Performance of Cat Retinal Ganglion Cells at Low Light Levels

W. R. LEVICK, L. N. THIBOS, T. E. COHN, D. CATANZARO, and H. B. BARLOW

From the Department of Physiology, John Curtin School of Medical Research, The Australian National University, Canberra, A.C.T. 2601 Australia; the School of Optometry, University of California, Berkeley, California 94720; and the Physiological Laboratory, Cambridge University, Cambridge CB2 3EG, England

ABSTRACT Responses of brisk-sustained cat retinal ganglion cells were examined using receiver operating characteristic (ROC) analysis. Stimuli were brief luminance changes superimposed upon a weak steady pedestal ranging from 27 to 47,000 quanta (507 nm) per second at the cornea. Overall quantum efficiencies of cells ranged up to ~13% and were compatible with previous estimates at absolute threshold. The main work was done on on-center cells, but a small sample of off-center units behaved similarly. Experimental ROC curves verified a set of qualitative predictions based on a theoretical treatment of performance, assuming that response variability resulted solely from quantum fluctuations. However, quantitative predictions were not fulfilled. The discrepancy could be resolved by postulating a source of added internal variance, $R$, the value of which could then be deduced from the experimental measurements. A ganglion cell model limited by a fixed amount of added variance from physiological sources and having access to a fixed fraction of incident quanta can account quantitatively for (a) slopes of ROC curves, (b) variation of detectability with magnitude of both increments and decrements, and (c) performance over a range of pedestal intensities. Estimates of the proportion of incident quanta used ranged up to 29% under some conditions, a figure approximately matching estimates of the fraction of corneal quanta that isomerize rhodopsin in the cat.

INTRODUCTION

Under thoroughly dark-adapted conditions, cat retinal ganglion cells may achieve sensitivity corresponding to an average of one or more nerve impulses per photon absorbed in visual pigment (Barlow et al., 1971). Unfortunately, a convincing demonstration of a deterministic, one-to-one relation between photon presentations and production of impulses is impractical, principally...
because of the stochastic nature of light: a weak light stimulus is determined only to the extent of its mean intensity. Fluctuations in the number of quanta are also important for another reason: they represent an irreducible source of variability that is responsible, at least in part, for the failure of ganglion cells to perform visual tasks without error. Just how large a part quantal fluctuations play is unknown. If they were paramount, we might expect to see some evidence of their particular statistical attributes in the responses of ganglion cells. It has generally been assumed (Hecht et al., 1942; De Vries, 1943; Rose, 1946; Barlow, 1956) that the number of photons acting in any particular stimulus is a random variable obeying the Poisson distribution, and this belief has been placed on a more secure experimental (Baumgardt, 1957) and theoretical (Mandel and Wolf, 1965, p. 271) footing. Thus, it might have been supposed that the discharge of retinal ganglion cells should also be Poisson, but this is not the case (Barlow et al., 1971). The evidence against the quantum fluctuation hypothesis is weak, however, because the Poisson signature of light would have been hidden by any type of signal transformation within the retina.

It was the aim of the present experiments to explore the extent to which response variability can be attributed to the unavoidable variability of quantal absorptions. The initial approach taken was to assume the simplest situation: that quantal fluctuations are the only significant source of variability. Certain predictions followed from this assumption that were tested experimentally. Not all the predictions were verified, and this led to a consideration of additional sources of variability intrinsic to the retina. To avoid the problems associated with signal transformation within the retina, we used the tool of receiver operating characteristic (ROC) analysis, as developed for the context of neural discharges (Cohn et al., 1975; Cohn, 1977). The special advantage of this method is that it bypasses complications arising from any deterministic, monotonic transformation preceding the ganglion cell responses and thus offers the possibility of revealing the signatures of the underlying probability distributions that govern performance. A preliminary abstract of this work has appeared (Thibos et al., 1978).

**METHODS**

*Preparation*

Experiments were conducted on 12 adult cats (2.4–3.9 kg) prepared under anesthesia with 2–4% halothane in gas mixture (70% nitrous oxide, 28.5% oxygen, 1.5% carbon dioxide). A tracheal cannula was inserted and the vago-sympathetic trunk was severed on the side of the ocular operation (left). After completion of surgery, halothane was omitted from the gas mixture. Neuromuscular blockade was obtained with gallamine triethiodide (5 mg·kg\(^{-1}\)·h\(^{-1}\)) and D-tubocurarine (0.4 mg·kg\(^{-1}\)·h\(^{-1}\)) in 5% (wt/vol) glucose solution given by continuous intravenous infusion at \(\sim 4\) ml/h, and artificial ventilation was provided. Body temperature was monitored by a subscapular probe and regulated at 37.5°C by feedback control of an electric heating blanket.

Eyelids and nictitating membrane were retracted with 0.5% neosynephrine eye-drops and 1% atropine eye-drops were applied to dilate the pupil. The cornea was
protected with a contact lens of zero power, and an artificial pupil of 3 mm diam was placed in front of the cornea and as close to the contact lens as possible. The carrier for the artificial pupil also included a light-tight tube and rack to support filters and spectacle lens correction. Because the experiments required up to 5 log units of neutral density in front of the pupil, an arrangement of overlapping strips of thick black felt was attached to the carrier to provide a light-tight enclosure around the eye and neighboring regions. With the aid of a photometer (model 721; Gamma Scientific, San Diego, CA) equipped with an integrating head, the attenuation provided by the felt was measured in the position of the animal as the ratio of fluxes after and before wrapping the integrating sphere in the same way as the ocular region of the animal's head. The factor was $< 2.8 \times 10^{-3}$. In addition, the whole preparation was enshrouded by a set of thick black curtains with a closely adapted slit for the pupil carrier. The attenuation caused by the curtains was estimated under working conditions from the ratio of fluxes registered at the position of the animal with the curtains closed or open. This factor was $< 5 \times 10^{-3}$. The highest level of stray light in the room came around midday from leakage past blackout blinds and thick black curtains over the windows. The ratio of this level to the dimmest room illumination (indirect lighting arrangement) was measured to be $6 \times 10^{-4}$. The unobstructed flux reaching the photometer head at the position of the animal in the dimmest room illumination was measured at 0.18 lm\cdot m^{-2}. From these data, the stray illumination reaching the surface of the animal’s ocular region with all of the screening in place and room illumination turned off was estimated at $1.5 \times 10^{-11}$ lm\cdot m^{-2}, corresponding approximately to $2.2 \times 10^{5}$ quanta (507 nm) m^{-2}\cdot s^{-1}. A further factor, not measured, would be the attenuation caused by pigmentation of hair, skin, and uvea. Even assuming these were completely transparent, the stray illumination falling on a receptive field center (area $< 5 \times 10^{-8}$ m²) would be $< 1.1 \times 10^{-3}$ quanta (507 nm) per second, which is already vanishingly small. An estimate was also made of the maximum stray light reaching the cornea through the artificial pupil under standard experimental conditions at midday. After attenuation by the usual 4 log units of neutral density before the eye, it amounted to $< 6 \times 10^{-5}$ quanta (507 nm) deg^{-2}\cdot s^{-1}, which is negligible.

