ENERGY AT THE THRESHOLD OF VISION

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LANGLEY[1] in 1889, after inventing the bolometer for measuring the energy of the solar spectrum, made the first determination of the minimum energy necessary to produce a visual effect. He found this to be 3×10^{-9} ergs for light of 550 mμ. Since then a dozen efforts have been made to redetermine this energy. Unfortunately, many of these attempts contained serious errors which invalidate them; indeed most of them involved no direct energy measurements, but relied on previously measured energy distributions in standard sources. Only three appear free from obvious error; these yield 0.66×10^{-10} ergs (Chariton and Lea[2]), 1.3–2.6 $\times 10^{-10}$ergs (von Kries and Eyster[3]), and 1.6–3.5 $\times 10^{-10}$ ergs (Barnes and Czerny[4]). Only the last values represent actual energy determinations by the authors.

These amounts lie so near the energy of a single quantum of light (3.84×10^{-12} ergs for 510 mμ) as to suggest that a small number of light quanta is necessary for a visual effect. Since the photodecomposition of visual purple in solution[5] probably has a quantum efficiency of 1, this would indicate that a small number of molecules is concerned in initiating a biological act, in particular a biological act involving the highest nerve centers. Because of these implications, we undertook last spring to make the measurements again, but under the best physical and physiological conditions so as to render the data reasonably definitive.

The physiological conditions which yield maximum retinal sensibility have been well explored in recent years. They involve dark adaptation, peripheral vision, small test fields, short exposures and selected portions of the spectrum. Our measurements were therefore made only after a 30-minute stay in the dark, with a circular retinal area subtending 10 minutes of arc situated 20° temporally on the horizontal axis of the retina, using homogeneous spectral light of wave-length 510 mμ presented as a flash 1/1000 second long, all of which are known to represent the best conditions.

The physical arrangements involved a ribbon filament lamp run on current from storage cells controlled with a potentiometer, a calibrated filter for coarse intensity variation and a calibrated wedge for fine intensity control, a double monochromator, a precision shutter, a fixed pupil, a diaphragm for test-field size and a fixation point. The energy at the pupil was measured on two occasions several months apart with excellent agreement using a Hilger linear thermopile and a Paschen galvanometer after due calibration with a standard carbon filament lamp.

The results have been consistent over several months. For a half dozen observers in the laboratory the minimum energy necessary for vision ranges between 2.2 and 5.7×10^{-10} ergs at the cornea. These small energies represent between 58 and 148 quanta of blue-green light.

These are the values at the cornea. Before one can know how many quanta are actually absorbed by the retina, at least three corrections must be applied. The first is reflection from the cornea; this is about 4 per cent., and is of only slight importance. The second involves loss by the ocular media between the outer surface of the cornea and the retina. Contrary to common opinion this loss is large. From the measurements of Ludvigh and McCarthy[6] it appears that at 510 mμ the ocular media transmit almost exactly 50 per cent. of the light entering the cornea of a young person, and less for an older one.

The next correction is more difficult to evaluate with precision and involves the percentage of the energy absorbed by the visual purple in the retinal rods. Koenig's[7] measurement of the visual purple in a human eye yields an absorption of only 4 per cent. of light of 510 mμ on the assumption that visual purple is evenly spread over the retina. Though astonishingly small, this value is like the 4 per cent. and 13 per cent. recently found by Wald[8] for the absorption of the rabbit and rat retinas, respectively. These figures are probably too low, because visual purple is not evenly distributed over the retina; it is missing from the fovea, and even in the periphery the density of rods varies obviously.

We have estimated the concentration of visual purple in the retina in a completely independent manner by comparing the percentage absorption spectrum of different concentrations of visual purple with the dim (rod) vision luminosity curve of the spectrum[9]

* Fellow of the Belgian American Educational Foundation.

