THE QUANTIC AND STATISTICAL BASES OF VISUAL EXCITATION

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At the present time we are still very far from having an entirely satisfactory theory of the mechanism of visual excitation.

In order to study this mechanism objectively we must take threshold excitation as the starting point, because it is there that the conditions are the simplest. Indeed, several authors have been led to formulate empirical laws, but none of these laws could provide a valid interpretation of the facts over the whole range of brightness. On the other hand, with none of the different theories is it possible to compute quantitatively the course of the phenomena investigated, unless one makes use of one or several parameters arbitrarily chosen so as to make the theory fit the experiments.

Contrary to the theories hitherto proposed, it seems obvious that in vision several mechanisms are involved and that they come into play one after another as brightness increases. In the present paper we shall put forward a theory which attempts to give a quantitative explanation of the liminal phenomena of vision without involving any arbitrary parameter.

This theory provides a basis for the further analysis of many other problems concerning supraliminal levels, especially those of brightness discrimination and visual acuity.

Absolute Threshold

We are now well aware that the photochemical theory of vision can at most explain the facts at the average levels of brightness only. The outstanding work of Hecht, Shlaer, and Pirenne seems to deny the possibility of explaining the mechanism of visual excitation by the mass action law. Indeed, according to these authors, 5 to 7 quanta, absorbed by receptor cells situated in a peripheral retinal area, subtending a visual angle of 10°, are the upper limit of the number of quanta necessary for producing a visual sensation, 60 out of 100 times. The number of rods contained in the above area (region IV, near periphery) is about 500, and the probability that 2 or more quanta are absorbed in the same rod is so slight that we may conclude that when the excitation is liminal, only one molecule of retinal purple is decomposed in each rod absorbing light. Now the photochemical theory claims that the level of sensation is conditioned by the degree of concentration of a certain substance produced by the decomposition of the visual purple; since the existence of absolute thresh-
old is a fact that cannot be denied, this threshold must correspond to a certain degree of concentration of that substance (liminal concentration). But the decomposition of a single molecule of visual purple in each rod absorbing light cannot provide more than a single molecule of efficient substance, perhaps even no more than a single atom or a single electron, for we know nothing about this entirely hypothetical substance. The only thing we are sure of is that, if it does exist, its molecular weight must be very slight in comparison with that of visual purple, for the molecular weights of the three purples, the visual, the yellow, and the white, have been found to be the same. It is therefore obvious that the mass action law—which is essentially a statistical law—cannot come into play at the threshold level. This law—and therefore the photochemical theory—cannot then account for the facts unless brightness is such that the average number of decomposed purple molecules in each rod is a non-negligible part of the total number of visual purple molecules contained in one single rod.

But this is the case only when the brightness reaches about 1 millilambert and the absolute threshold is about 10,000 times lower, even if one allows for pupillary aperture variation.

Afterwards Van der Velden found that 2 quanta may produce a liminal sensation when they are absorbed in a small peripheral retinal area and the time interval between them does not outlast a certain constant. This constant is furnished by experiment. Van der Velden uses a statistical method already employed by Hecht, Shlaer, and Pirrme. It consists in computing the number of positive responses in relation to the logarithm of stimulus brightness. The curve thus obtained must be a Poisson exponential expansion curve, characteristic of the number $n$ of independent events, that is of quanta necessary to induce excitation. Indeed, as $n$ is a small number, the average number $N$ of quanta absorbed during a flash will not always be equal to $n$. On account of the chance distribution of the quanta contained in a small flux, $q$ quanta ($q: 0, \ldots, n-1, n, n+1, \ldots$) will be absorbed and Poisson's law makes it possible to compute the probability $P_{n,q}$ that the number of quanta absorbed during a single test will be equal to $q$:

$$P_{n,q} = \frac{N^n}{e^N q!}$$

$e$ being the basis of Naperian logarithms. When the retina absorbs more than $n$ quanta, of course we also experience a visual sensation. We must therefore compute the probability for $n$ or more quanta to be absorbed, among those carried by a flash which on the average provides $N$ quanta to the retina. For each value of $n$, we thus obtain a definite Poisson curve, steeper and steeper as the parameter $n$ increases. Fig. 1 shows a “family” of these curves in which the abscissae are fractions and multiples of $N_1, N_2$, being the average number of quanta absorbed by the retina when the flash intensity is liminal,
and the ordinates percentages of the probability for \( q \) to be superior or at least equal to \( n \).

In order to compute \( n \), we must use stimulus intensities which will vary from a fraction to a multiple (e.g. twice) of the liminal intensity. Then, for each brightness \( b \) given, we write down the proportion of positive responses, the corresponding abscissa being \( b/b_l \) when \( b_l \) is the liminal brightness.