The effectiveness of the light exclusion arrangements was confirmed by monitoring ganglion cell discharge under the following test situation. The light path through the artificial pupil was attenuated by 4 log units with neutral density filters, a value typical of that used in experiments, and the dimmest room illumination was alternately turned on and off. The actual luminance of the external stimulus field under these two conditions was $3 \times 10^{-2}$ cd\cdot m^{-2} and $< 3 \times 10^{-6}$ cd\cdot m^{-2}, respectively. Through the artificial pupil and filters the apparent luminances were each 4 log units lower. Alternating between these two levels of room illumination had no effect on ganglion cell discharge frequency, which indicated that light scattered into the eye from room illumination was insignificant. Nevertheless, to be quite sure that scattered light was negligible, room illumination was turned off during experimental runs.

Recordings were obtained from the vicinity of retinal ganglion cells with tungsten-in-glass electrodes introduced across the vitreous through a cannula penetrating the coats of the eyeball ~6 mm behind the limbus (Cleland and Levick, 1974). First, the discharge from a single cell was isolated and then the cell's functional class was established by testing with hand-held black and white stimuli (Cleland and Levick, 1974) against a uniformly grey tangent screen of luminance not less than $\sim 10^{-2}$ cd\cdot m^{-2}. The room illumination for these conditions was provided by indirect lighting. Correct focus was established for a specified stimulus distance by observation of
responses to photographic square wave grating patterns of various spatial frequencies with different lenses in place close to the eye. The appropriate adjustments of lens power were applied for different working distances.

Light Stimulators

The stimulus source was a green light-emitting diode (LED) based on gallium arsenide phosphide (MV5253; Monsanto Co., St. Louis, MO). It was driven by a feedback circuit (Cohn, 1972) supplying regulated currents in the range 0–35 mA under computer control. The most commonly used form of stimulation consisted of a steady level of light output (pedestal level) with superimposed, transient, upward (increment) or downward (decrement) rectangular steps. Stimulus magnitude was expressed as a fraction \( m \) of the pedestal level. The LED was mounted in a horizontal, matte, white surface carried upon an X-Y translation stage. An aluminized front-surface mirror was positioned to intercept the line of sight of a receptive field and project it vertically down onto the LED. To secure accurate centering of the stimulus, receptive fields were mapped by turning the LED on and off at different positions with a 2 or 3 log unit filter in front of the pupil.

Light Calibrations

Several methods were used and all were in close agreement. The primary calibration was conducted in Canberra by comparing the LED with a tungsten filament lamp traceable (PT 18159) to the National Standards Laboratory, CSIRO, Sydney, using the Gamma Scientific photometer with monochromator head model 700. This yielded the absolute spectral emission curve of the LED (full width at half-maximum = 27 nm), from which the scotopic luminous intensity was determined: \( 2.76 \times 10^{-3} \) scotopic cd at a current of 20 mA. A supplementary calibration was made by applying the same methods to a second similar LED. This was then mailed to Berkeley, where a different type of calibration was performed involving the use of a silicon sensor having spectral and absolute calibration traceable to the National Bureau of Standards (NBS Standard Sensor E-13; California Optoelectronic Industries, Palo Alto, CA). The Canberra and Berkeley results agreed closely (14 and 14.1 \( \mu \)W/sr, respectively). Other measurements with an SE1 photometer (Salford Electrical Instruments, Salford, England) and a J16 photometer (Tektronix, Inc., Beaverton, OR) gave concordant results. The luminous region of the LED had a diameter of 5 mm and its angular subtense was in the range 0.2–0.5° in different experiments.

Stimuli are stated in terms of the scotopically equivalent number of quanta of wavelength 507 nm passing the artificial pupil. The reflection factor of the front-surface mirror (0.84) was measured using the LED and mirror in their working positions. The distance from LED to pupil was 62–147 cm. When a spectacle lens was used, the calculation included a factor to account for reflection losses at front and back surfaces (4% each) and for magnification and displacement of the apparent entrance pupil. Over the series of experiments, the range of factors was 0.868–1.008. Neutral filters (nominal densities 0.5–4) were calibrated in situ. The number of photons at different diode currents was estimated from an experimental curve of relative light output against diode current, measured under steady state conditions. We checked that the peak wavelength of emission (561 nm) increased by no more than 2 nm when current increased from 2.74 to 30.04 mA.

Analysis of Impulse Trains

The computer (H-P 2100; Hewlett-Packard Co., Palo Alto, CA) was programmed to present an interleaved sequence of up to seven different increment and decrement
stimuli of controlled amplitude, timing, and duration. Each stimulus was arranged to occur early in a phase lasting ∼1 s, which allowed sufficient time for the effects to settle before the following stimulus. One of the phases was usually reserved for the no-stimulus condition (steady pedestal level). The complete sequence was recycled continuously. On command from a keyboard the computer began to accumulate peri-stimulus time histograms (PSTHs) and pulse-number distributions (PNDs) from the train of nerve impulses (cf. Barlow and Levick, 1969a). The PSTHs of a preliminary experiment were used to define the latency and duration of responses (Fig. 1, left) required for subsequent scoring of the count for each particular phase into its PND (Fig. 1, right) in the main experiment. Some cells were subjected to a series of experiments, each at a different pedestal level. Although response latency varied inversely with pedestal, response duration was constant and so a count gate of fixed duration was suitable for an entire series. In the case of the no-stimulus phase, the count gate was repeated after intervals equal to the gate duration to acquire as many independent samples of the ongoing discharge as possible and thus reduce sampling variance. A continuous chart-recording of mean impulse rate was made throughout all runs as a check for stationary behavior (Levick and Williams, 1964). In what follows, each cycle of presentation is called a trial.

