RB-102

QUANTUM EFFECTS IN HUMAN VISION

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I. Introduction

The familiar story of forsaking one's gem-studded back yard to look for diamonds abroad takes on a particularly ironic twist in the case of the quantum theory of radiation. Planck made a magnificent excursion into radiation theory to establish the fact that radiation is not a smooth flowing continuum of energy but rather a finely divided stream of separable and countable bits of energy called quanta or photons. To the layman, Planck's demonstration was far from simple. It was a highly technical argument showing that only by the assumption of such discrete bits of energy could one account for the experimentally known spectrum of radiation from an incandescent body. Later, more direct and simple evidence for photons was supplied by the experiments on photoemission. In these experiments, the energies of electrons ejected from a solid by light were traceable easily to the discrete energies of the photons that ejected them.

What is ironic is that this same granular nature of light was all the while imposing its inescapable limitations on what the early scientists could literally see in their dimly-lit libraries and laboratories. In fact, if the present writer is not deceived by his own observations, the early workers had only to glance up at some shadowed wall to see directly the granularity of the radiation they were intently investigating. This is not to suggest that acceptance of the quantum theory of radiation would have been hastened by pointing out its visual effects. Agreement comes more slowly in the field of vision than in the purely physical sciences.

Perhaps, it is even more to be wondered, once the quantum nature of radiation had been established now some half century ago, that it was not immediately used to outline the absolute limits of visual performance. Only in the last few years has this limitation been seriously recognized, and then mainly by a small group of research workers whose business it is to supplement and extend the range of human vision by electronic devices. The several attempts to "see" down to the fluctuation limits imposed by x-ray photons both in medical and industrial radiography are the most current examples[4,5,11,13,15],

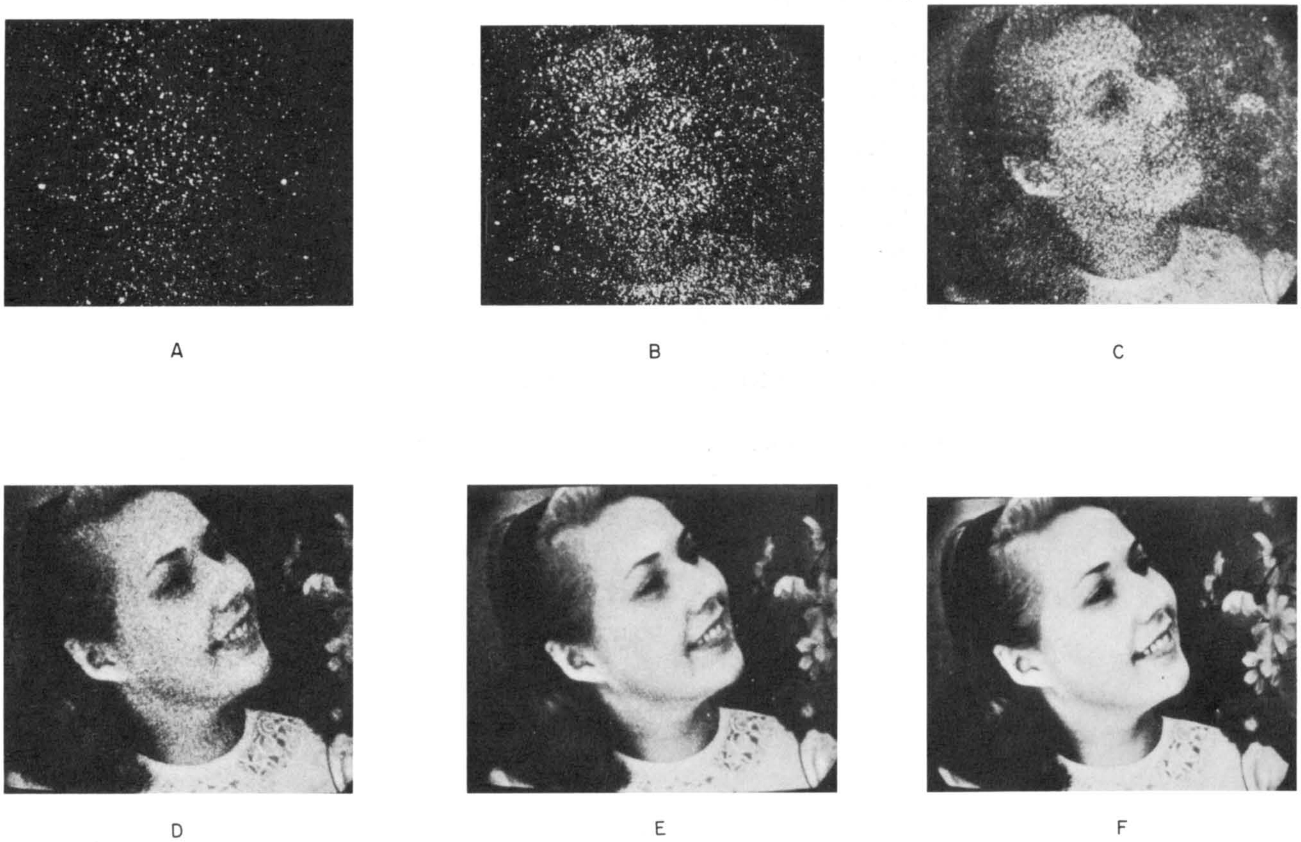

Fig. 1 – Series of photographs showing the quality of picture obtainable from various numbers of photons. The luminance values shown were computed from the numbers of photons assuming a storage time of 0.2 seconds, a pupil diameter of about 6 millimeters, a viewing distance from the life-size subject of four feet and a quantum efficiency for the eye of 10 percent.

16,22. The somewhat longer standing problem of developing a television camera tube to match the human eye is another example[14, 19c, 21, 24].

The problem of the quantum (or photon) limitations to vision can be quite simply stated. At any given light intensity, one counts the total number of photons entering the eye during its storage time. From the total number of photons, one computes or constructs (see Fig. 1) the best picture permitted by the random properties of the photons. One then compares this picture with what one actually sees. If the two are the same, the conclusion must be that visual information is determined by the finite number of photons entering the eye. This conclusion is absolute and is independent of one's choice of physiological or chemical mechanisms to be associated with the visual process.

If, on the other hand, this comparison shows that we actually see less than what is theoretically permitted, two conclusions are possible. The simplest would be to say that only a fraction of the stream of photons incident on the eye eventually contributes to forming our visual image. For example, it is known that half the light is reflected or absorbed in the inert lens and optical fluids before it reaches the retina. It is also reported that the sensitive retinal elements themselves, the rods and cones, absorb only a fraction of the light incident on them. This conclusion would still refer our visual information back to the finite stream of photons but would make use of only a fraction of that stream.

The second broad conclusion formally possible is that all of the light goes to forming a visual image but that there are local limitations imposed on what we can see. One kind of limitation could be of the "threshold" type in which a minimum number of photons must be accumulated before a sensation is triggered off. Much of our visual information would then be abortive. Another kind of limitation could come from what might generally be called "system noise". This is a familiar term in electrical communications used to describe the level of local disturbances in a receiver. An incoming signal must exceed this level before it can be detected. A more homely parallel is that the buzzing or ringing sounds one sometimes experiences in his ears obviously interfere with what he can hear. Possible evidence for local disturbances or "noise" in the visual system will be discussed later. Whatever the local limitation postulated, one must take care that it does not deteriorate the theoretical picture too much. For example, if we actually see half of what is theoretically possible, the local limiting mechanism should not cause more than this factor of two deterioration. As obvious as this caution may appear, it is not trivial. A long standing model, used to explain dark adaptation and identified by the phrase "bleaching of the visual purple", has maintained an apparently healthy existence in spite of the fact that its consequences are in patent violation of the limits set by the photon nature of light. In this sense, a knowledge of the absolute limits set by the photon nature of light can help to sift out various proposed visual mechanisms.

An actual comparison between what one sees and and what one should theoretically see, if he made use of every incident photon, shows that our visual performance parallels closely the theoretical limits over a range of light intensity of seven powers of ten. Even though our actual performance is a power of ten lower than the theoretical limit, the close approach to theory over this large range of light intensities strongly suggests that the finiteness of the incident stream of photons rather than some local mechanism in the eye controls our visual performance.

II. Quantum Limitations to Vision

1. *Limitations Imposed by Finite Number of Photons*

Suppose we wish to construct a picture making use of small white dots all having the same size. Pictures formed in this way are common experience in display signs and somewhat less common in certain paintings executed by stippling. The minimum number of white dots required is evidently given by the number of picture elements to be resolved. Such a picture would, however, lack half tones, at least in areas of elemental size. If we wish to make a good picture, we might ask that each picture element be capable of showing a brightness difference from its neighboring elements of one percent. Now, if we are in complete control of how we dispose the white dots, we would need only one hundred dots per picture element. In this way, neighboring elements having ninety-nine and one hundred dots respectively would display the required one percent difference in brightness. The total number of dots required is then one hundred times the number of picture elements. We ask now whether this requirement entails any serious limitation on the performance of the eye.

