ENERGY, QUANTA, AND VISION*

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I

Threshold Energies for Vision

The minimum energy required to produce a visual effect achieves its significance by virtue of the quantum nature of light. Like all radiation, light is emitted and absorbed in discrete units or quanta, whose energy content is equal to its frequency ν multiplied by Planck's constant h. At the threshold of vision these quanta are used for the photodecomposition of visual purple, and in conformity with Einstein's equivalence law each absorbed quantum transforms one molecule of visual purple (Dartnall, Goodeve, and Lythgoe, 1938). Since even the earliest measurements show that only a small number of quanta is required for a threshold stimulus, it follows that only a small number of primary molecular transformations is enough to supply the initial impetus for a visual act. The precise number of these molecular changes becomes of obvious importance in understanding the visual receptor process, and it is this which has led us to the present investigation.

The first measurements of the energy at the visual threshold were made by Langley (1889) with the bolometer he invented for such purposes (Langley, 1881). He found the energy to be 3×10^{-9} ergs for light of 550 mμ. Langley worked before the physiology of vision was understood, so that he used the wrong light and took none of the precautions now known to be necessary; even so, his results are too high only by a factor of 10.

In the fifty years since Langley there have been eleven efforts to redetermine the minimum energy for vision. We have carefully studied all these accounts and have done our best to evaluate the measurements. Unfortunately, many of them contain serious errors which invalidate them. Most of them involved no direct energy determinations; instead, the investigators relied on previously measured energy distributions in standard sources and made elaborate computations from them. Only a few can be considered as reliable.

After Langley, the earliest paper is by Grijns and Noyons (1905). Their data differ widely from all other measurements and cannot be accepted even

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uniformly illuminated field is varied in large steps by the neutral filters F, and in a gradual way by the neutral wedge and balancer W. The size of the field is controlled by the diaphragms D. Its exposure is fixed by the shutter S, and is initiated by the subject.

For the record it is necessary to describe the apparatus and calibrations in detail. The double monochromator is made of two individual constant deviation mono-chromators, M_1 and M_2, which are arranged for zero dispersion by means of the reversing prism RP. In this way, all the light passes through an equal thickness of glass, and assures a uniform brightness of the field lens FL. The exit slit of M_1 has been removed, and the entrance slit of M_2 serves as the middle slit of the combined double monochromator. The entrance and exit slits of the combination are kept at 1.2 mm., which corresponds to a band width of 10 mμ centered at 510 mμ. The middle slit, before which the shutter is placed, is kept at 0.1 mm.
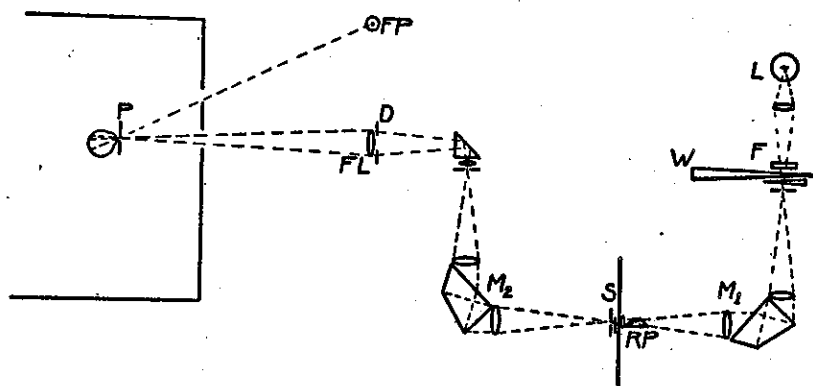

FIG. 1. Optical system for measuring minimum energies necessary for vision. The eye at the pupil P fixates the red point FP and observes the test field formed by the lens FL and the diaphragm D. The light for this field comes from the lamp L through the neutral filter F and wedge W, through the double monochromator M_1M_2 and is controlled by the shutter S.