Receiver Operating Characteristic (ROC) Curves
Any pair of PNDs produced in a particular run could be used to generate an ROC curve in the following way. Let $C_i(n)$ be the fraction of area of the $i$th PND to the
right of \( n \) (including the block at \( n \)). The plot of \( C_i(n) \) against \( C_j(n) \) for varying \( n \) is the ROC curve for the \( i, j \) pair of stimulus conditions. The abscissa (labeled \( P[\text{false positive}] \) in the figures) is usually reserved for the \( C_i(n) \) applying to the phase containing ongoing discharge in the presence of unchanging pedestal (no-stimulus condition). The above formulation covers the case where the stimulus condition corresponding to the \( C_i(n) \) causes an increase in the discharge on average, i.e., an incremental response (e.g., increment of luminance on the center of an on-center cell, or a decrement of luminance on the center of an off-center cell). When the stimulus condition on average causes a decremental response, the convention is to generate the ROC by plotting \( 1 - C_i(n) \) against \( 1 - C_j(n) \). The set of numbers \( n \) of impulses (abscissas of PNDs) is not explicitly designated on the ROC graph but stands in a one-to-one correspondence with the set of points constituting the ROC. A detailed description of the construction of ROCs is given by Cohn et al. (1975).

An ROC expresses the performance achievable by a detector using the counts of gated nerve impulses to make decisions as to whether a luminance change signal had been presented. It reflects one of two strategies, depending upon the stimulus condition and type of ganglion cell: (a) in the case of stimuli that on average produce an increase in discharge frequency (i.e., an increment of light occurring in an on-component of receptive field, or a decrement occurring in an off-component), report that a stimulus occurred when \( n \) or more impulses occurred on a given presentation; otherwise, report that stimulus did not occur; (b) in the case of stimuli that on average decrease discharge frequency (i.e., decrement of light in an on-component, or increment in an off-component), report that a stimulus occurred when \( n' \) or fewer impulses occurred on a given presentation; otherwise, report that stimulus did not occur. Typical ROC curves are shown in Figs. 3 and 4.

There is a stochastic element in the responses of retinal ganglion cells and it is this that concerns us in this paper; the same stimulus in the same conditions produces variable responses, and the same response can result from stimuli of different intensities. ROC analysis has definite advantages in handling the variable element of the relationship because it deals only with the pairs of cumulative probabilities that trace out the ROC curve. Any deterministic monotonic transformation of the stimulus-response relation leaves the ROC curve unaffected (Egan, 1975) and one thus isolates the nondeterministic element for study.

According to theory (Cohn et al., 1975; Cohn, 1977; Thibos et al., 1979), the coordinate points of a Poisson ROC curve will fall very near a straight line when plotted with cumulative Gaussian scales for abscissa and ordinate. The line is characterized by (a) its intercept with the negative diagonal (line of slope \(-1\) through the point \(0.5, 0.5\)), called the \( d' \) axis, and (b) its slope. The scale of this \( d' \) axis is established by the position of ROC curves when the underlying pair of probability density functions have Gaussian form with equal standard deviations. The value of \( d' \) is defined as the difference in means of the densities divided by their common standard deviation. A scale of \( d' \) is constructed along the negative diagonal by marking its intersection with various Gaussian ROC curves generated by setting \( d' \) to a range of values. When cumulative Gaussian scales are used on the two coordinate axes, the scale of the constructed \( d' \) axis is conveniently linear with its unit equal to the distance between the probability points \((0.5, 0.5)\) and \((0.5085, 0.6915)\).

The above definition of \( d' \) determines its meaning. It measures the discriminability of the pair of conditions under test (usually stimulus plus pedestal against pedestal alone). The greater \( d' \) is, the more discriminable are the two conditions.

Fitting a straight line to a set of experimental ROC points is complicated by the fact that both coordinates are random variables subject to sampling variance (Ogilvie
and Creelman, 1968). Strictly an iterative maximum-likelihood method attaching lower weights to the tails of the PNDs would be needed (Finney, 1971). Instead, a simple procedure was used by applying linear regression to the set of points after transformation to Gaussian deviates having the same cumulative probability (Hastings, 1955, sheet no. 62). Sufficient accuracy for present purposes was achieved simply by excluding those points for which either coordinates fell outside selected bounds of probability. The bounds depended upon the number of trials in the run and were chosen after inspection of the computer-plotted ROC points. For 1,000 trials, the bounds $0.01 \leq P \leq 0.99$ were commonly used. When progressively stronger responses are analyzed, the ROC curve shifts outwards to the upper left of the coordinate grid and eventually becomes indeterminate. In such cases, an approximate value of $d'$ was obtained as the difference in means of the PNDs divided by the geometric mean of their standard deviations.

**Estimation of Overall Quantum Efficiency**

In line with previous ideas (Rose, 1946; Jones, 1957; Barlow, 1962), overall quantum efficiency, $F$ (same as the "detective quantum efficiency," $Q$, of Jones, 1959), of a ganglion cell can be defined for a specified task as follows. It is the ratio of the least quantity of light required by an ideal detector to achieve a particular level of performance to the actual amount of light required by the ganglion cell achieving that level of performance. In the Appendix, a formulation of the definition is given that yields $F$ in terms of $d'$ and stimulus parameters (Eq. 3, p. 424).