The final limit of resolution of the eye is set mechanically by the size of its receptor elements, the rods and cones. One of these elements is about a micron in diameter and subtends an angle of about one minute of arc at the eye lens. Let us consider a picture element containing a number of rods or cones and subtending an angle of 2 minutes at the eye lens. We can extrapolate this small angle out to the scene we are viewing and count how many photons enter the eye from the intercepted scene element. At a scene brightness of ten foot lamberts, a representative value for indoor lighting, the number of photons aimed at the picture element per second is 10^6. Since the storage or exposure time of the eye is 0.2 second, the number of photons per picture time is 2×10^5. This number is large compared with the 100 photons required to reproduce a brightness difference of one percent. *Accordingly, if we were free to dispose the incoming photons in a regular array, the number of photons available would be far in excess of that needed for an excellent picture.* And this would still be true for illuminations well below that of moonlight.

In reality, however, we are not free to dispose of the photons as we wish. We must accept them as they come and they come at randomly spaced times. This randomness makes a heavy demand on the number of photons needed to reproduce small brightness differences.

2. *Limitations Imposed by the Random Character of Photons*

It is well known and well established that an average number of random events has associated with it fluctuations from the average whose root mean squared (rms) magnitude is equal to the square root of the average number. This relation applies equally to photons falling on the eye, electrons emitted from a hot body, rain drops falling on a pavement (if the rain drops are independent of each other) and to the random walks, common in diffusion problems. The meaning of the relation becomes clear from a representative test. Consider a square foot of surface to be uniformly illuminated. The word "uniformly" means that the average number of photons falling on each square inch is the same over all the surface. Thus if we count the number of photons falling on each of ten neighboring square inches during a time of one second, these numbers will not be the same. We can take an average of the ten numbers and compare it with a similar average taken elsewhere on the surface, the two averages would be closely the same. The fractional discrepancy would be reduced if we made the count for a minute instead of a second and, in fact, would approach zero as the averaging time increased indefinitely.

Once having defined the average number of photons falling on each square inch per second, we can return to the set of ten numbers giving the *actual* numbers of photons falling on each of the square inches in a time of one second. If we take the differences between each of these ten numbers and the average, square each difference, average the squared differences and take the square root of the average, this number will be the root mean squared (rms) fluctuation. It will also be close to the square root of the average number of photons. If the operation were repeated many times and an average of these rms values taken, the rms value so obtained would approach even closer to the square root of the average number of photons.

The well-known steps, leading up to the rms fluctuation have been deliberately repeated here to emphasize that the concept is a mathematical measure of the fluctuations. It is a highly convenient measure. For example, in circuit theory the rms fluctuations in a steady current can be treated immediately as a current from which the fluctuation (noise) power can be computed. On the other hand, and this is the kernel of the present argument, the rms, fluctuation does not immediately inform one how large a signal is needed to be distinguishable from random fluctuations. The signal is the difference in average brightness or number of photons between two neighboring areas. That difference or signal, to be discussed shortly, is found from experiment to be detectable when it is about five times the rms fluctuation.

All of the necessary concepts are now at hand for recomputing how many photons per picture element are required to see a brightness difference of one percent between neighboring elements. In the absence of random fluctuations, it was immediately clear that only one hundred photons were required. In the presence of random fluctuations, the number will be considerably larger. What we ask quantitatively is that the difference in average numbers of photons between neighboring elements be one percent of the average number* and, further that the difference be five times the rms fluctuations associated with the average number. Let the average numbers be N_1 and N_2. Then, approximately*, the two conditions are expressed by:

$$N_1 - N_2 = 10^{-2} N_1 = 5\, N_1^{1/2} \tag{1}$$

From Eq. (1) we get:

$$N_1 = 250{,}000 \text{ photons per picture element.}$$

This is in striking contrast to the 100 photons previously computed in the absence of fluctuations and is close to the 2×10^5 photons available from a ten foot-lambert scene. *In brief, the number of photons available to the eye at the comparatively high brightness of ten foot lamberts is just sufficient to produce an excellent picture.*

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* Strictly one should take some kind of mean between N_1 and N_2 for the average number. It is not important here since N_1 and N_2 are nearly the same.

At lower scene brightnesses down to absolute threshold in the neighborhood of 10^{-6} foot lamberts, the fluctuation-limited picture quality must steadily decrease.

The comparison between the actually perceived picture quality and the theoretical fluctuation-limited quality is carried out in a later section. At this point it is useful to translate Eq. (1) into readily observable quantities.

3. *Fundamental Relation:* $BC^2\alpha^2 = constant$

Eq. (1) of the previous section can be re-written in terms of the number of photons *(n)* striking the retina per unit area and the element of area (s^2) under consideration.

$$(n_1 - n_2)s^2 = 5\,(n_1 s^2)^{1/2} \qquad (2)$$

If Eq. (2) is squared and all of the variables brought to the left side, it may be written as

$$n_1\,[(n_1 - n_2)/n_1]^2\, s^2 = constant \qquad (3)$$

In this form we can readily replace the three factors with quantities proportional to them: n_1 with the average scene brightness B, $(n_1 - n_2)/n_1$ with the contrast C between neighboring elements and s with the angular size α subtended by the test element under consideration. Eq. (3) then becomes the simple fundamental relation:

$$BC^2\alpha^2 = constant \qquad (4)$$

The constant includes the storage time t of the eye, the threshold signal-to-noise ratio k, the diameter D of the pupil opening of the lens, a factor θ giving the fraction of photons incident on the eye that are eventually used in forming the picture and a factor depending on the units of B, C and α. For B in foot lamberts, C in percent contrast and α in minutes of arc the constant is [19b]:

$$constant = 5(k^2/D^2 t\theta) \times 10^{-3} \qquad (5)$$

where D is measured in inches, t in seconds and k has the value 5. In the example discussed in the previous section, B was 10 foot lamberts, C one percent and α two minutes of arc. The value of the constant, then, for full use of every incident photon is 10. This value is based on a pupil diameter of four millimeters.

The series of photographs in Fig. 3 were used to test Eq. (4) as well as to derive an experimental value for the threshold signal-to-noise ratio k. Fig. 3 is what a perfect eye would see when looking at the original pattern shown in Fig. 2 under various illuminations. The adjective "perfect" refers to the fact that each white dot (visible particularly in the first three pictures of the series) is an actual trace of a single photon reflected from the original pattern and entering the photomultiplier*. The gain of the photomultiplier and subsequent television amplifier was sufficient to show traces of the individual photons on the kinescope from which Fig. 3 was photographed.

The original test pattern, Fig. 2, consisted of black discs along the top row decreasing in diameter by a factor of two in each step. The second row is a repetition of the first except that the discs are now grey, with 50 percent contrast. In the third row the contrast is 25 percent and in the fourth, 12 percent. The pattern was so designed that at each level of illumination the demarcation line between the resolvable and unresolvable parts of the pattern should be a 45 degree line if Eq. (4) is valid. Also this demarcation line should move one step to the right for each factor of four increase in illumination. The illumination in successive pictures was increased by a factor of four each time. Both these expectations were born out in a careful examination of the originals of Fig. 3. Actually each picture of Fig. 3 is in itself a confirmation of Eq. (4) and serves to give several independent estimates of the threshold signal-to-noise ratio. The slight shading in the pictures and the variations in the sizes of the white dots reflect experimental difficulties not entirely overcome but not having a serious effect on the conclusions.

4. *Threshold Signal-to-Noise Ratio*

The statement or the assumption is frequently made in communications that a just detectable signal is one that is equal to the noise* of the receiving system: in brief that the threshold signal-to-noise ratio is unity. This is a quite reasonable assumption to make in the absence of experimental data. It is also a statement that might be erroneously confirmed if the noise is not properly defined. For example, the noise is sometimes loosely used to refer to the "envelope" noise on a cathode ray tube display. The so called "envelope" noise is some six to eight times (depending on viewer and viewing conditions)

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* The television light spot scanner arrangement used to obtain the photographs of Fig. 3 is described in reference 19b.

*In communications, the term "noise" is used to refer to the fluctuations in signal currents both in video as well as audio systems. "noise" is used in the present paper interchangeably with "fluctuations".

larger than the accurately definable rms noise. Also, one may easily overlook certain integration effects that reduce the actual value of noise below that read on a meter. It is, for example, common to specify the signal-to-noise ratio in a television system by measurements on, or by analysis of, the wide-band amplifier. It must be borne in mind that this signal-to-noise ratio applies only to areas of picture element size viewed in single pictures. In viewing an actual picture, the eye can integrate several successive television pictures and thereby improve the signal-to-noise ratio. Further, if elements larger than picture element size (as determined by the passband of the amplifier) are under consideration, the signal-to-noise ratio is higher in accordance with Eq. (4).