The field lens FL magnifies the exit slit by a factor of 2, and thus yields an image of it 2.4 mm. wide and over 10 mm. high at the pupil P. The image is sufficient to cover uniformly not only the pupil P, but also the linear thermopile used for the energy calibration. The pupil mount at P and the field lens FL are connected by a carefully diaphragmed and blackened tube. The 2 mm. circular pupil P used for the visual measurements can be replaced by a slit 2 mm. wide and 10 mm. high behind which is the receiving surface of the thermopile for energy measurements.

S is a precision shutter made of two parts. One part is a thin circular aluminum disc with a small sector of 10.8° removed and properly balanced. It is run at 1800 R.P.M. by means of a synchronous motor, and therefore permits light to pass through the middle slit for 1/1000 second during each revolution. The other part is a polar relay shutter, which, by means of a phasing commutator on the shaft of the synchro-nous motor, is opened for only one passage of the rotating disc aperture whenever the subject releases a push button.

The essentials of the shutter are shown in diagrammatic detail in Fig. 2. On the same shaft with the disc there is mounted a commutator having a "live" sector, which together with the brush occupies somewhat less than 90°. Two brushes are arranged on this commutator 90° apart, and are so phased with the A.C. line voltage that one of these brushes receives only a positive impulse while the other receives only a negative impulse. These impulses control a polar relay PR_2, which then actuates a pair of single pole, double throw micro switches, MS_1 and MS_2. These are arranged with their springs in opposition in such a manner that the switches are in equilibrium
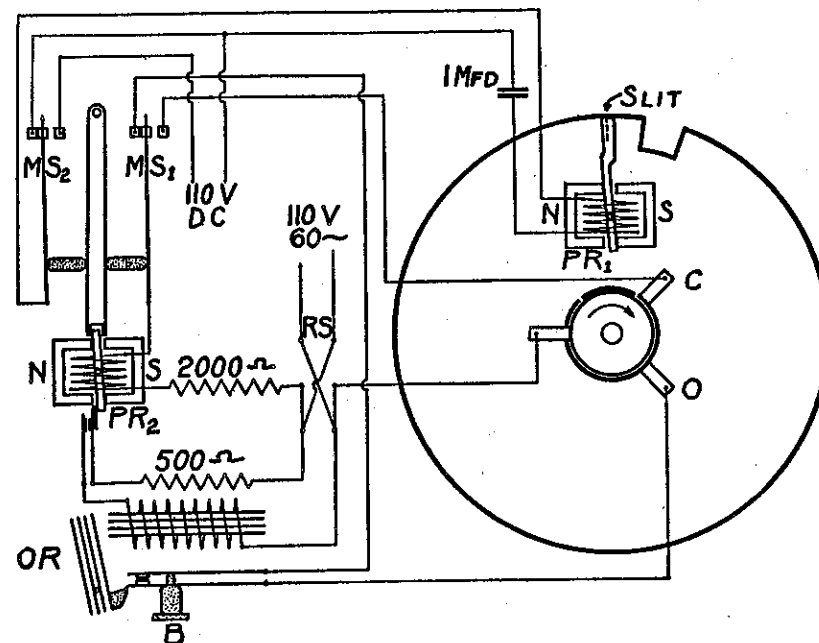

FIG. 2. Shutter for obtaining a single exposure of 1/1000 second. The details are described in the text.

at either of their two positions, and require but a small force and movement to kick them over to their other positions. Micro switch MS_1 is in series with the winding of PR_2, and in one position connects with the opening brush O and in the other position with closing brush C. The other micro switch, MS_2, charges and discharges a 1 μfd. condenser from the 110 volt, D.C. line through the polar relay PR_1. These impulses in and out of the condenser actuate PR_1 whose armature movement then uncovers and covers the middle slit.

The operation is seen by following a single cycle of operation of circuit and shutter. Fig. 2 shows the apparatus during its rest or closed period. The 110 volt, 60 cycle power enters through a pole-reversing switch, RS, to the neutral brush on the com-mutator. The impulse through the closing brush C is blocked, since it enters an open

IV

Visual Measurements

From the subject's point of view, an experiment involves the report of whether or not he has seen a flash of light after he has opened the shutter for an exposure. Fixation of the red point need not be continuous, a circumstance which avoids undue fatigue. The observer is told by the operator that conditions are set and that he should try a flash when he is ready. He fixates

TABLE II

Minimum Energy for Vision

Each datum is the result of many measurements during a single experimental period, and is the energy which can be seen with 60 per cent frequency. $\lambda = 510 \, m\mu$; $h\nu = 3.84 \times 10^{-12}$ ergs.