1 S. P. Langley, *Phil. Mag.* (5), 27: 1, 1889.

2 J. Chariton and C. A. Lea, *Proc. Roy. Soc.* A, 122: 304, 1929.

3 J. v. Kries and J. A. E. Eyster, *Z. Sinnesphysiol.*, 41: 394, 1907.

4 R. B. Barnes and M. Czerny, *Z. f. Phys.*, 79: 436, 1932.

5 H. J. A. Dartnall, C. F. Goodeve and R. J. Lythgoe, *Proc. Roy. Soc.* A, 164: 216, 1938.

6 E. Ludvigh and E. F. McCarthy, *Arch. Ophth.*, 20: 37, 1938.

7 A. Koenig, *Sitzungsber. Akad. Wiss. Berlin*, 577, 1894.

8 G. Wald, *J. Gen. Physiol.*, 21: 795, 1938.

9 S. Hecht and R. E. Williams, *J. Gen. Physiol.*, 5: 1, 1922.

corrected for quantum effectiveness[10] and ocular media absorption.[6] The comparison rests on the fact that the shape and width of the percentage absorption spectrum of a substance varies with its concentration, and that the corrected luminosity curve must represent the percentage absorption curve of a particular concentration of visual purple in the retina. Using the average of the almost identical measurements of frog's visual purple made by Chase and Haig,[11] by Lythgoe[12] and by Wald,[8] we find that visual purple absorption and retinal luminosity coincide for such a concentration of visual purple that at 510 mμ the absorption is between 10 and 20 per cent. An absorption above 20 per cent. is definitely excluded, and one may therefore take this as an upper limit; it is still of the same order of magnitude as the values found by Koenig and by Wald.

If we apply these three corrections to the minimum perceptible energy, the range of 58 to 148 quanta at the cornea becomes as an upper limit 5 to 14 quanta absorbed by the retina. It is quite probable that the higher value, which is given by the oldest (48 years) observer, is the result of a much higher absorption by his lens, and that the range is really much smaller than would appear.

The area on the retina in which these few quanta are absorbed contains about 500 sensitive receptor cells. The likelihood, therefore, that 2 quanta will be taken up by a single rod cell is only about 4 per cent. We can then conclude that in order to see, it is necessary for only 1 quantum of light to be absorbed by each of 5 to 14 retinal rods. Taking a quantum efficiency of 1 for visual purple, this means that one molecule of visual purple needs to be changed in each of 5 to 14 rods in order to produce a visual effect.

This is indeed a small number of chemical events; but by virtue of its very smallness one may test its reality in an entirely independent manner.

The energy calibration of the light gives merely the *average* number of quanta per flash. Each flash will not always deliver this average number; sometimes the flash will yield fewer, sometimes more quanta. Since each quantum absorption in the retina is a discrete, independent and random event, the actual number of such retinal events which any given flash provides will vary according to a Poisson probability distribution.

The virtue of the Poisson distribution is that its properties depend only on the value of the average number. Assume for the moment that for us to see a flash of light, the retina must absorb n quanta; obviously we shall also see it if the retina absorbs more than n quanta. From the Poisson distributions one can then compute the probability that n or more quanta will be delivered to the retina in a given flash when the average number of quanta delivered by that flash is known. These computed values are shown in Fig. 1.

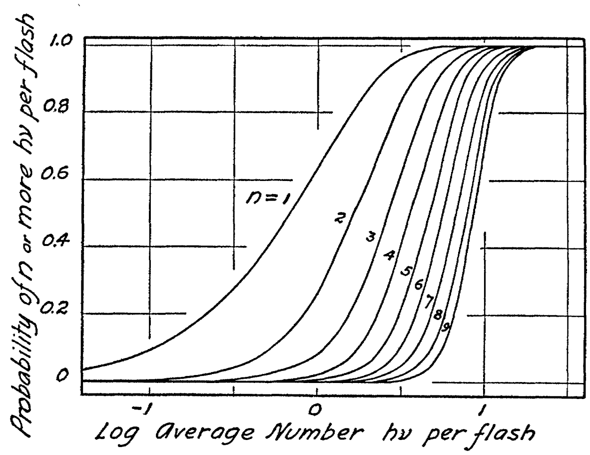

FIG. 1. Relation between the average number of quanta (hν) per flash of light and the frequency with which the flash will contain n or more quanta, computed in terms of the Poisson probability distribution.

The significant feature of Fig. 1 is that the shape of the probability distribution is fixed and different for every value of n; the curve becomes steeper as n increases. It therefore follows that if the probability distribution could be determined by experiment, its *shape* would automatically reveal the value of n corresponding to it. What is equally important is that in the experimental procedure for determining the probability distribution, the absolute values of the average number of quanta per flash are not necessary for comparison with the distributions in Fig. 1. Because of the logarithmic plot, the relative values of the average number are adequate to determine n.

Experimentally one should see a flash whenever it yields n or more quanta of light to the retina. On frequent repetition of a flash of given average quantum content, the frequency with which the flash is seen will depend on the probability with which it yields n or more quanta to the retina. When this frequency is determined for each of several intensities, a frequency distribution is secured whose shape, when plotted against the logarithm of the average energy content, should correspond to one of the probability distributions in Fig. 1 and thus show what the value of n has been.

We have made determinations of this kind. Unknown to the observer, the experimenter varies the intensity of the light. The observer elicits the flash,

[10] H. J. A. Dartnall and C. F. Goodeve, *Nature*, 139: 409, 1937.