What can be stated here with confidence, based on simple inspection of Fig. 3, is that a signal just equal to the rms noise is *not* detectable. If it were detectable it would mean that one could remove one of the photon specks in Fig. 3a or Fig. 3b and the removal of that photon would be detectable by another person. Since the noise is the square root of the signal, one photon in these pictures represents a signal of unity and also a noise of unity. In fact, the questions of what the threshold signal-to-noise ratio means, and what its approximate value is, can also be answered by simple inspection of these figures. One poses the problem: what is the smallest number of photons that must be removed so that the removal is detectable. The removal of photons from a given area corresponds to the insertion of a black disc of that same area in the original test pattern. By such an inspection of Fig. 3 or, its equivalent, and by noting the size of black discs that are just detectable in these photographs, it was concluded that about 25 photons had to be removed to get a clear indication that something was missing. The twenty-five photons represent a signal of twenty-five and a signal-to-noise ratio of five. Hence, the origin of the value five for threshold signal-to-noise ratio. Another way of stating

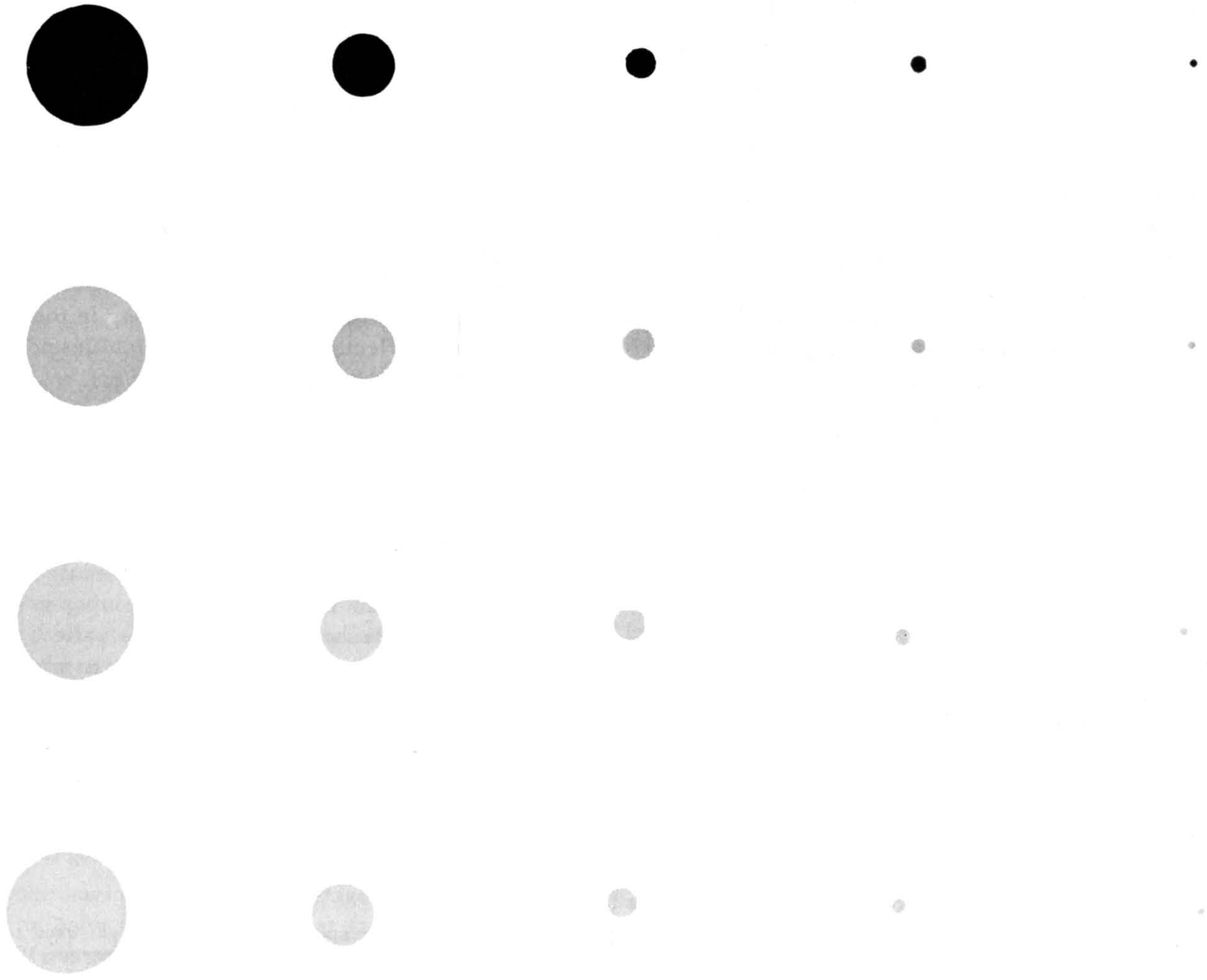

Fig. 2 – Test pattern used for series of photographs in Fig. 3.

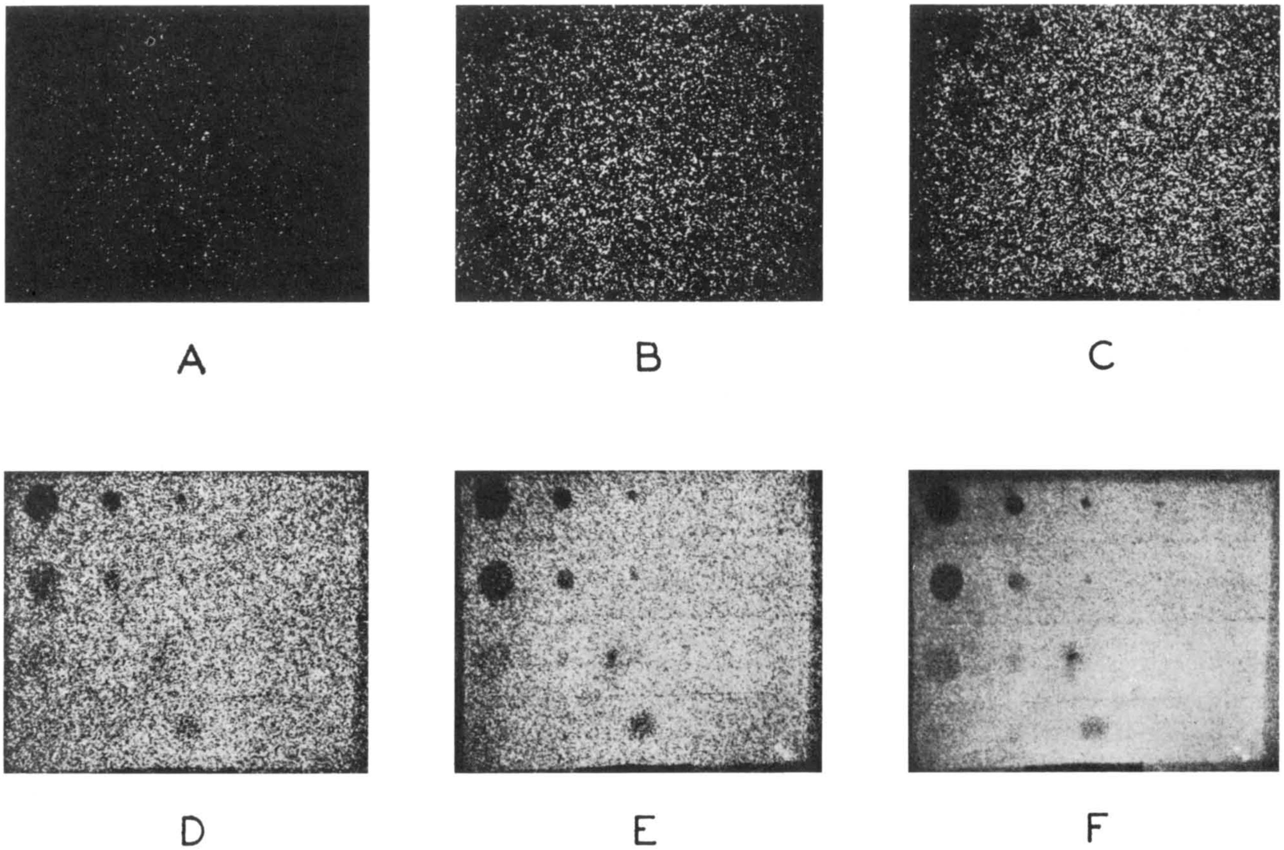

Fig. 3 – A series of light spot scanner pictures of the test pattern in Fig. 2, using increasing numbers of photons. The photon density increases by a factor of four for each step in the series A – F.