Observer	Energy	No. of quanta	Observer	Energy	No. of quanta
	ergs $\times 10^{10}$			*ergs $\times 10^{10}$*	
S. H.	4.83	126	C. D. H.	2.50	65
	5.18	135		2.92	76
	4.11	107		2.23	58
	3.34	87		2.23	58
	3.03	79			
	4.72	123	M. S.	3.31	81
	5.68	148		4.30	112
S. S.	3.03	79	S. R. F.	4.61	120
	2.07	54			
	2.15	56	A. F. B.	3.19	83
	2.38	62			
	3.69	96	M. H. P.	3.03	79
	3.80	99		3.19	83
	3.99	104		5.30	138

the red point, and at the moment which he considers propitious, he exposes the light to his eye. The operator changes the position of the wedge, or removes or introduces a filter until he is satisfied with the precision of the measurements.

In the early measurements we considered that the threshold had been reached when the observer saw a flash of light at a given intensity six times out of ten presentations. Later the measurements were made somewhat more elaborately. Each of a series of intensities was presented many times and the frequency of seeing the flash was determined for each. From the resulting plot of frequency against intensity we chose the threshold as that amount of light which could be seen with a frequency of 60 per cent.

During 1940 and 1941 we measured the threshold for seven subjects. With four we made several determinations each, extending over a year and a half; one subject we measured on two occasions 3 months apart; and two we measured only once. For all these observers the minimum energy necessary for vision ranges between 2.1 and 5.7 $\times 10^{-10}$ ergs at the cornea. These small energies represent between 54 and 148 quanta of blue-green light. The results for the individual subjects are in Table II, and are given as energy and as the number of quanta required.

It is to be noticed that these values are of the same order of magnitude as those of von Kries and Eyster, and of Barnes and Czerny, but almost twice as large. Because of the fairly wide ranges, these previous measurements and our own overlap to some extent, and it is conceivable, though not probable, that their observers may actually have needed somewhat smaller energies than ours. Chariton and Lea's results, however, are much too small. Actually their value of 17 $h\nu$ is an extrapolation to zero frequency of seeing; if we take as threshold a 60 per cent frequency, their data come more nearly to 25 $h\nu$. This is still too small a value, and is probably in error, as will be apparent in later sections of our paper.

V

Reflections and Absorptions

The values in Table II, as well as those of previous investigators, are the energies incident at the cornea. Nevertheless the tacit supposition has generally been made that they represent the actual energies necessary to initiate a visual act. It is important to recognize that this assumption is incorrect. Before one can know how many quanta are required to start the visual process, one must apply at least three corrections to the measurements.

The first is reflection from the cornea. This is about 4 per cent and is obviously of not much importance. The second involves loss by the ocular media between the outer surface of the cornea and the retina. It has been common opinion that this loss is small. However, the measurements of Roggenbau and Wetthauer (1927) on cattle eyes, as well as the recent measurements of Ludvigh and McCarthy (1938) on human eyes, have shown that this loss is large. From the values of Ludvigh and McCarthy it appears that at 510 $m\mu$ the ocular media transmit almost exactly 50 per cent of the light entering the cornea of a young person, and less of an older one.

The next correction is much more difficult to evaluate with precision and involves the percentage of the energy absorbed by the retinal elements themselves. Since visual purple is the photosensitive substance concerned in this particular act, light which is not absorbed by it is visually useless. One cannot assume that visual purple absorbs all the light incident on the retinal cells. The fraction which it does absorb must be found by experiment.

Koenig (1894) determined the absorption of the total amount of visual

upper curve represents 20 per cent maximal absorption, while the lower curve is 5 per cent maximal absorption.

TABLE III

Absorption Spectrum of Visual Purple

Average of data from Chase and Haig (1938), Wald (1938 b), and Lythgoe (1937).