A second method of calculating overall quantum efficiency was that introduced by Barlow (1962) for psychophysical work and applied subsequently to ganglion cell data (Barlow et al., 1971). Experiments were required in which a number of different stimulus strengths had been interleaved in the trial. The calculation was based on the probability of reaching or exceeding a criterion number of impulses as a function of stimulus strength. Attention was restricted to a criterion number that yielded points well spread around 50% probability, because these have the greatest reliability. Probits of probability were plotted against the square root of stimulus quanta and a best-fitting straight line was drawn by eye (Finney, 1971), taking care to give smaller weights to points having probabilities approaching 0 or 1. $F$ is one-quarter of the slope of the line.

**RESULTS**

In preliminary experiments, the performance of ganglion cells was observed to vary according to their functional class. To minimize this heterogeneity, it was decided to concentrate on just one of the classes, the on-center brisk-sustained ganglion cells (Cleland and Levick, 1974). Recordings were deliberately confined to the same patch of retina in each animal ($\sim 5^\circ$ below and temporal to the center of the area centralis) in the interests of further minimizing possible heterogeneity of performance. A few experiments were also done on off-center brisk-sustained units.

**Stimulus-Response Relations**

In previous work (Barlow et al., 1971), the means and variances of PNDs were used to infer the number of quantum absorptions from the ganglion cell response, but this method depends upon the linearity of the stimulus-response relation and for this reason only weak stimuli could be used. With
In the present stimulus configuration, it was usually the case for on-center cells that the magnitude of the response to a decrement stimulus was less than that to an equal-magnitude increment. An example where the effect was evident is shown in Fig. 2. The part of the stimulus-response relation corresponding to increments above the pedestal level is well fitted by a straight line, but the points for decrements are systematically displaced above the line. The effect is barely perceptible in the left-hand curve, where the pedestal intensity was very low, but is more obvious on the right, where the pedestal was about three times more intense. The common occurrence of similar nonlinearities was one factor urging us to use ROC analysis.

**Figure 2.** Stimulus-response relations for 200-ms increments, decrements, and pedestal level at two intensities of pedestal (arrows): squares 30, circles 94 quanta (507 nm) per 200 ms. Response is mean spike count per gate interval (180 ms). Number of trials: 145 and 400, respectively. Stimulus: centered LED subtending 0.45°. On-center brisk-sustained cell (J-1-6,7,12).

**Qualitative Comparison of ROC Curves with Predictions**

If the variability in the responses of ganglion cells results from the inherent Poisson variability of the light stimuli, then the ROC curves should have the form derived by Thibos et al. (1979). This leads to the following predictions for both on- and off-center cells: (a) ROC points should fall on straight lines when graphed on probability coordinates; (b) \( d' \) for a decrement stimulus should be greater than \( d' \) for an equal-magnitude increment (Eq. 1, p. 423); (c) ROC slope should be greater than unity for decrements and less than unity for increments (Eq. 2, p. 423); (d) expressed as a function of modulation, \( d' \) for decrements should have an accelerating form, and for increments, a decelerating form (Eq. 1).

Prediction b follows directly from the fact that the variance of the Poisson distribution for a decrement is smaller than that for an equal-magnitude increment; the detectability of the decrement is greater because of less
overlap with the Poisson distribution of the common pedestal. This effect is exaggerated by an increase in modulation depth and this leads to prediction d. The slope of an ROC curve is related to the ratio of variances of the underlying distributions; this leads to prediction c. Prediction a is not intuitively obvious.

Fig. 3 illustrates representative results conforming to the first three predictions. Both ROC curves closely approximate straight lines. The decrement ROC intersects the negative diagonal of the graph at a greater distance \( d' = 1.59 \) from the chance (positive) diagonal than the increment ROC \( d' = 1.25 \). This indicates that the decrement had greater detectability than the increment. Furthermore, the slope of the decrement ROC is greater than that of the increment ROC.

Additional Control Observations

All three observations result from the variance of the response to a decrement being less than that for an increment, and they are as expected if response variability is caused by stimulus variability. But they might also be explained...
by a Poisson process whose mean, and hence variance, was directly associated with the response magnitude itself and was not traceable to the stimulus. For this reason the results for an off-center brisk-sustained cell shown in Fig. 4B are of particular interest. If response variance had increased with the mean number of impulses, the ROC curve for increments and decrements would have had the opposite features to those of the on-unit in Fig. 4A, but in fact the features are the same. This points to the variability being traceable to stimulus variance.

Performance of ganglion cells did not always match the above predictions and so in these instances was not limited by quantal fluctuations alone. The reasons for this occasional result are of interest because they show the ways in which suboptimal performance can happen. Departures from expectations occurred if ganglion cell behavior was nonstationary because of receptive field movement relative to the stimulus during the experiment or because of cyclic maintained discharge (Rodieck and Smith, 1966; Levick and Williams, 1964). Departures also occurred if strong pedestal intensities were used or if the count gate was not optimally positioned relative to the response. By opening the count gate to include a greater portion of the ongoing discharge, it was possible to imitate the effects of strong internal noise that became the dominant factor limiting performance. Both nonstationarity and improper count gate could play a role in explaining certain results from human psychophysical experiments (see Discussion).

**Figure 4.** (A) ROC curves for 100% increment (open circles) and decrement (filled circles) of a pedestal subtending 0.43° and supplying 61 quanta (507 nm) per stimulus duration (500 ms); count gate duration, 400 ms; number of trials, 1,000. Regression lines were fitted to points as in Fig. 3. The inset at lower right is the mean rate recording for a representative 17-min section of the 50-min run showing an irregular but stationary pattern. On-center brisk-sustained cell (H-1-8). (B) The same for an off-center brisk-sustained cell (K-1-5): pedestal (0.47°) supplied 8.7 quanta (507 nm) per stimulus duration (200 ms); count duration, 145 ms; number of trials, 1,000.
Fig. 5B shows ROC curves from a representative run in which three different magnitudes of both increment and decrement were interleaved in the sequence of presentations. At all levels of stimulus strength the central portions of the ROC curves are satisfactorily fitted by straight lines. Points toward the ends of ROC curves depend upon uncommon events and are therefore relatively more subject to sampling variance. Detectabilities and slopes were greater for decrements than for equal-magnitude increments. Detectabilities for both increments and decrements increased with magnitude of the stimulus. Fig. 5A bears out the fourth prediction of the quantum fluctuation hypothesis: detectability of decrements is an accelerating function of stimulus magnitude, whereas that of increments is decelerating. The solid lines through the points are theoretical and will be considered in the Discussion.

\[ d' \text{ vs. Stimulus Magnitude} \]

In a few experiments, units demonstrated stationary behavior long enough to extend observations like those of Fig. 5 over a range of pedestal intensities. This allowed more searching tests of the quantum fluctuation hypothesis, but attempts were often thwarted by unstable performance, eye movements, or loss of the recording. The practical difficulties were eased by restricting the number of trials to 400 or 200, but problems then arose because of sampling variance of \( d' \) and slope.