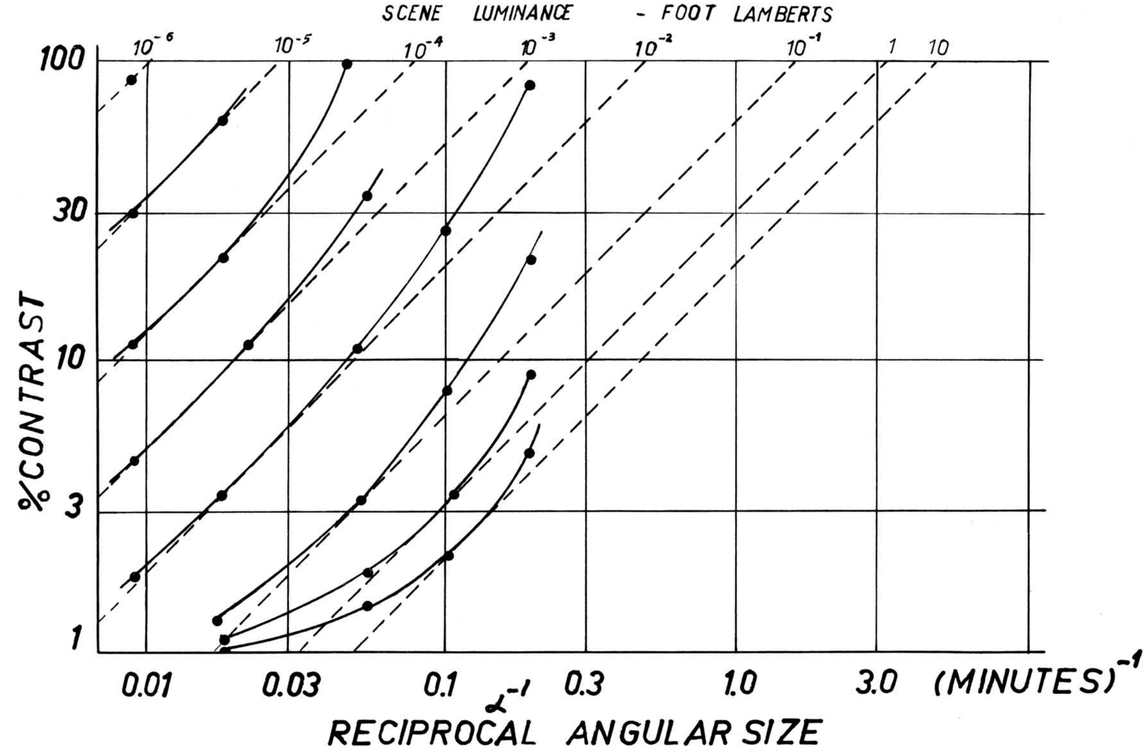

Fig. 4 – Comparison of performance data for the eye (computed from Blackwell) with ideal performance curves.

the problem is that there are already present in the uniformly illuminated areas of Fig. 3 statistically formed "holes" in the distribution of photons of a magnitude approaching twenty-five photons. To avoid confusion with these spurious "black" areas a real black area must be somewhat larger.

These last statements can be made more quantitative. Consider a uniformly illuminated area and within this area consider a test area containing an average of 100 photons. The rms fluctuation associated with the test area is ten photons. One now asks, "how many photons must be removed from the test area in order that the removal be detectable?". If one assumes that a signal-to-noise ratio of unity is detectable, only ten photons need be removed. But then, one asks, "what are the chances of seeing another area, the same size as the test area, that has ten photons missing by accident?" The answer is that approximately one out of three such areas picked at random will show this deviation. If the test area occupies a small fraction, say 10^{-5}, of the field of view, one will see about 3×10^4 spurious deviations. For a signal-to-noise ratio of two, there will be about 10^4 spuriour test areas. At a signal-to-noise ratio of three, the number of spurious test areas is 300 and at a signal-to-noise ratio of four it is 6. Finally, a signal-to-noise ratio of five would reduce the chance of finding a single spurious test area in the whole field of view to less than a tenth. Thus, threshold signal-to-noise ratios between 4 and 5 would appear to be safe. Moreover, the threshold signal-to-noise ratio ought to become somewhat smaller the larger the test area. The improved performance shown in Fig. 4 for larger area test elements could be interpreted as reflecting this decrease in threshold signal-to-noise ratio*.

III. Quantum Efficiency Of The Eye

1. *Comparison with Visual Data*

Some of the most thorough data on the performance of the eye have been reported by Blackwell.[2] Part of his data has been replotted in Fig. 4 in a form to be readily compared with the fundamental relation (Eq. (4)) derived from purely statistical reasoning. The experimental data show the threshold contrast detectable as a function of the reciprocal angle subtended by the test object and at various scene brightnesses ranging from 10^{-6} foot-lamberts to 10 foot-lamberts. The data were taken with white light and are uncorrected for pupil opening. Tangent to the best performance at each value of scene luminance are drawn dotted lines with 45-degree slope representing the type of ideal performance expected from Eq. (4). The experimental curves depart from the 45-degree lines both at small contrasts and small angular sizes. Since the smallest detectable contrast and smallest detectable angle are set by local limitations in the eye and not by the statistical fluctuations in the incoming photons, one would expect the experimental data to depart from the statistically-derived 45-degree lines as these limits are approached. Even at lower illuminations, where the statistically-limited resolution is well below the limit set by the rods and cones, the eye must perform a quite ingenious technical feat in order to approach ideal performance. That is, for low-contrast areas it must pool the information from hundreds or thousands of rods in order to perceive the low-contrast area while, at the same time, it must reduce the pooling effect for high-contrast areas where higher resolution is statistically possible. It is conceivable that some of the incoming photons are diverted from picture forming receptors to monitoring receptors whose function it is to control the amount of local pooling.

From the 45-degree lines in Fig. 4 and from data published by Reeves[18] on the size of pupil opening as a function of scene illumination, one can compute, with the aid of Eq. (4), the effective quantum efficiency of the eye. The meaning of an effective quantum efficiency of 10 percent, for example, is that the performance of the eye is equal to that of an ideal fluctuation-limited device making use of 10 percent of the incoming photons. The effective quantum efficiencies, rounded out to the nearest half percent, are listed in Table I. They are shown for white light as derived directly from Blackwells data in Fig. 4. A second column of efficiencies is shown for blue-green light*. These are simply the white-light efficiencies multiplied by three, since blue or green light, depending on the brightness range, requires only one third as many photons to produce a given brightness as does white light. To obtain the efficiencies in Table I, an exposure time of 0.2 second and a threshold signal-to-noise ratic of 5 was used. If there is any change in these parameters

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* Careful measurements by Tol et al[25] on a two millimeter test element lead them to estimate the threshold signal-to-noise ratio at a value between 3 and 4.

* At high lights, the maximum efficiency of the eye is in the green at 5500 Å; at low lights it moves to the blue at 5100 Å.

Table I

Brightness	Effective Quantum Efficiencies in Percent		
Foot Lamberts	White Light	Blue-Green Light 5100 Å to 5500 Å	Blue-Green Light at the Retina
10^{-6}	3	9	18
10^{-5}	4	12	36
10^{-4}	3	9	18
10^{-3}	2	6	12
10^{-2}	2	6	12
10^{-1}	2	6	12
1	1.5	4.5	9
10	1	3	6

as a function of brightness, the exposure time is almost certain to decrease and the threshold signal-to-noise ratio to increase with increasing brightness. Both these changes would be in the direction of reducing the change in quantum efficiency from low lights to high lights.

Two facts are of striking importance in Table I. First, the quantum efficiencies are relatively high at low light levels. Second, there is remarkably little change in the quantum efficiency from 10^{-6} foot-lamberts to 10 foot-lamberts. The change by a factor of four as shown in the table is an upper limit and is insufficient, as discussed later, to support the "bleaching of the visual purple" model for dark adaptation.

The last column of Table I is labeled "Effective Quantum Efficiencies for Blue-Green Light at the Retina". The values here are twice those in the previous "Blue-Green" column. Since it is known that only half the light incident on the eye arrives at the retina, it is worth separating out this factor. The last column, then, is a measure of how much of a discrepancy must still be accounted for between the actual and the theoretically perfect performance of the retina as a picture device.

A small part of this discrepancy can undoubtedly be ascribed to incomplete absorption of the light in the receptor elements*, to some reflection and to some absorption by non-sensitive tissues separating the receptor elements. Perhaps a more significant source of the discrepancy lies in the many functions the eye performs. Color vision at scene brightnesses above 10^{-1} foot-lamberts is one of the most important. If, as some theories have held, there are different receptors for different parts of the spectrum, most of the remaining discrepancy would be accounted for at high lights because only a half or a third of the light would be absorbed in the "right" receptors.

There are other functions that might tap off some of the light on to monitoring cells. The adjustment of the high gain process that must intervene between the retina and the optic nerve pulses is one such function. Electrical recording of pulses on single nerve fibers by Hartline[8] has shown that some receptors are active only transiently when the light is increased or decreased but not when it remains constant. These cells might indeed be monitoring the magnitude of the high gain process. The additional function of monitoring the number of receptors that must pool their information has already been mentioned.