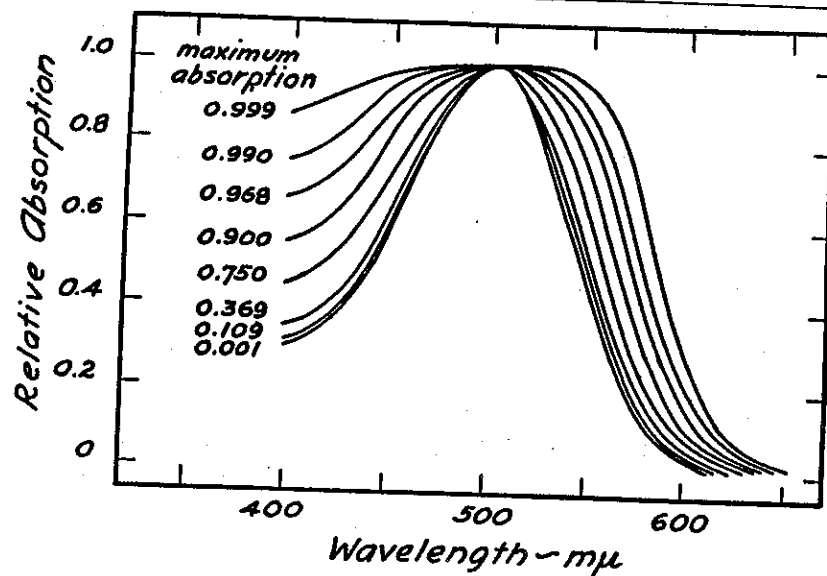| $\lambda - m\mu$	Density	$\lambda - m\mu$	Density	$\lambda - m\mu$	Density
400	0.306	480	0.900	560	0.321
410	0.317	490	0.967	570	0.207
420	0.353	500	1.000	580	0.131
430	0.408	510	0.973	590	0.0805
440	0.485	520	0.900	600	0.0473
450	0.581	530	0.780	610	0.0269
460	0.691	540	0.628	620	0.0150
470	0.811	550	0.465		

FIG. 4. Percentage absorption spectra of various concentrations of visual purple. For convenience in comparing the shapes of the curves, their maxima have all been equated to 1 and superimposed. The actual fraction absorbed at the maximum is shown for each curve. It is apparent that with increasing concentration the absorption curve steadily increases in width.

For comparing the luminosity and absorption data, it is well to confine our attention mostly to the long wave half of the luminosity curve because of the larger number of points involved. From the comparison it is apparent that the 5 per cent maximum absorption curve describes the points quite well, but

TABLE IV

Rod Luminosity Distribution in Spectrum

The original energy luminosity data of Hecht and Williams (1922) in column 2, when divided by the corresponding wavelengths in column 1, yield the quantum luminosity values in column 3 after being multiplied by a factor so that the maximum at 511 $m\mu$ equals 1. When these values in column 3 are divided by the ocular media transmission data in column 4 from Ludvigh and McCarthy (1938), they yield the spectral luminosity distribution at the retina given in column 5 after multiplication by a factor so that the maximum at 502 $m\mu$ is 1.