A representative result is shown in Fig. 6. Over the lower 1.4 log unit range of pedestal intensities, the general form of the relations between \( d' \) and predicted by the quantum fluctuation hypothesis. The solid lines through the points are theoretical and will be considered in the Discussion.

**Figure 5.** (A) \( d' \) as function of modulation magnitude for increments (open circles) and decrements (filled circles) of a pedestal (0.46°) delivering 78 quanta (507 nm) per stimulus duration (500 ms). The count gate duration was 400 ms and the run contained 600 trials. The solid curves are theoretical and are based on parameters \( R = 35.0, U = 0.095 \), estimated from \( d' \) measures for 100% increment and decrement. (B) ROC curves corresponding to the six points in A. Solid lines are linear regressions. On-center brisk-sustained cell (G-3-15).
and stimulus magnitude shown earlier was maintained. This result did not hold for stronger pedestals and a more detailed evaluation of these data will be deferred to the Discussion.

**Overall Quantum Efficiency**

The agreement between estimates of overall quantum efficiency derived from probit analysis (Barlow et al., 1971) and from $d'$ was checked. Fig. 7A shows that the two estimates were closely concordant over a sample of units from different animals at various low backgrounds (pedestal intensities ranging from 27 to 8,000 quanta [507 nm] per second at the cornea). Values from 10 to 13% obtained from several units are comparable to the quantum efficiency measured in the absence of pedestal illumination (Barlow et al., 1971).

On the right side of Fig. 7, overall quantum efficiency (calculated by the $d'$ method) is plotted as a function of modulation depth. There is clearly a

![Graph showing overall quantum efficiency](image-url)
A good deal of variability between preparations, but rather less in any one preparation at different modulations. The data show a slight trend for quantum efficiency for the deepest decrements to be less than that for the largest increments. This result supports the notion of added variance that is required for the quantitative modeling of ROC data considered in the Discussion.

**DISCUSSION**

**Quantitative Comparisons**

The qualitative agreement of results in Figs. 3–6 with the predictions from quantum fluctuations suggested that response variability was due at least in part to stimulus variability and so encouraged us to pursue the comparison quantitatively. To do this, it is first supposed (stage I analysis) that response variability is entirely attributable to stimulus variability. This is the model of an ideal photon detector with a single parameter, the fixed fraction of stimulus photons utilized in generating the observed responses. A measurement of $d'$ under a particular experimental condition is then sufficient to predict the value of $d'$ at other stimulus strengths. In addition, the slopes of
the corresponding ROC curves should be predictable from stimulus modulation (Eq. 2, p. 423).

In Table I the pivotal quantity is \( d^+ \), the measurement of \( d' \) for an incremental stimulus. The value of this parameter is used to predict (stage 1 of analysis) \( d^- \), the detectability of a decremental stimulus of the same magnitude. The predictions are somewhat greater than measured values for modulations of 67% but the discrepancy becomes extreme with 100% decrements. Detectability should become infinitely great in the latter circumstance because quantal fluctuations are reduced to zero. Predicted slopes of ROC curves are reasonably close to measured slopes except for ROCS from 100% decrements. To put this assessment of results on a quantitative footing requires knowledge of the sampling distributions of \( d' \) and ROC slope. Explicit expressions for these are not known, but they have been evaluated empirically for the case of Poisson-distributed input signals and have been shown to be approximately Gaussian with standard deviation \( \sqrt{3/N} \), where \( N \) is the number of trials per ROC (Thibos et al., 1979). By taking this result as a guide for interpreting the present results, it can be concluded that the discrepancies are greater than can be accounted for by sampling error.

### Table I

**Quantitative Analysis of Performance**

| Cell  | Pedestal* | Size | Modulation | Prediction (stage 1)$^2$ | ROC slope | Prediction (stage 1)$^2$ | Prediction (stage 2)$^3$ | \( F \) | \( U \) | \( R^4 \) | Trials |
|-------|-----------|------|------------|--------------------------|-----------|--------------------------|--------------------------|-----|-----|------|-------|
| F-3-9 | 206       | 0.43 | \(+0.67\)  | 1.34                     | 0.89      | 0.92                     | 0.93                     | 0.025 | 0.051 | 58.4 | 600   |
|       |           |      | \(-0.67\)  | 1.79                     | 2.01      | 1.10                     | 1.15                     | 0.020 |       |      |       |
| G-9-8 | 87.5      | 0.21 | \(+0.67\)  | 1.25                     | 0.97      | 0.92                     | 0.94                     | 0.051 | 0.071 | 45.6 | 600   |
|       |           |      | \(-0.67\)  | 1.59                     | 1.88      | 1.19                     | 1.20                     | 1.10  | 0.037 |      |       |
| G-3-12 | 21.9     | 0.46 | \(+1.0\)   | 1.30                     | 0.88      | 0.89                     | 0.96                     | 0.109 | 0.291 | 50.4 | 1,000 |
|       |           |      | \(-1.0\)   | 1.52                     | \(\approx\) | 1.16                     | \(\approx\) | 1.06  |      |      |       |
| H-1-8 | 61.1      | 0.43 | \(+1.0\)   | 1.60                     | 0.97      | 0.89                     | 0.94                     | 0.059 | 0.117 | 82.0 | 1,000 |
|       |           |      | \(-1.0\)   | 2.01                     | \(\approx\) | 1.20                     | \(\approx\) | 1.10  |      |      |       |
| H-1-28 | 194      | 0.43 | \(+1.0\)   | 1.85                     | 1.00      | 0.89                     | 0.93                     | 0.025 | 0.042 | 178  | 1,000 |
|       |           |      | \(-1.0\)   | 2.47                     | \(\approx\) | 1.51                     | \(\approx\) | 1.15  |      |      |       |
| I-2-6 | 19.1      | 0.45 | \(+1.0\)   | 1.09                     | 0.96      | 0.89                     | 0.94                     | 0.088 | 0.178 | 26.8 | 1,000 |
|       |           |      | \(-1.0\)   | 1.56                     | \(\approx\) | 1.09                     | \(\approx\) | 1.09  |      |      |       |
| I-3-5 | 19.1      | 0.45 | \(+1.0\)   | 1.16                     | 0.90      | 0.89                     | 0.94                     | 0.100 | 0.181 | 21.3 | 800   |
|       |           |      | \(-1.0\)   | 1.50                     | \(\approx\) | 1.11                     | \(\approx\) | 1.11  |      |      |       |
| K-1-5 | 8.7       | 0.47 | \(+1.0\)   | 0.72                     | 0.95      | 0.89                     | 0.96                     | 0.084 | 0.243 | 22.7 | 1,000 |
|       |           |      | \(-1.0\)   | 0.83                     | \(\approx\) | 1.15                     | \(\approx\) | 1.06  |      |      |       |