2. *Quantum Efficiency Derived from Absolute Threshold*

It has been known for a long time that only about 100 photons need be incident on the eye in order to give a visual sensation. To carry out the above experiment the eye is completely dark adapted and then exposed to a series of light flashes. The magnitudes of the light flashes are at first below the threshold of seeing and later increased until the observer gives reliable responses that he sees the flash. This measurement, then, is a measurement at absolute threshold – that is, a single white area against a black background.

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*If one takes the setimates of Hecht [9b] or of Dartnall and Goodeve [6] for the light absorption by receptor elements, namely about 20%, the differences between the efficiencies in the last column of table I and 100% are mostly accounted for and in one instance (10^{-5} foot lamberts) are over accounted. The writer finds it difficult to believe, however, that the eye wastes 80% of the light.

It occurred to Hecht[9a], and apparently independently to a group of Russians[3] that one could make use of the transition curve from "not-seeing" to "seeing" in order to compute the actual number of photons taking part in the visual sensation. Qualitatively, if only one or two of the hundred incident photons were finally used, the transition from "not-seeing" to "seeing" would be relatively slow. It would occupy perhaps a factor of two in incident light intensity. This argument is based on the statistical fluctuations to be associated with a small number of random events. At the other extreme, if all hundred of the incident photons were used, the transition would be relatively steep, occupying only about a ten percent change in light intensity. The argument is a quite reasonable one. The results obtained, however, by Hecht[9b], by Brumberg[3] and more recently by van der Velden[26] show a disturbing spread. Hecht concluded that only 7 out of the hundred quanta were used, Brumberg's values ranged from 25 to 50, while van der Velden has concluded that the number should be 2. Van der Velden has gone into great detail to discuss the mathematical statistics of this method. These arguments the writer has not evaluated*. What does occur to the writer is a parallel between the problem of determining the quantum efficiency of the eye and the same problem for a photomultiplier.

One can, of course, easily measure the quantum efficiency of a photomultiplier by taking the ratio of the electron current leaving the photocathode to the photon current incident on the cathode. The parallel operation cannot readily be carried out for the eye. There is, however, a second simple method for measuring the quantum efficiency of the photomultiplier. One can measure and compare the signal current (average output current) and the noise current coming out of the multiplier. This ratio is the signal-to-noise ratio in the output stage of the photomultiplier. It should also be closely equal to the signal-to-noise ratio of the current leaving the photo cathode of the photomultiplier. Knowing the signal-to-noise ratio of the cathode current, the current itself may be directly computed. The ratio of the cathode current to the current of photons incident on the cathode then gives the quantum efficiency of the photocathode. This precedure is essentially what the writer has carried out in order to compute the quantum efficiencies for the eye shown in Table I. For the eye, the signal-to-noise ratio of the output was estimated from its half-tone discrimination characteristic. From this ratio the effective number of photons at the retina was computed and compared with the number of incident photons to obtain a value for the quantum efficiency.

What is to be emphasized about this procedure is that it can be carried out at scene brightnesses well above absolute threshold. At these scene brightnesses, the noise from the incoming photons is likely to be greater than possible local noise sources in the retina. The latter can be significant and can mask the measurement of quantum efficiency at extremely low values of scene brightness.

To continue the parallel with the photomultiplier, if one tried to carry out the method of Hecht and others to determine its quantum efficiency, one would use small flashes of light on the photomultiplier until a reliable signal was obtained. This procedure would not necessarily give the quantum efficiency of the photomultiplier. In the absence of light, one can still observe currents in the output stage of photomultiplier. These signals come from thermionic emission from the photocathode, from leakage currents, from stray gas ions and possibly from cosmic rays. The magnitudes of these local noise sources would normally confuse any measurement of the quantum efficiency of the photomultiplier carried out at absolute threshold. In brief, the local noise sources are greater than the noise of the incoming photons. At light intensities well above absolute threshold, the reverse is true.

The writer, for the above reasons, is inclined to place more reliance on quantum efficiency measurements of the eye carried out at light intensities well above absolute threshold than on those carried out at absolute threshold.

IV. Some Problems Of Vision

1. *Primary and Secondary Processes*

It is essential to an understanding of the eye that one distinguish between primary and secondary processes. This is just as true for an understanding of its intimate chemistry as it is for an understanding of its performance. Separation of primary and secondary processes is a well-recognized prelude to an analysis of those man-made com-

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* Baumgardt[1] has repeated and confirmed van der Velden's measurements. He also confirms the conclusion that the basic retinal units (a unit may be a collection of hundreds of receptors) is triggered off by two photons. He goes on further to show, however, that it would not alter the agreement with experiment to assume that two or even more of these basic units need to be triggered off before a recognizable sensation is transmitted to the brain. This argument of Baumgardt's would allow van der Velden's results to be consistent with the higher quantum efficiencies shown in Table I. If only one basic unit needed to be triggered, the best quantum efficiency that van der Velden could offer would be perhaps two percent, to be compared with the twelve percent in the blue-green column of Table I.

petitors to the eye – photomultipliers, photographic systems, and television camera tubes. All of these devices, including the eye, are subject to the same statistical limitations in the incoming stream of photons and the same principles of physics and chemistry in the subsequent development of detectable signals.

The primary process is clearly the absorption of incident photons. Present knowledge of quantum physics makes it almost certain that the photons are absorbed by electrons – as opposed to ions. The electron may be liberated into the vacuum as in a photoemitter; it may be liberated (or made free) within the solid as in photoconductors and as in the silver bromide crystals of photographic film; or it may be raised to an excited state from which its energy may cause the dissociation of molecules or may trigger off one of many possible photochemical reactions.

It is not important which of these types of absorption takes place in the primary process. What is important is that all of the photons be absorbed in the same way and in such a way as to be countable by their subsequent physical or chemical effects. Only then can all of the information be drained out of the incoming stream of photons.

In the photocathode of a photomultiplier, only a fraction of the absorbed photons succeeds in liberating electrons into the vacuum where they can be counted by the multiplier; in photographic film, only a fraction of the internally liberated electrons arrives at opportune spots in the crystal where they can contribute to (or be counted by) the developability of grains; in a photoconductor, some of the liberated electrons may be associated with longer-lived, higher-gain centers than others and, thereby, pre-empt the counting process. Accordingly, it is not sufficient that all of the photons be absorbed by the same type of electronic process, but they must all be able to contribute equally to the subsequent train of events. The fraction of incident photons so absorbed is the quantum yield of the primary process and determines the maximum fraction of incoming information that can finally appear in the output of the picture recording device. The intermediate or secondary processes may deteriorate the information but they cannot recover the information lost in the primary process.

The secondary processes are those that intervene between the primary absorption of photons and the final presentation of the picture. The energies of photons are microscopic compared with the energies normally associated with perception. On the microscopic scale, the energy of a photon is large compared with the thermal energy of an atom and can thereby trigger off normally improbable* events to make itself visible on a macroscopic scale. A well-known example is that of the silver bromide grains in ordinary photography. The energy of the few photons absorbed by the silver bromide grain is sufficient to change the state of only a few atoms of silver. To become visible, the state of all 10^{10} atoms of silver in the grain must be altered. Thus the secondary process here provides a gain or amplification of ten billion times. The same order of gain intervenes between the photo-surface of a television camera tube and the final viewing audience.

A rough estimate of the energy of a single pulse in the optic nerve can be made based on the estimated values: pulse height 10^{-3} volts, nerve fiber resistance 10^3 ohms, and pulse duration 10^{-3} seconds. This estimate yields an energy of 10^{-12} joules or a value over a million times larger than the few photons known to be able to trigger the pulse. Undoubtedly, then, the secondary processes in the eye must provide a considerable gain in energy just as in the other systems of picture recording.

Not only is it common in picture recording systems, for the secondary processes to provide a high gain, but this gain must be variable. The energy level of presentation, as measured by the brightness of motion picture or television screens, is relatively constant, while the energy level in the primary process, as determined by the scene or image brightness, may vary over many powers of ten. The variable gain of the secondary processes must match this variable ratio between final presentation and initial image brightnesses*. (In photography and television, the gain of the secondary processes includes also the ratio of final picture area to initial image area).

In photography and television the range of scene brightnesses transmitted is in the order of a thousand, that is, from about one to a thousand foot-lamberts. In the case of human vision, this range is about a billion fold extending from 10^{-6} foot-lamberts to 10^3 foot-lamberts. The importance of a variable gain mechanism in the secondary process of the eye is accordingly even greater than in photography or television where it is already known to exist. In spite of our lack of knowledge about the presentation level in the brain, we can be reasonably confident that it does not vary by the factor of a billion just cited. Our ability to discriminate absolute brightnesses in a uniformly lit white enclosure (in the absence of the tell-tale objects of common experience) is notoriously poor. Further, the measurements of Hartline[8] on the optic nerve fibers of the crab show that the electrical signals passed on to the brain vary only as the logarithm of the light intensity.