| $\lambda - m\mu$	Energy luminosity at cornea	Quantum luminosity at cornea	Ocular transmission	Quantum luminosity at retina
412	0.0632	0.0779	0.116	0.336
455	0.399	0.447	0.410	0.545
486	0.834	0.874	0.472	0.926
496	0.939	0.964	0.490	0.984
507	0.993	0.998	0.506	0.986
518	0.973	0.957	0.519	0.921
529	0.911	0.877	0.540	0.812
540	0.788	0.743	0.559	0.665
550	0.556	0.515	0.566	0.455
582	0.178	0.155	0.596	0.131
613	0.0272	0.0226	0.625	0.0181
666	0.00181	0.00139	0.672	0.00104
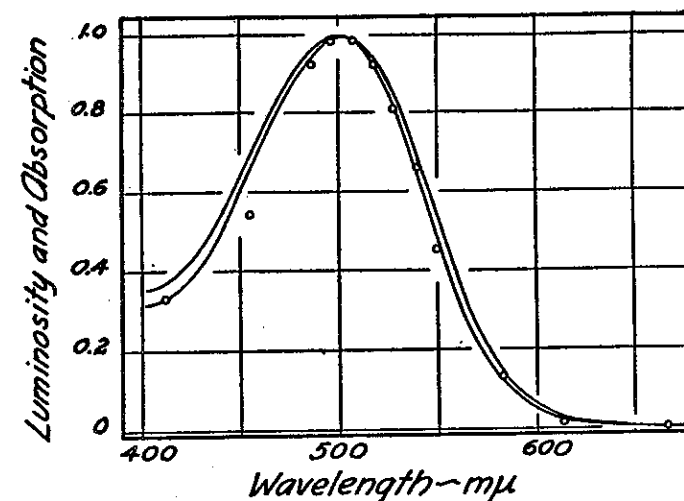
FIG. 5. Comparison of scoptopic luminosity at the retina with visual purple absorption. The points are the data of Hecht and Williams corrected for quantum effectiveness and ocular media transmission. The curves are the percentage absorption spectra of visual purple; the upper curve represents 20 per cent maximal absorption, and the lower one 5 per cent maximal absorption. All curves have been made equal to 1 at the maximum, 500 $m\mu$, for ease in comparison.

steeper as n increases. It follows from this that if the probability distribution could be determined by experiment, its shape would automatically reveal the value of n corresponding to it.

Another and equally important feature of Fig. 6 is that the relationship is expressed in terms of the logarithm of the average number of quanta per flash. Therefore, for comparison with the distributions in Fig. 6, the experiments need not employ the absolute values of the average number of quanta delivered per flash, but merely their relative values.

The experiments may then be made quite simply. On many repetitions of a flash of given average energy 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 measured for each of several intensities, a 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. 6, and should thus show what the value of n has been.

IX

Frequency of Seeing

We have made determinations of this kind. The experimenter varies the intensity of the light by placing the wedge in specific positions unknown to the observer. The observer then elicits the flash whenever he is ready, and merely reports whether he has seen it or not. The intensities are presented in a deliberately random sequence, each for a specific number of times, usually 50. The procedure is simplified for the operator by a series of accurately made stops against which the wedge may be rapidly set in predetermined positions. A complete series in which six intensities are used requires about $1\frac{1}{2}$ hours of continuous experimentation composed of two or three periods of intensive work.

The comfort of the observer is of great importance and this must be at a maximum. It is equally important that fixation should not be rigidly continuous because this is fatiguing. Above all, the observer must be on guard to record any subjective feelings of fatigue the moment they become apparent. The experiment is much facilitated by the fact that the observer controls the occurrence of the flash, and can set it off only when he is thoroughly fixated and ready for an observation.

The data for the three observers who engaged in this experiment are given in Table V. One experiment for each observer is plotted in Fig. 7. The points in the figure record the percentage frequency with which a flash of light is seen for flashes of average quantum content shown in the abscissas. Comparison with the curves in Fig. 6 shows that the measurements are best fitted by Poisson distributions in which n is 5, 6, and 7 quanta per flash. For the two other

experiments in Table IV, n is 7 and 8. No special statistical methods are necessary to determine which curve fits the data, since smaller and larger values of n are easily excluded by the simplest visual comparison.

TABLE V

Energy and Frequency of Seeing

Relation between the average number of quanta per flash at the cornea and the frequency with which the flash is seen. Each frequency represents 50 flashes, except for S. H. for whom there were 35 and 40 for the first and second series respectively.