* Quanta (507 nm) per stimulus duration.

\( ^2 \) Stage 1: assumes fixed fraction of stimulus quanta utilized.

\( ^3 \) Stage 2: based on two-parameter (\( U, R \)) analysis including added variance.

\( ^4 \) Equivalent quanta per stimulus duration.

\( ^5 \) Stimulus duration 500 ms; count duration 400 ms.

\( ^6 \) Stimulus duration 100 ms; count duration 100 ms.

\( ^7 \) Stimulus duration 200 ms; count duration 145 ms. Off-center brisk-sustained cell; all others are on-center brisk-sustained cells.
Reference to the original PSTHs for 100% decrements provides the clue to the source of the discrepancy. Removal of all of the light did not remove all of the variability in impulse frequency; it is the variability of the residual discharge that has forced detectability to remain finite. In the next section (stage 2 analysis), the ideal photon detector model of ganglion cell performance is expanded by an additional parameter, \( R \), to handle the variability of the residual discharge.

**Dark Light and Added Variance**

The existence of an intrinsic retinal noise has been recognized previously and its effects have been calculated both on psychophysical performance (Barlow, 1956) and on neurophysiological responses (FitzHugh, 1957; Barlow and Levick, 1969b; Barlow et al., 1971). These effects are not unimportant, for the noise is thought to determine the level of the absolute threshold and to cause the maintained discharge of the ganglion cells in total darkness. To account for the residual discharge, it is natural to suppose that there is an intrinsic retinal source of random events that are additional to and independent of the events originating from quantal absorptions. However, the mean rate of these random events is not necessarily fixed and the present analysis will enable a distinction to be raised further on between “dark light” and “added variance.” The former is the minimum added variance that would be expected in the undisturbed retina left in darkness, whereas the latter is a figure derived from the analysis of the present experiments, in which a pedestal level of light illuminates the receptors and is briefly modulated to provide the stimulus. In other words, we have now been led to change from the idea of intrinsic noise as an invariable “dark light” that cannot be eliminated, to the idea that it contributes an “added variance” that may be different under different conditions. Note that “added variance” is additional to the variance associated with the steady pedestal level or the various stimulus levels of light used. Furthermore, it is an entirely different concept from that of “equivalent background brightness” (Crawford, 1947; Barlow, 1964; Barlow and Sparrock, 1964; Blakemore and Rushton, 1965) used in the interpretation of threshold changes after the bleaching of substantial fractions of visual pigment. The fraction of visual pigment bleached in the present experiments is miniscule in effect even as the argument of an exponential.

**Quantum Efficiency and Quantum Utilization**

The incorporation of added variance in a model of ganglion cell performance calls for a reconsideration of the meaning of quantum efficiency, \( F \). Although \( F \) is measured in terms of the attenuation of light necessary to reduce the performance of an ideal detector to that of the system studied, it reflects losses of performance caused both by actual attenuation of light as well as by the addition of unrelated noise events. The formulation now to be presented segregates these two classes of performance-reducing effects in a way that is not possible with only a single measure, \( F \). Besides the added variance \( R \), a new parameter \( U \) is introduced to stand for the fraction of input quantal variance that is converted into stimulus-dependent response variance. In the
model considered, it is supposed that there is a random deletion of input photons so that only a fraction of them contributes effectively to performance. \( U \) stands for that fraction and for convenient reference is called "quantum utilization." Unlike \( F \), the value of \( U \) is unaffected by the presence of intrinsic noise. With no intrinsic noise, \( F \) and \( U \) are equal; otherwise, \( F \) provides a lower bound on \( U \). Under the low light levels of the present experiments, a major component of both \( U \) and \( F \) is the fractional reduction in the number of quanta passing the entrance pupil to the number effectively absorbed in visual pigment. A more comprehensive model would be required to deal with further classes of performance-reducing effects such as multiplicative noise (Lillywhite and Laughlin, 1979; Teich and Saleh, 1981; Lillywhite, 1981; Laughlin and Lillywhite, 1982). Whether this development is needed will be determined by how well the present two-parameter model represents the experimental observations.

**Three Tests of the Formulation**

Estimation of two model parameters \( U \) and \( R \) requires a pair of measurements of performance, for example, estimates of \( d' \) for equal-magnitude incremental and decremental stimuli (Appendix: Eqs. 7 and 8). Knowledge of \( U \) and \( R \) then allows the following predictions to be made of other aspects of performance and of performance under other stimulus conditions.

**ROC CURVES**

The different slopes of the ROC curves for increments and decrements are not entirely unrelated to the different \( d' \) intercepts, but they were not used in the estimation of \( U \) and \( R \), and so may be tested against the model's predictions (Appendix: Eq. 5). Table I (prediction, stage 2) illustrates the comparison on eight experiments each of \( \geq 600 \) trials. The significance depends upon the sampling variances of both measured and predicted ROC slopes. Taking \( \sqrt{3/N} \) as a rough guide to sampling error (Thibos et al., 1979), one can draw the conclusion that the measured ROC slopes agree with the predicted ROC slopes to within the accuracy of the experiment.