The arguments for the existence of a variable gain mechanism between retinal receptors and optic nerve fibers may appear to have been labored too much. The

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* The probability that an atom take on from thermal vibrations the energy of a photon of green light in one second is less than 10^{-20}. This means that grains approaching 10^{20} would be stable against thermal triggering.

* If the quantum yield of the primary process is less than unity, the same fractional value of image brightness is to be used.

writer can say only that such a mechanism must play an important role in many visual phenomena, two of which are discussed below, and he has not seen the variable gain mechanism separated out in other analyses of vision*.

2. *Dark Adaptation*

Once the separation of primary and secondary processes is recognized, the way is opened for a simple interpretation of some well-known visual phenomena. Dark adaptation is one example. Its characteristics have been repeatedly explored. The major facts are these: If a person enters a dimly lit room after having been exposed to normal high-brightness levels of about one hundred foot-lamberts, he finds at first that he sees little or nothing. After a time he begins to discern objects not at first visible. After a half hour he can see objects whose brightness is a thousand to ten thousand times lower than what he could see when he first entered the darkened room. The improvement in vision with time in the dark is called "dark adaptation". The problem is: how to interpret the factor of a thousand or more improvement in seeing.

Hecht[9a] and others have turned the problem around and have suggested that one starts with maximum visual sensitivity in the dark. In the dark, or near absolute threshold, the sensitive material in the retina, called "visual purple", absorbs about 20 percent of the incident light. As the ambient brightness is raised, the "visual purple" tends to bleach out and accordingly to absorb less of the incident light*. Finally at high light intensities, it absorbs less than one thousandth of what it absorbed near absolute threshold. In brief, the true sensitivity of the eye has been depressed by a factor of a thousand. If the process is now reversed, and one enters a darkened room, time is required for the visual purple to be regenerated. Dark adaptation is then identified with the regeneration of visual purple.

The significance of the "bleaching of the visual purple" model for dark adaptation is far reaching. It means that the sensitivity of the eye at normal seeing levels is one thousandth what it is at low light levels. If one takes the quantum efficiency of the eye at low light levels to be about 10 percent, then the quantum efficiency at high light levels must be less than 0.01 percent. One compares this value with values in the neighborhood of a few percent shown in Table I. The latter were deduced from purely statistical considerations without reference to any particular assumptions about the retinal mechanism. The values in Table I are absolute minimum values for quantum efficiencies. The eye must absorb at least these fractions of the incoming light in order to see what it does. (It may actually absorb more light to be used for other visual functions). Whatever uncertainties are involved in computing the quantum efficiencies in Table I, it is highly unlikely that the error would be even a significant fraction of the factor of several hundred, needed for reconciliation with the bleaching theory.

To restate the argument in a positive manner, the change in quantum efficiencies in Table I from 10^{-6} foot-lamberts to 10 foot-lamberts is only a factor of three. A factor of more than a thousand is needed to account for the known facts of dark adaptation. Changes in the quantum efficiency or sensitivity of the primary process cannot, therefore, account for dark adaptation. (See also Rushton[20]).

If dark adaptation is not assignable to the primary process, its interpretation must be found in a secondary process. One such secondary process has already been described that appears to fit readily, namely, the variable gain mechanism that amplifies the energy of a few absorbed photons to the energy level of optic nerve pulses. At low lights, this gain must obviously be set high. As the light intensity is increased, the gain is reduced as evidenced by the measurements on the energy flow in the optic nerves. The frequency of nerve pulses increases slowly, only logarithmically with increasing light intensity[8].

The reduction in gain does not mean a lower sensitivity but only that less amplification is needed to present the information to the brain. A common parallel is found when we tune a radio receiver from a weak to a strong station; the gain of the receiver is reduced to match the presentation level of our hearing. The reduction in gain does not reduce the information transmitted. If we now tune back again to the weak station, we find that it is not audible until the gain is once more increased.

Similarly, if we re-enter a darkened room after being exposed to high light intensities, time is required to re-set the gain mechanism at its maximum value. The steady improvement in seeing reflects the steady increase in amplification provided by the gain mechanism. Whether one describes this transient as an increase in sensitivity (a description the writer regards as confusing) or as a temporary mismatch of gain is not so important as it is to recognize that it is a transient, that it is associated with a secondary process and that the steady-state sensitivity of the eye changes very little from low lights to high lights.

It is worth likening the gain mechanism to one other familiar system. The resolving power of a microscope is commonly defined in terms of its objective lens. The magnification that follows the objective is to some extent incidental. A minimum value, called the useful magnifi-

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* De Vries[27b] makes passing mention of possible triggering action of the absorbed photons.

* For a recent review of the "visual purple" mechanism, see G. Wald[28].

cation, is needed to present to the observer all of the information resolved by the objective lens. Magnifications greater than this value may add convenience but do not add information.

There is no difficulty in conceiving of a high gain mechanism in the retina. The chemical literature provides numerous examples of catalytic processes in which a small number of atoms of one type can facilitate reactions in large numbers of atoms of another type. Moreover, the human system is already skilled at devising the powerful triggering mechanisms that allow heavy muscular activity to be controlled by the relatively microscopic energy of nerve impulses. Finally, the decrease in gain at higher light levels would follow naturally if the amount of material available to be triggered is limited. The writer wonders, here, whether the substance called visual purple is not the triggered material responsible for the high gain rather than the material responsible for the absorption of light. Bleaching or exhaustion of the visual purple at high light intensities would then be more easily understandable.

The present model for dark adaptation has separated the visual processes into a primary process (the absorption of photons) that controls the amount of information received by the eye and a secondary process, a gain mechanism, that determines the level of presentation of the information. These are separate operations and conceivably can act independently. In fact, it is the time lag in re-setting the gain mechanism that is used to account for dark adaptation. Another example of independent action is discussed in the following section.

3. *Luminosity and Information*

It is known that at high brightnesses, the eye sees closely the same fine detail in red, green or blue light as in white light. Luckiesh and Taylor[12] performed the following test. They started with equal high brightnesses of red and blue light and observed that the fine detail visible under both illuminants was the same. Next, they inserted neutral filters in front of each illuminant to reduce their radiance by a factor of a hundred. The detail visible under each illuminant was reduced but remained mutually the same. On the other hand, the apparent brightness – called luminosity – of the blue illuminant was considerably greater than the red illuminant. The quantitative results in this test are not of particular concern here. What is significant is that qualitatively the information transmitted by the red and green illuminants did not change at the same rates as did their luminosities.

A simple interpretation of the above test can be made in terms of the primary and secondary visual processes. The insertion of a neutral filter reduced the number of photons reaching the eye from each illuminant by the same factor. Hence, the information transmitted by the two illuminants (determined by the number of photons absorbed in the primary visual process) remained equal. The luminosity, on the other hand, is determined both by the number of photons absorbed and by the gain of the secondary process. If the secondary processes for the two illuminants are taken to be different and to provide different gains at low brightnesses, the higher luminosity of the blue illuminant can be accounted for.

For example, it is known from Hecht's work that low-light vision is provided by the system of rods as opposed to the cones. The rods must accordingly have a higher gain secondary process associated with them than do the cones. Further, the rods are sensitive to blue and green light but have very little response for red light.

4. *Seeing Noise*

It is natural to inquire about the magnitude of the gain process in the eye. If the performance of the eye is to be limited by the noise of the incoming photons, the gain must at least be sufficient to make this noise visible. A smaller gain would entail a loss of information. A larger gain, on the other hand, would add no more information but might contribute the annoyance of a prominent noisy background. The series of photographs in Figs. 1 and 3, particularly the first three in each series, show the kind of pictures we would see at low lights if the gain in our visual system were considerably higher than it is. If the gain were freely at our disposal, it is possible that some individuals might prefer such a gain setting. Most people, however, would set the gain carefully at the point where the noise was just visible. At least this would be true if we can take television viewing practices as a guide. Here, the gain is freely at the disposal of the viewer and one seldom finds it set so high that the background noise becomes distracting.

Whether it was through the influence of a kind of personal choice or a result of natural economy, the evolutionary processes appear to have set the gain at each brightness close to the threshold of noise visibility. At normal brightness levels, it would be difficult to persuade oneself that visual noise can be perceived. At low brightnesses, however, in the neighborhood of 10^{4} foot-lamberts the writer is confident from his own observations that visual noise is readily "seeable". This is particularly true for large uniformly-lighted areas. A dimly-lit wall takes on a fluctuating granular appearance reminiscent of a noisy television picture or a grainy motion picture screen. An important corollary to this observation is that the noise is absent in neighboring black areas. Whatever one may conclude about the fluctuations, at least they do not originate as independent local noise in this observer's visual system.