| S. H.		S. H.		S. S.		S. S.		M. H. P.	
No. of quanta	Frequency	No. of quanta	Frequency	No. of quanta	Frequency	No. of quanta	Frequency	No. of quanta	Frequency
	per cent		per cent		per cent		per cent		per cent
46.9	0.0	37.1	0.0	24.1	0.0	23.5	0.0	37.6	6.0
73.1	9.4	58.5	7.5	37.6	4.0	37.1	0.0	58.6	6.0
113.8	33.3	92.9	40.0	58.6	18.0	58.5	12.0	91.0	24.0
177.4	73.5	148.6	80.0	91.0	54.0	92.9	44.0	141.9	66.0
276.1	100.0	239.3	97.5	141.9	94.0	148.6	94.0	221.3	88.0
421.7	100.0	386.4	100.0	221.3	100.0	239.3	100.0	342.8	100.0
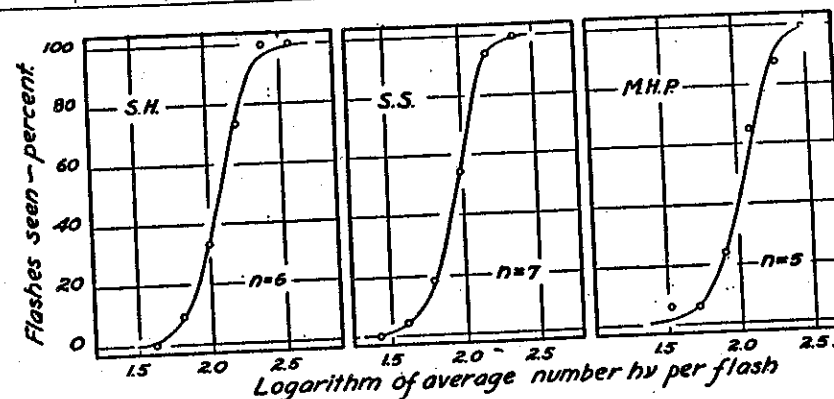
Fig. 7. Relation between the average energy content of a flash of light (in number of $h\nu$) and the frequency with which it is seen by three observers. Each point represents 50 flashes, except for S.H. where the number is 35. The curves are the Poisson distributions of Fig. 6 for n values of 5, 6, and 7.

From these measurements it is apparent that the number of critical events in the retina required to produce a visual effect lies between 5 and 8. These values are in such good agreement with the results determined by the straightforward physical measurements already described that we must consider them as the actual number of quanta absorbed by the retina.

subject to a similar physical variation as at the absolute threshold itself. Only experiment can decide this.

The fact that for the absolute visual threshold the number of quanta is small makes one realize the limitation set on vision by the quantum structure of light. Obviously the amount of energy required to stimulate any eye must be large enough to supply at least one quantum to the photosensitive material. No eye need be so sensitive as this. But it is a tribute to the excellence of natural selection that our own eye comes so remarkably close to the lowest limit.

SUMMARY

1. Direct measurements of the minimum energy required for threshold vision under optimal physiological conditions yield values between 2.1 and 5.7 $\times$ 10^{-10} ergs at the cornea, which correspond to between 54 and 148 quanta of blue-green light.

2. These values are at the cornea. To yield physiologically significant data they must be corrected for corneal reflection, which is 4 per cent; for ocular media absorption, which is almost precisely 50 per cent; and for retinal transmission, which is at least 80 per cent. Retinal transmission is derived from previous direct measurements and from new comparisons between the percentage absorption spectrum of visual purple with the dim-vision luminosity function. With these three corrections, the range of 54 to 148 quanta at the cornea becomes as an upper limit 5 to 14 quanta actually absorbed by the retinal rods.

3. This small number of quanta, in comparison with the large number of rods (500) involved, precludes any significant two quantum absorptions per rod, and means that in order to produce a visual effect, one quantum must be absorbed by each of 5 to 14 rods in the retina.

4. Because this number of individual events is so small, it may be derived from an independent statistical study of the relation between the intensity of a light flash and the frequency with which it is seen. Such experiments give values of 5 to 8 for the number of critical events involved at the threshold of vision. Biological variation does not alter these numbers essentially, and the agreement between the values measured directly and those derived from statistical considerations is therefore significant.

5. The results clarify the nature of the fluctuations shown by an organism in response to a stimulus. The general assumption has been that the stimulus is constant and the organism variable. The present considerations show, however, that at the threshold it is the stimulus which is variable, and that the properties of its variation determine the fluctuations found between response and stimulus.

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