**DETECTABILITY VS. STIMULUS STRENGTH**

If the model parameters \( U \) and \( R \) are fixed for a particular ganglion cell and independent of stimulus parameters, a second test of the formulation may be developed on experiments where several different levels of incremental and decremental modulation were interspersed. The predicted dependence of \( d' \) on \( m \) (Appendix: Eq. 4) was calculated on the basis of estimates of \( U \) and \( R \) derived from one pair of modulations. Fig. 5 illustrates a representative result. The solid curves are the predicted relations. They pass exactly through the pair of points used for determining \( U \) and \( R \) as expected, but also fit the other points quite well.

**DETECTABILITY VS. PEDESTAL INTENSITY**

The final quantitative test of the ganglion cell model with fixed parameters was an attempt to fit a field of data points involving joint variation of modulation depth and pedestal intensity on the basis of estimates of \( U \) and \( R \) obtained at just one of the conditions examined, namely 100% increments and decrements of a pedestal of 94 quanta. Fig. 6 shows the best of three examples. The predicted relations
between $d'$ and modulation are shown by the solid curves, which necessarily pass through the corresponding measured values (upright triangles on the right) and provide a reasonable fit to measurements at lower modulations. Corresponding pairs of curves were calculated for other values of pedestal from the same estimates of $U$ and $R$ and it will be seen that these fit the data reasonably well for pedestals of 30 and 820 quanta. However, the predicted curves for 9,330 quanta clearly diverge from the experimental points, even at the lowest values of $d'$.

The conclusion is that with only two express parameters, quantum utilization factor and added variance, the model provides a comprehensive description of the ganglion cell's performance over a significant range of conditions towards the low end of the pedestal intensity scale.

**Significance of Quantal Fluctuations**

The central aim of these experiments was to assess the extent to which ganglion cell performance is limited by the stochastic nature of light and to what extent it is limited by the stochastic nature of the retina. From the foregoing analysis, it can be concluded that ganglion cells behave as if these two sources of variability were independent and additive. If the variance contributed by the pedestal is $P$ and that contributed by the intrinsic retinal noise is $R$, then quantal fluctuations contribute the fraction $P/(P + R)$ to the total. For the eight experiments of Table I, the range of this fraction was 0.28–0.78 and the average was 0.48. It can therefore be concluded that for the low light level conditions of these experiments, quantal and physiological variability were of about equal importance.

How the relative importance of quantal and retinal noise might vary with stimulus conditions is not yet fully understood. From results of experiments at a fixed level of pedestal illumination, such as illustrated in Fig. 5, the value of $R$ appears to be independent of the magnitude of stimulus increment or decrement. It also appears that $R$ remains roughly constant as pedestal level varies over a limited range, about 30-fold for the unit of Fig. 6.

**Relevance to Human Psychophysics**

The quantum efficiency of cat retinal ganglion cells is significantly greater than that measured in human psychophysical experiments (see Barlow, 1977, for review). One possible explanation for this discrepancy is that central neurons are uncertain as to which ganglion cell carries the response to a visual stimulus (Nachmias and Kocher, 1970) and uncertain also as to the timing of the response in the impulse train (Lasley et al., 1976). This notion of "channel uncertainty" has been used previously to explain why human performance does not always appear to be quantum limited (Cohn et al., 1974; Cohn and Lasley, 1974; Greenhouse and Cohn, 1978). Barlow (1977) suggests that random variation in threshold criterion of central neurons could also be a major contributing factor to human quantum inefficiency.

The control experiments of the present study provide some neurophysiological basis for these ideas. The type of channel uncertainty envisaged...
by Nachmias and Kocher (1970) occurs in a ganglion cell when uncontrolled eye movements cause the stimulus to wander across the cell's receptive field; the result is nonstationary, suboptimal performance. Uncertainty about the timing of stimuli and responses also leads to suboptimal performance and reduced quantum efficiency. This was demonstrated by experiments in which the count gate for nerve impulses was deliberately widened to include more than just the central plateau of the ganglion cell's response waveform.

Comparison with Previous Measurements

The range of quantum efficiencies for dark-adapted cat ganglion cells of the on-center class reported by Barlow et al. (1971) was 4–16% (relative to quanta at the cornea), which agrees with the present results of 2–11% (Table I) using a different stimulus paradigm and different methods of estimation.

Estimates of quantum utilization ranged up to 29%. These values are of the same order as an estimate of the fraction of corneal quanta absorbed in rhodopsin (24%) determined by retinal densitometry in the cat (Bonds and MacLeod, 1974) and are at the center of the range (12–54%) suggested by Barlow (1977) for the proportion of quanta at the cornea that causes isomerizations in the rods. The comparison cannot be pushed too closely because the computed values of $U$ are affected by the combined sampling variance of two $d'$ estimates. The lower bound set by $F$ is more reliable because it depends on the sampling variance of just one $d'$ estimate. The order of accuracy for estimates of $U$ was obtained by two methods. First, it is supposed that estimates of $d'$ were distributed like those of computer simulations of 1,000-trial runs with Poisson signals, which had standard deviations of $\pm 0.05$ (Thibos et al., 1979). Calculations of $U$ for the three units of Table I with the highest $U$ were repeated with all combinations of new values of $d'$ $\pm 0.05$. For cell G-3-12, the worst-case choice of $d'$ values would reduce $U$ from $\sim 29\%$ to $\sim 20\%$. For two other cells the reductions would be: from 24 to 13% (cell K-1-5), from 18 to 14% (cell I-3-5). Second, a 1,000-trial ganglion cell experiment was simulated with parameters typical of the best units: $U = 0.30$, $R = 20$, $P = 13.3$, $m = \pm 1.0$. The resulting values of $d'$ were then used to estimate these given values of model parameters $U$ and $R$. The mean of 100 estimates of $U$ by this method was 0.36 with SD = 0.20 and the mean $R$ was 27 with SD = 21.