The curve thus obtained must coincide with one of the graphs of Fig. 1. This method led Van der Velden, experimenting on two observers, to state that \( n = 2 \). Van der Velden uses as abscissae the logarithm of \( b \); Hecht, Shlaer,

![Fig. 1. Poisson's law. The proportion of positive responses to weak stimuli in relation to stimulus brightness and number \( n \) of quanta necessary to induce a sensation. Threshold brightness is chosen as abscissa unit.](image-url)
that, depending upon his physical and psychological condition, one of our subjects saw the flash one day when his retina absorbed 4 quanta, another day when it absorbed 10 quanta, experiments always being preceded by a 50 minute adaptation. Training also plays an important part, and in order to find $n$ we must not use average values but select and train the observers beforehand. Fig. 2 shows quite a homogeneous run which furnished the value of $n = 5$. The best performances of the best observers will give a number $n$ which will be the absolute threshold. Therefore it seems justifiable to accept 2 quanta as sufficient to excite, that is to induce a propagated action potential. But this excitation will not necessarily produce a sensation.

The Conditions of Liminal Excitation

According to several authors, among whom we shall quote only Blondel and Rey, Pîeron, and Graham and Margaria, one always notes a time $\tau$ which de-
pends on the size of the test area and on the position of that area on the retina, and is such that \(bt = \text{constant when } t \leq \tau\). This applies to foveal as well as to peripheral vision, and to large retinal areas as well as to very small ones. If we take into account this fact on one hand and Van der Velden's result on the other, we are led to express the conditions of liminal excitation as follows:

Liminal excitation is caused by the absorption of 2 quanta of light, happening, in a time interval \(t \leq \tau\), inside a retinal area to which we shall give the name of quasi-independent unit. This unit is such that in each region of the retina it is the largest area possible within which Ricco's law \((bS = \text{constant})\) is valid; \(\tau\) is a time constant which is to be found experimentally.

Thus we see that the quantic and statistical theory of visual excitation which we here put forward does not assume any "ad hoc" mechanism nor any arbitrary parameter.

**Liminal Brightness in Relation to the Size of the Retinal Area**

**Stimulated—Ricco's, Piper's, and Piéron's Laws**

Ricco's law is an expression of the fact that, given certain space-time conditions, we observe what is usually called "total summation." According to this law, liminal intensity varies inversely to the stimulated areas; that is to say, when we use quantic terminology, the number of quanta likely to induce liminal excitation is a constant whatever the size of the retinal area stimulated. Nowadays we know that Ricco's law is not valid for all the regions of the retina nor for areas of every size. The most outstanding exceptions are the foveal region and any peripheral area above a certain size which varies according to the retinal region involved (Piéron; Graham and Margaria). For instance, in region IV (near periphery) which spreads between 12°30' and 20° from the foveal center, Ricco's law is strictly valid for circular test areas, the visual angle of which varies from about 2' to 1° (see Graham and Margaria and this paper, p. 281). This has been tested with white and blue light.

Let us therefore suppose, for the time being, that any retinal region is made up of quasi-independent units (according to our definition of this term, see above). In this case, liminal excitation can only take place when 2 quanta are absorbed, during a time interval \(t\) sufficiently small, by two rods belonging to the same unit; that unit contains, in this retinal region, about 18,000 rods (Osterberg).

When the test area involves several of these units, by which law, then, should Ricco's law be replaced?

Let us call \(k\) the number of these stimulated units, and compute the probability that 2 quanta (or more) among \(q\) will be absorbed by the same unit, \(q\) being the number of quanta absorbed in the test area. This probability is equal to 1 minus the probability that the opposite event does happen; that is to say, that each of the \(q\) quanta is absorbed by a separate unit.
Now if \( \frac{k!}{(k-q)!} \) is the number of favorable combinations and \( k^q \) the number of possible combinations, it follows that

\[
P_{k,q} = 1 - \frac{k!}{(k-q)k^q} \quad q \leq k
\]

We are then looking for a number \( q \) such that \( P_{k,q} = 0.5 \) (threshold condition) and we may therefore write

\[
P_{k,q} = 0.5 \quad \text{or} \quad \frac{k!}{(k-q)k^q} = 0.5
\]

The function \( P_{k,q} \) has this particular characteristic, that when \( k \) is not too small, its value remains practically constant when one multiplies \( k \) by \( a \) and \( q \) by \( \sqrt{a} \), where \( a \) is any positive number. It follows that the liminal energy increases as the square root of the test area when the latter contains several of those units. This is Piper's law which, empirical at first and verified only in certain conditions of area, region, and time, becomes now a basic law, valid everywhere that we deal with a homogeneous population of units inside which Ricco's law is valid.

Indeed, Graham and Margarla have observed that Piper's law holds good for the retinal region investigated by them, when the visual angle of the test area varies from 1 to 3° in diameter. Since they have not used larger areas, we still have to prove that the same law applies also when the stimulated areas have larger diameters, but not larger than the limits of the investigated retinal region.

Let us now examine the course of liminal energy as influenced by the size of the area, inside the outer fovea, the diameter of which is 1°20' (Polyak). If the cones were a homogeneous population, Piper's law would be valid over the whole range of the outer fovea. But this is not so. In the very center of the fovea, the diameter of the cones is minimum and it increases towards the foveal periphery.