The writer knows of only one other published interpretation of the graininess of large dimly-lit areas in terms of visual noise. The terms used by de Vries[27a] to describe the granular appearance are quite similar to those used here. (De Vries also published one of the first attempts to account for visual performance at high lights in terms of photon noise. His quantum efficiencies, based on a signal-to-noise ratio of unity, are almost a hundred times smaller than the values shown in Table I.) The writer has also found from an informal canvass of his colleagues that most of them describe the appearance of dimly-lit scenes in terms consistent with a visual noise interpretation.

The advantage of large uniformly-lit areas for seeing noise is well known from experience with television and motion picture screens. In fact, a device used to obscure the noisiness of early motion picture films was to break the background screen up into a high contrast, checkerboard array of wallpaper patterns or objects. The discrimination of the eye for half tones is markedly deteriorated in the neighborhood of a sharp black-to-white transition.

5. *Eigenlicht*

One frequently finds the statement that a completely dark room does not appear as dark as one in which there are at least local patches of light. In fact, in utter darkness, the sensation of a grey light, appearing to originate within the eye (eigenlicht), is often reported. Another sensation in utter darkness is that of visual strain.

All of these observations are consistent with what one might expect from a high gain mechanism in the eye. In a partially-lit dark room, the magnitude of gain is set by the visible areas. The other areas then appear completely black. If the room is devoid of any visible light, there is nothing objective by which the eye can calibrate its gain mechanism. Under these conditions, one can readily believe that the gain is turned up to its maximum useful value, that is, until local system noise or disturbances are visible. This would account both for the appearance of eigenlicht and for the severe strain of trying to distinguish objective from subjective sources of light sensations. Indeed, knowing the tendency of observers to see regular patterns in an array of purely random noise, one can speculate that the source of some optical hallucinations may lie in the random character of the eigenlicht.

6. *Visibility of Noise in Television and Motion Pictures*

There is no doubt that the conditions under which we see noise in a television picture, or its counterpart graininess in a motion picture, are of considerable economic consequence. The size and brightness of picture screens, the grain size of photographic film, the intensity of studio lighting and the transmitter power of a broadcast station all hinge on the visibility of noise. The aim, of course, is not to see the noise.

The most succinct criterion for not seeing noise in a picture is that the noise originating in the outside picture be less than the noise of the photons entering our eye. It is often more convenient to deal with the parameter signal-to-noise ratio, that is, the ratio of average brightness to statistical fluctuations in brightness. In these terms, we ask that the signal-to-noise ratio of the television picture or motion picture be greater than the signal-to-noise ratio of our visual image.

Some immediate consequences of this criterion of seeing noise are familiar experiences to most people. Television pictures, because they are usually brighter than motion pictures, must have a better signal-to-noise ratio to avoid being considered noisy. Similarly, as the brightness of motion picture screens has been increased, finer grained (less noisy) films have had to be used. The converse experience is an interesting one. If one is presented with a noisy television picture, he can convert it into a "good", noise-free picture by the simple expedient of holding a neutral filter in front of his eyes[19a]. It is important to have the neutral filter covering the observer's eyes rather than just the television screen. If the neutral filter covers only the television screen, it is still true that the noise is "filtered" out, but then the observer concludes that the picture is poor because it is dark. The judgement "dark" is made by comparing it with surrounding objects. If, on the other hand, the neutral filter covers the observer's eyes, the brightnesses of both the television screen and the environs are reduced by the same factor. The television picture does not suffer by comparison with the environs. Further insofar as one's judgement of the absolute level of brightness is poor, the first order effect of the neutral filter is not that of reducing brightness but only of removing the noise.

The action of a neutral filter on the visibility of noise is especially efficient when one compares it with other methods of noise reduction. For example, large reductions in noise power, as read on a meter or as observed on an oscilloscope, can be made by reducing the bandwidth of the television system. The reduction in bandwidth, of course, cuts out both the fine detail in the picture as well as the fine-grained noise. Similar large reductions in noise power can be conveniently effected by slight defocusing of the scanning beam in the television receiver or by slight optical defocusing of the motion picture projection lens. While the total noise power may be reduced by a factor of ten, the noisiness of the picture remains substantially unchanged. The reason is that bandwidth reduction and optical defocusing selectively remove the noise from the high-frequency end of the spectrum. That is, both the fine-grained noise and the fine-grained picture detail are filtered out leaving still intact the noise associated with larger areas. But, in a well-balanced system, the eye sees noise in large areas as well as in small areas. Thus, cutting out the small-area noise and picture detail does not alter the annoyance of noise in the larger areas. The observer concludes, then, that in spite of the large reduction in total or integrated noise, the picture is still noisy.

In contrast to bandwidth reduction or optical defocusing, the use of a neutral filter reduces the visibility of noise uniformly for large as well as small areas. By Eq. (4), a reduction in brightness (B), reduces the half-tone discrimination of the eye equally for all values of elementary picture area. The neutral filter has, incidentally, one other effect in its favor. The apparent contrast of the picture is increased, because the gamma (in the photographic sense) of the eye is larger at lower scene brightnesses.

7. *Light Amplifiers*

The phrase "light amplifier" has a certain magic sound that has encouraged extravagant speculations of being able to see in substantial darkness. "Given a device that intensifies the light just before it enters our eyes, what is to prevent us from extending our vision indefinitely?" The physician who spends almost half an hour dark-adapting his eyes and then is only barely able to discern the tell-tale patterns on a fluoroscopic screen must surely wonder how much he could profit from such a device. It is here that a recognition of the quantum limitations to vision finds its most direct application. A light amplifier *can* provide a significant but not an unlimited gain in seeing.

The simplest estimate of the gain to be derived from a light amplifier comes from Table I. The quantum efficiencies shown in Table I for white light and for blue-green light range in the neighborhood of five percent. This means that the eye is already apprehending five percent of the total information incident on it. The most that a light amplifier, interposed at the eye, can do is to increase the five percent utilization of information to 100 percent. Sturm and Morgan[22], and Morton, Ruedy and Krieger[15] also concur in estimating the useful gain of a light amplifier to be about twenty times.

To realize a significant gain over the human eye, the photosensitive element of the light amplifier must have a correspondingly higher quantum efficiency than the eye. This is generally not true for the photo-emissive cathodes used in vacuum-type light amplifiers. Their quantum efficiencies for white light approach closely that of the eye. Light-sensitive elements making use of photoconductivity, on the other hand, can achieve quantum efficiencies close to 100 percent[29].

There are other conveniences in using a light amplifier that are not to be confused with the fundamental gain in information of a factor of twenty. A light amplifier allows the physician to dispense with the time for dark adaptation. A light amplifier can make use of lenses having a larger diameter and light gathering power than the eye lens. It is true that "night glasses" do the same for the eye directly. However, it is more convenient to attach these heavy optics to a light amplifier. The light amplifier also permits the observer to be at a remote location, possibly safer and more confortable.

Light amplifiers have a variety of forms. Electron image tubes[15] have received the most attention. More recently, several solid-state, flat-screen light amplifiers have been described[10, 17]. One must not overlook the fact that any photographic system is potentially a light amplifier. Insofar as the final viewed picture is brighter than the original, light amplification has taken place. This is not usual for orindary photography. However, one frequently finds television pictures displayed at ten or more times the brightness of the original scene. A common experience is that the waning minutes of a late fall football game often take on a brighter aspect in the picture presented by a television receiver than in the original.

V. Some Problems For The Future Research

The vast amount and the fruitful variety of research centered on the visual process needs no rehearsal here. It is perhaps sufficient to mention that in the last century contributions have come from biologists, chemists, physicists, bio-chemists, bio-physicists, zoologists and a variety of medical specialists. The proposals that follow are meant in no way to reflect on the significance of the body of knowledge already amassed or being acquired. What can, in all propriety, be suggested, is that a sense of proportion would surely redistribute some of the effort toward a better understanding of the role of quantum limitations to vision. Such an understanding will not of itself uncover the visual mechanism. It can, however, by its very independence of mechanism and by its severe restrictions on the economy of photons, help to weed out those proposed mechanisms that are too wasteful of the photon stream.

1. Quantum Efficiency

The quantum efficiency of the eye is a measure of the minimum fraction of the incident light that the eye must use (independent of mechanism) to enable it to see what it, in fact, sees. Because this fraction is close to unity, it becomes a powerful tool in discriminating against those visual mechanisms that are too profligate of light energy.

Consider, for example, three commonly quoted factors: a factor of 1/2 giving the fraction of incident light reaching the retina; a factor of 1/3 if there are three different types of receptors for effecting color vision; a factor of about 1/5 for the fraction of light absorbed by the light sensitive material in the retina. If these three factors are combined, the maximum quantum efficiency of the eye could not exceed three percent. But the middle column of Table I based simply on what the eye sees shows quantum efficiencies greater than three percent.