[11] A. M. Chase and C. Haig, *J. Gen. Physiol.*, 21, 411, 1938.

[12] R. J. Lythgoe, *J. Physiol.*, 89: 331, 1937.

and reports whether he saw it or not. This is done for six intensities which are presented in a deliberately random sequence, each for 50 times. A series takes about one and one half hours.

The data for us three are given in Fig. 2. Com-

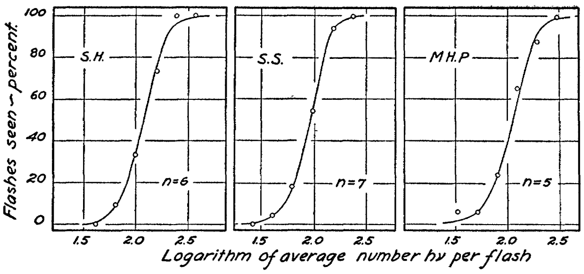

FIG. 2. Relation between the average number of quanta delivered by a flash of light at the cornea and the frequency with which the observer sees the flash. The curves are the computed Poisson distributions taken from Fig. 1. Each point represents 50 observations.

parison with the curves in Fig. 1 shows that the measurements are fitted best by Poisson distributions in which n is 5, 6 and 7 quanta per flash. Smaller and larger values of n are definitely excluded. Thus the number of critical physical events necessary in the retina in order to produce a visual effect lies between 5 and 7. This is in excellent agreement with the results determined by the straightforward physical measurements. We must therefore consider them as the actual number of quanta absorbed by the retina for the initiation of a visual act.

In applying the Poisson probability distribution, we have assumed that a constant number of quanta is necessary in order to see a flash of light. In view of the supposed variability of an organism from moment to moment, we have considered the consequences of assuming this number n to vary. An example will make this clear. Suppose that the biological variation lies between 5 and 9 quanta per visual act, and that it has an ordinary probability distribution. The curves in Fig. 1, weighted in such a way and averaged, yield a curve which is identical with the ones in Fig. 1 for $n = 5$ or 6. Thus when biological variation is imposed upon the physical variation there occurs no change in the essential characteristics of the physical distribution and only a small decrease in the value of n. When, as in Fig. 2, the measurements yield n values of 5, 6 or 7, these represent lower limiting values for the physical number of quanta.

In considering the nature of fluctuations in response given by an organism, it has always been assumed that the stimulus is constant and that the organism is variable. The present evaluation of our measurements shows however that at the threshold, where only a few quanta of energy are involved, it is the stimulus which is variable, and that the nature of its variability determines the variation encountered between response and stimulus.

SCIENTIFIC EVENTS

THE COLLEGE OF SURGEONS, LONDON

THE following account of the damage by air raids to the Royal College of Surgeons, London, is given in the London *Times* for May 21:

Irreparable losses, including most of the Hunterian Collection, were suffered by the Royal College of Surgeons in Lincoln's Inn Fields, whence the society moved from their eighteenth-century hall in the Old Bailey. Incendiary bombs first fell on the roof of the building, but just as a watcher was giving the alarm a high-explosive missile struck No. 5 room of the museum. Only two persons on the premises were slightly injured. In spite of great damage to the interior the fabric of the college is more or less intact, but the museum buildings have suffered severely, and fire also gutted an adjoining building containing solicitors' offices and the College of Estate Management.

The most valuable specimens in Dr. John Hunter's collection, purchased by the Government for £15,000 two years after his death in 1793 and presented to the college, are probably safe under the débris, having previously been moved into reinforced sections of the subbasement. The collection of portraits and pictures, including Reynolds's portrait of Hunter, are safe in the country, and the part of the records still at the college had been stored in strong rooms that withstood the blast and flames.

But thousands of museum pieces are gone, among them the skeletons of kangaroos brought by Captain Cook from Australia, and the comparative osteology collection of 4,000 specimens acknowledged to be the finest in the world. Much of the material antedated British Museum specimens, and, as Professor Cave, the assistant conservator, said yesterday, the greater part of the wonderful work of Sir Richard Owen and Dr. William Flower has been undone.

All Dr. Hunter's eighteenth-century furniture, which was in the president's room, was destroyed. The original surgical instruments used by Lister were recovered, but many others were lost. Though the oldest mummy in the world, that of Ra Nefer, an Egyptian nobleman who died, it is said, about 2900 B.C., was destroyed, many mummies of popular interest have been salved.

By a grim coincidence the invaluable Army Medical War Collection, containing plaster casts of every type of wound, was also destroyed, as were the council room and lecture theater.