the exact background level where the t.v.i. curve switched into near Weber performance. This suggests that one underlying mechanism or structure may account for both the adaptation and spectral sensitivity effects observed by Whittle. For example, Whittle’s data can be accounted for in terms of the two-stage DCR retinal gain control model discussed in the Introduction. In the DCR model, a Weber gain control is assumed to exist in the photoreceptors and a noise gain control at the ganglion cell level. In this model, the transition from square-root to Weber behavior occurs at the background level at which the cones begin to adapt, which should be wavelength-dependent as a result of cone spectral sensitivity. Below this background level, the retinal gain is determined solely by the proximal noise gain control mechanism, for which it is reasonable to expect that the homo- and heterochromatic conditions should be superimposed, as is the case in Whittle’s data.

Although our data strongly supports the existence of an inverse square-root gain control mechanism in scotopic vision—and at least suggests that a similar mechanism operates in photopic vision—the data do not prove the existence of a noise gain control per se. That is, we have no direct evidence that the inverse square-root gain control is achieved by a mechanism which bases its adjustment on an actual measure of the photon fluctuation level. An alternative possibility is that the square-root law results from a deterministic gain control based on a measure of the mean background.

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**Fig. 4.** Photopic t.v.i. and brightness matching data for an 8 ms, 3.5’ target presented foveally on an 11’ background. The target was red, produced by a long-pass filter with the cut at 600 nm. The background was white. Targets appeared ~0.5° below a dim green fixated cross. The solid lines are composed of three segments of slopes 0, 0.5 and 1.0 exactly and were superimposed on the data by eye; the dotted line is the same as the solid line, only shifted up and slightly left. Actual slopes for the middle and top portions of the curves are: LGB threshold, 0.478 (middle) and 0.904 (top); LGB brightness, 0.491 and 0.853. For subject EY threshold, 0.487 (middle) and 0.854 (top); EY brightness, 0.464 and 1.25.
illuminance, rather than the root-mean-square fluctuation level. A deterministic gain control of this type might have evolved to perform the same function that would be served by a gain control based on a measure of the fluctuation level. A deterministic square-root gain control would also suffice to account for the cellular threshold data of Donner, Copenhagen and Reuter.

A square-root gain control serves just as well any other luminance-dependent gain control in protecting the optic nerve from being overwhelmed by uninteresting fluctuations at high background levels. The specific advantage of the square-root gain control, over say, a Weber gain control, is that it keeps the level of noise in the visual system constant as the background level is increased. The increase in root-mean-square fluctuation level due to photon noise is exactly compensated for by a square-root gain control. Thus, the visual brain need not be designed to take into account different noise levels in the input, since the gain control acts to fix the noise level of the cortical input. A further advantage of having the square-root gain control implemented as a noise gain control is that the exact compensation for input noise level would be generalized: non-Poisson statistical fluctuations would be automatically compensated for, and if one area of the visual field was noisier but of the same mean luminance as the remainder of the visual field, a compensatory gain control would be applied.

One completely deterministic alternative to DCR-like models is the model proposed by Sperling [28]. Sperling’s model was based on a two-stage RC-circuit model as an analogue of shunting inhibition. For our purposes, the model can be thought of essentially as having two deterministic square-root gain control stages which operate in series. The two gain control mechanisms become effective at different backgrounds, resulting in a square-root t.v.i. segment at low background levels (where only one stage operates), and a Weber segment at high levels (where both stages operate). If one assumes that only one of these stages operates under scotopic conditions, then Sperling’s model could also account for our threshold and brightness matching data.

Of these two models, we think that the DCR model (with the second stage being either a noise gain control, or deterministic square-root gain control) is more physiologically plausible. This is because a Weber gain stage is already known to exist in the rod photoreceptors of many mammals, including primates [29,30]. Given the well-documented psychophysical Weber’s law in photopic vision, it is natural to postulate that the cones also use a Weber adaptation mechanism at high backgrounds. However, a Weber mechanism in the photoreceptors is inconsistent with the Sperling [28] model, where the Weber gain control arises from a combination of two sequential square-root gain stages, both of which are assumed to exist beyond the stage of canter surround spatial filtering.

It is interesting to ask at what background level Weber photoreceptor adaptation becomes important in humans. Kraft et al. [31] have recently attempted to provide an answer to this question for human rods. Their somewhat surprising answer is that human rod adaptation does not occur below about 1 log scot. td. of background intensity. Our data in Fig. 2 (as well as the data of Sharpe et al.) clearly show that most (possibly all) of scotopic adaptation occurs below this level, suggesting that the square-root gain control mechanism is perhaps the dominant source of neural adaptation for rod vision. If the DCR retinal model applies to human vision, the psychophysical data implies that the Weber rod adaptation should only begin to appear at mesopic levels. Furthermore, if the DCR model is also an adequate model for cone vision then Weber adaptation in the cones should occur at 2 log td. of background intensity, where we begin to see Weber adaptation in our psychophysical data. If it turns out that cones do not show any adaptation, this would rule out the photoreceptor stage, but not the noise gain stage of the DCR model.

Some evidence for a square-root gain control at the ganglion cell level is seen in the classic recordings of Barlow and Levick [32] and Sakmann and Creutzfeldt [33], in which the spiking rate of cat ganglion cells exhibited a square-root law dependence on the background. In a rarely cited experiment, Barlow and Levick [34] attempted a direct test of a retinal noise gain hypothesis. We will briefly describe it here as it is the best direct evidence for a noise gain control (as opposed to a deterministic square-root gain control) of which we are aware. They used a pattern consisting of a moving array of light and dark spots to produce a background with greater dynamic noise variance than a uniform field of the same intensity. Although they noted an increase in the variance of the optic nerve spike train in response to the field of moving dots as compared to the uniform field, the manipulation produced a much larger effect on the gain of the ganglion cell. The ‘noisy’ background produced a quantum/spike ratio that was seven times larger than that produced by a uniform background of equal intensity. Altogether, the threshold of the cell on the noisy background was increased by a factor of about 21, compared to the threshold of the cell adapted to the uniform background. A factor of three was accounted for by the increased variability of the maintained discharge, and a factor of seven was accounted for by the reduced gain.

Barlow and Levick concluded that noise is ‘important in controlling the quantum/spike ratio, or gain, of the retina.’
Through computer simulation work and mathematical analysis [35–37], we have shown that noise gain control arises automatically as a byproduct of modeling ganglion cell spike generation with either an integrate-and-fire model [38] or a closely related spike generation model in which the neural threshold is elevated after each spike. In the integrate-and-fire type of spike generation model noise gain control arises from a statistical hyperpolarization of the neuron resulting from the neural reset mechanism. In the second type of model (threshold accommodation) noise gain control arises from a statistical elevation of the neural threshold. In both classes of spike generation models, the average distance between the threshold and the intracellular potential grows like the standard deviation of the input noise level. Hence, a square-root gain control falls out naturally from using either type of spike generation model and assuming that the dominant source of noise in the ganglion cell input is due to photon fluctuations. In light of the converging evidence from psychophysics and physiology for the existence of a retinal noise gain control, direct physiological tests of specific noise gain models (including, but not limited to, ours) would appear to be a worthwhile next step.

References