One may, indeed, take issue with the accuracy of the results listed in Table I, and that is precisely the argument intended here. A quantity of such fundamental importance as the quantum efficiency of the eye merits more than one set of investigations by one investigator. This statement does not overlook the several papers[1,3,9a,26,27b] reporting on the minimum number of quanta used by the eye at absolute threshold. Table I, if anything, deemphasizes measurements at absolute threshold and reports quantum efficiencies over a range of ten-million fold in light intensity.

The quantum efficiencies in Table I were computed by comparing what the eye sees, given a certain number of quanta, with what an ideal device would see with the same number of quanta. There are other more direct ways of measuring quantum efficiencies. These involve a simple side-by-side comparison of the human eye with other picture recording devices of known quantum efficiency. For example, let an observer and a television camera view the same test pattern side by side. The observer need then only compare what he sees of the test pattern with what he sees reproduced on the television monitor to decide whether his quantum efficiency is greater or less than that of the television camera. The great virtue of this method is that one is not dependent on a knowledge of the storage time of the eye or of the threshold signal-to-noise ratio. Since the same observer compares the original and reproduced patterns, the same storage time and threshold signal-to-noise ratios are effective and their influence on the comparison cancels out.

It is true that there are some uncertainties about the quantum efficiency of the television camera. For this reason the supporting evidence from other comparisons is desirable. The increased sensitivity of recent photographic films would make a comparison between an observer and a motion picture camera of special interest. Finally, the comparison of an observer and a light-spot scanner as described in reference[19b] has the virtue that the quantum efficiency of the photomultiplier pick-up can be accurately defined. What one would prefer in this arrangement is a scanner giving visible light in the range of 5000-5500 Å. Since present cathode-ray-tube scanners emit in the near ultraviolet, a mechanical scanner would have some advantage.

2. Threshold Signal-to-Noise Ratio

The significance of the threshold signal-to-noise ratio has already been described in an earlier section. It need only be mentioned that independent estimates by other observers would be helpful in arriving finally at a reliable figure. A quite extensive set of measurements was made by Tol et al[25]. They have concluded that the threshold signal-to-noise ratio lies between three and four as opposed to the value five proposed by the present writer. It is likely that the threshold signal-to-noise ratio depends on the angular field of view as well as the scene brightness. Little or nothing is known of these dependencies.

3. Storage Time of the Eye

There is reasonably good agreement that the physical storage time of the eye is close to 0.2 second and that it varies very little from extreme low lights to high lights. It is worth trying to confirm this value in other ways. There is an interesting method of making an independent check that to the writer's knowledge has not been carried out.

Consider a test pattern like that shown in Fig. 2 and photographed on a single frame of grainy film. That is, only part of the test pattern is detectably reproduced owing to the film noise. If, now, the test pattern is photographed on successive frames by a motion picture camera and projected as a normal motion picture, the observer should see more of the test pattern. The increased visibility comes from integrating out the noise of successive frames and is a measure of how many frames are so integrated or stored. Tol et al[25] present evidence that the physical storage time of the eye can be extended significantly by memory. An exaggerated example of integrating out the noise is the series of photographs in Fig. 3. Here, the first photograph in the series represents one field of a television picture. The improved reproductions in the later photographs of the series were obtained by letting the camera record or store an increasing number of frames by increasing its exposure time.

4. *Color Vision*

It is known that below a tenth of a foot-lambert one's ability to distinguish colors rapidly disappears. It would be interesting to know how much of a role fluctuations in the incoming photon stream play in this transition from color to monochrome vision. Modern electronic color television systems would be an excellent guide. Especially, those color-slide scanners in which the lignt transmitted by the color slide is picked up by three photomultiplier tubes[23] would allow one to observe how rapidly the color reproduction is obscured by photon noise at low illuminations.

The transition from color to monochrome vision at low lights may also have arisen from a "tactical decision" as a part of the evolutionary processes. It is true for most man-made picture recording systems that more light is wasted by reproducing in color than by reproducing in monochrome. If the same is true for the eye, it could easily have been more important for survival to transmit at low lights a moderately-well-defined monochrome picture than a poorly-defined color picture.

5. *Variable Gain Mechanism*

The arguments of the earlier sections have emphasized that the understanding of dark adaptation is likely to come not from the primary mechanism of light absorption in the retina but from the secondary reactions that are triggered off by the absorption of light. The absorption coefficient of the light-sensitive material is not likely to vary much from high lights to low lights. The magnitude of the triggered reactions must on the other hand undergo large changes. It is possible that observations reported on the bleaching of visual purple may alternatively be interpreted as bleaching of the triggered material.

6. *Optic Nerve Pulses*

Information is transmitted from the retina to the brain by a train of nerve pulses all having the same amplitude. The number of these pulses per second is a measure of the light intensity at the retina. But the measurements of Hartline[8] have shown that the rate of pulse transmission increases only slowly, possibly logarithmically, with increase in light intensity. A consequence of this relation is that at higher light intensities each nerve pulse represents a larger number of photons. Since the percentage fluctuations decrease as the average numbers of photons increase, the timing of each nerve pulse should become more precise. In the other extreme, at low lights, where the nerve pulses represent one or a few photons, the spacing of pulses should be quite random.

A careful examination of the trains of nerve pulses at various light levels should reflect the signal-to-noise ratio of the photon stream. At low lights, improvements in signal-to-noise ratio may be conveyed chiefly by an increase in the number of pulses per second. At high lights, improvements in signal-to-noise ratio may be conveyed chiefly by a greater regularity of spacing of the pulses. Measurements of the signal-to-noise ratio associated with the train of nerve pulses could yield directly the number of photons giving rise to these pulses. The electronic parallel is that a measurement of the signal-to-noise ratio of the output current of a photomultiplier gives directly the number of electrons per second leaving the photocathode or, what is the equivalent, the number of photons per second that are absorbed by the photocathode and that emit electrons.

7. *Visibility of High Energy Radiations*

There is good evidence that x-rays are observable by direct absorption in the retina. This is not particularly surprising for example, there are many materials known to become photoconducting or luminescent when exposed to optical radiation. In all these materials, the same effects can be brought about by a variety of electron-exciting radiations including x-rays, gamma rays, alpha rays, beta rays and other nuclear radiations. While optical radiations result in only one excited electron per absorbed photon, the high-energy radiations may excite hundreds or thousands of electrons for each high-energy photon or particle absorbed. Since the eye is known to respond at absolute threshold to only a few photons or electron excitations, it is surprising that no one has reported seeing any of the high-energy radiations directly. In particular, the frequency of cosmic rays is such that one would expect to see an occasional track traced out in the retina by a cosmic ray striking almost parallel to the retina. Is it possible that evolutionary processes have developed some ingenious mechanism for discriminating against cosmic radiation since no useful purpose would be served by detecting it?

VI. Vision And Evolution

In a very real sense one can be confident that evolutionary forces have attained close to an absolute goal in the visual process. The absolute goal is to perceive all of the information contained in the stream of photons incident on the eye. The eye approaches this goal in the range of wavelengths of 5000 to 5500 Å. Not only the human eye, but also the eyes of lower forms of animals have crowded close to this absolute limit.

It is true that many man-made devices have extended the range of human vision. These extensions include sensitivity to other spectral ranges (infrared and ultraviolet), longer storage times (photographic film), longer focal lengths (telescopes), shorter focal lengths (microscopes), shorter resolving times (photomultipliers) and larger light gathering power (Schmidt lens). It is also true that other animals like hawks have a finer resolving power than the human eye or, like lemurs, a higher-speed eye-lens. In all of these instances, it is not so much a question of improving on the performance of the human eye as it is of choosing another theater of operation. The parameters: storage time, spectral range and focal length define the field of application of the optical device. Once having made a selection of these parameters, the fundamental performance is measured by the ability of the optical device to make use of all incident photons. This the human eye does almost to perfection.

The particular choice of optical parameters for the human eye has been made for obvious evolutionary reasons. Its spectral response is peaked to match the sun's radiation in the daytime and shifts in twilight vision to match the blue light scattered from the sky after the sun has set. The storage time of the eye is closely matched to the speed of response or reaction time of the rest of the human system. The mechanical fineness of the rod-and-cone structure of the retina is internally self-consistent with the diffraction limits set by the diameter of the eye lens. Perhaps one can decipher in the particular choice of rod-and-cone size something of the primitive life habits of man. The hawk makes good use of an even finer structure in tracking down its prey from great heights. In fact, a most fascinating account of the great variety of adaptations of the visual system to living habits is given by Detwyler[7].

It would be interesting to know more about the time scale associated with these evolutionary changes. Suppose the use of fire as a night illuminant had come at a much earlier date. Would there be a nocturnal red-shift in our eye response as there is now a twilight blue-shift?

Whatever the time scale of evolution, it remains true that no single man-made device yet matches the eye for compactness, versatility, long life and high performance throughout seven decades of light intensity.

Albert Rose

Albert Rose

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