The conclusion is that the highest values of $U$ found for retinal ganglion cells agree with the estimate of effective rod absorptions to within the accuracy of our experiments. If $U$ indeed matches the ratio of isomerizations to incident quanta, the implication would be that all isomerizations (and hence all photoreceptors) in the excitatory receptive field center contribute to the ganglion cell response.

Estimates of dark light were also made by Barlow et al. (1971). Expressed as equivalent quanta at the cornea per receptive field center per second, the range was 4.5–128. Similarly expressed, the range of data in Table I is 43–436. Thus, the present experiments lead to considerably higher values than the previous derivation from the maintained discharge level and responses...
to weak flashes. In the present series, there were no experiments for which both types of estimates were made on the same cells, so the implications of the comparison should be regarded as suggestive only. Furthermore, the success of the analysis developed in this paper depended critically on the responses to decrements and this implied that a pedestal had to be used. It would certainly be possible to conduct experiments without a pedestal and to let the analysis for $R$ be based on measurements of $d'$ for a pair of incremental stimuli, but the outcome would depend on smaller differences and would require more trials than were found necessary in the present work to achieve useful reliability. It may be worth attempting because of the importance of the result. If estimates of added variance made in the presence of a pedestal are greater than the dark light estimated in its absence, it would imply that transduction was noisier at higher sustained rates of quantum absorption.

**Multiplicative Noise**

Lillywhite and Laughlin (1979), Lillywhite (1981), and Laughlin and Lillywhite (1982) have inferred the presence of a source of noise arising from the transduction of quantal absorptions by locust photoreceptors. The effect is to generate a stimulus-dependent variance in excess of the quantum fluctuation noise. A model of multiplicative noise has also been proposed for cat retinal ganglion cells (Teich and Saleh, 1981) and human visual system (Teich et al., 1982). This is different from the “added variance” of the present model because its magnitude increases in proportion to stimulus intensity. Several results bear on the question of multiplicative noise. First, the finite detectability and finite ROC slope with 100% decrements exclude the possibility that such transduction noise could be the only source of retinal noise in the present experiments. Second, it can be shown that “transduction noise” superimposed on quantum fluctuations theoretically leads to ROC curves having slopes closer to unity than is the case for the homogeneous Poisson process. This leads to a distinctly poorer fit with the present experimental observations. Finally, when the quantum utilization factor $U$ matches the fraction of quanta actually absorbed in visual pigment, multiplicative noise can be set aside because the surplus response variance is then totally accounted for by “added variance,” which is constant for increments and decrements.

**Appendix**

The form of ROC curves for detection of Poisson signals is described in detail elsewhere (Thibos et al., 1979). When plotted on Gaussian axes, the Poisson ROC consists of a series of nearly collinear points. A line passing through these points has slope and intercept (at the negative diagonal, i.e., the $d'$ axis) given approximately by:

$$d' = |m| \sqrt{P(1 + m)^{-1/4}},$$  
(1)

$$\text{slope} = (1 + m)^{-1/6},$$  
(2)

where the mean number of quanta at the cornea per stimulus duration provided by the pedestal is $P$ and by the pedestal plus signal is $P + mP$. The appearance of the
absolute value of modulation parameter $m$ in Eq. 1 preserves the convention that $d'$ shall be positive for both increments ($m > 0$) and decrements ($m < 0$).

**Overall Quantum Efficiency**

Definition of $F$: the ratio of the least quantity of light required by an ideal detector to achieve a particular level of performance divided by the actual amount of light required by the ganglion cell to achieve the same level of performance. By convention, equality of performance is met by equality of $d'$. Eq. 1 written for the ideal detector and rearranged becomes:

$$F = d'^2 \sqrt{1 + m/Pm^2}.$$ (3)

**Two-Parameter ($U, R$) Model**

It is supposed that ganglion cells use only the fraction $U$ of quanta incident on the cornea. Intrinsic retinal noise is modeled as an independent random process generating events confusable with the events associated with the absorption of quanta from pedestal and stimuli. Its magnitude is expressed as the intensity of a real light source that would add the same variance $R$ (same units as pedestal) to the distribution of input events. The justification of this representation is as follows. If the retinal noise process is due to the superposition of many independent sources of variability, then it, like the input quantal events, will be Poisson (Cox and Lewis, 1966). As the superposition of two independent Poisson processes is also Poisson, the ROC slope and $d'$ for the model are immediately known by substituting $U(P + R)$ for pedestal intensity and $m' = mP/(P + R)$ for modulation into the performance Eqs. 1 and 2:

$$d' = |m'| \sqrt{U(P + R)(1 + m')^{1/4}};$$ (4)

$$\text{slope} = (1 + m')^{-1/6}.$$ (5)

If the process adding variance has some unspecified distribution of mean $R'$ and variance $R$, it is necessary to fall back on an intuitive definition (Sakitt, 1973; Thibos et al., 1979) of $d'$: the difference of means divided by geometric mean of standard deviations, but the result is the same.

The unknowns $U$ and $R$ can be estimated experimentally by measurements of $d'$ for an increment ($d'_+$) and decrement ($d'_-$) of the same magnitude $m$. The ratio $r = d'_-/d'_+$ yields the effective modulation strengths:

$$m' = (r^4 - 1)/(r^4 + 1),$$ (6)

from which $R$ and $U$ can be obtained:

$$R = P[(m/m') - 1];$$ (7)

$$U = d'd'_-(1 - m'^2)^{1/4}/Pmm'.$$ (8)

Valuable technical assistance was rendered by Mrs. Erika Vander Pol. We appreciated the fine technical contributions of Mr. L. M. Davies, Mr. R. M. Tupper and staff, and members of the Photographic Unit. P. Hutton provided valuable help in the calibration of light sources. The project was supported in part by grants EY01481(NEI) and BNS76-18829(NSF) and a Visiting Fellowship (ANU) to T. E. Cohn. L. N. Thibos was supported by Postdoctoral Fellowship 5F32EY05039-02(PHS), and D. Catanzaro by Vacation Scholarships (1977, 1978, ANU).

*Received for publication 17 December 1981 and in revised form 2 April 1983.*
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