When we measure the foveal threshold for red light, for areas of increasing size, we must expect that Piper's law will be affected according to the density of the cones. On account of the fact that the cone diameter increases from the center towards the edge of the fovea, the threshold intensity must decrease more slowly than the square root of the ratio of the stimulated areas increases.

1 The first quantum may be chosen between \( k \) units, the second between \( k - 1 \), \( \ldots \) the \( q \)th between \( k - q \). The product \( k(k-1)(k-2)\ldots(k-q) \), which is the number of favorable combinations, may be written \( \frac{k!}{(k-q)!k^q} \).

2 For values \( k: 2, 8, 50, 200, 800 \) and \( q: 2, 4, 10, 20, 40, \) we compute \( P_{k,q}: 0.5-0.599-0.618-0.626-0.629. \)
It does not matter whether we use Östergberg's or Polyak's data to compute the number of cones in circles of different diameter, having as center the center of the fovea. Those data vary from 1 to 2, but the cone density ratios of any two circles of different diameters, computed from Östergberg's figures, are practically equal to those computed from Polyak's findings. According to Östergberg, the numbers of the cones contained in circles 50, 100, and 200 µ in radius, having the foveal center as center, are respectively 1,050, 3,050, and 8,150. Östergberg counts also rods in circles over 100 µ in radius, while Polyak definitely denies the existence of rods inside circles smaller than 200 µ in radius. The number of receptors inside those circles—either cones or rods—according to Östergberg is 1,050, 3,050, and 9,100. Polyak's data allow us to compute the number of cones contained in circles respectively 50, 125, and 200 µ in radius. These numbers are the following: 2,250, 9,350, and 18,600.

In order to compute the coefficient of spatial summation, let us apply Piper's law. If \( n_1 \) is the number of cones contained in a circle, the radius of which we shall call \( a_1 \), and if \( n_2 \) is the number of cones contained in a second circle, the radius of which we shall call \( a_2 \), \( a_2 > a_1 \), according to Piper's law we shall have:

\[
\frac{n_2}{n_1} = \sqrt{\frac{S_2}{S_1}} = \left( \frac{n_2}{n_1} \right)^{0.8}
\]

When replacing the ratio \( \frac{n_2}{n_1} \) by \( \frac{S_2}{S_1} \), where \( S_1 \) and \( S_2 \) are respectively the areas of the two circles, we may compute easily:

\[
\frac{n_2}{n_1} = \left( \frac{S_2}{S_1} \right)^{0.97}
\]

Now Piéron, for areas from 6' to 2° in diameter, finds 0.30 the summation coefficient; Elsberg and Spotnitz, for areas from 8' to 36' in diameter, find a coefficient varying between 0.33 and 0.30. Let us note that Piéron, as well as Elsberg and Spotnitz, has experimented with stimuli lasting several seconds, which affects the results because of fixation-micronystagmus effect. Now, when the tested areas are small, this effect is relatively greater than it is for bigger areas, and it seems possible to ascribe to it the numerical gap between theory and experience. We intend to take up again in the near future the same investigations, but with short flashes as stimuli, in order to check whether this effect is actually the only cause of the observed gap.

Here we must raise the question: what is, inside the fovea, the nature of the quasi-independent unit? Foveal histology teaches us that it is more than probable that each foveal cone is linked to its own ganglion cell by the medium of its individual bipolar cell. We are then justified in surmising that the quasi-independent foveal unit is made up of one cone only or, at least, of a small
number of cones forming a functional color vision unit. The comparison of the peripheral and foveal thresholds, interpreted by means of probability calculations, will provide us with a definite answer, but it would take too long to discuss this important question here, and we shall deal with it in a future paper.

At any rate we are justified in stating that Elsberg and Spotnitz's observations, relative to very small foveal areas, cannot provide a satisfactory answer to this question. Indeed, their experimental conditions are not guaranteed against the intervention of two artefacts; viz., micronystagmus and fixation point intervention. It will indeed be useful to take up their observations again, however difficult it is, for they are liable to provide very valuable information.

Threshold Brightness in Relation to Stimulation Time and Size of Test Area

If \( b \) is the liminal brightness that corresponds to a stimulation time \( t \), what must be the course of the function \( bt = f(t) \)?

When made on a well circumscribed retinal region, experiments (Piéron, Graham and Margaria) always yield curves of the same type; \( bt \) remains constant up to a certain limit, then rises quite abruptly and continues to rise, but more and more slowly. From the point where they cease to be horizontal straight lines (Bunsen-Roscoe's law) these curves are similar to parabolas (Piéron).

Though it is often asserted that \( b \) becomes constant as soon as \( t \) reaches a certain value called "summation time" (temps utile in French), we have not been able to find any trace of experiments yielding the above result, the only exception being those of Blondel and Rey who operated with mixed (foveal and parafoveal) vision. But these experimental conditions are too complex to yield results liable to be taken into account in the discussion of the present question. Why then do so many authors assert that \( b \) becomes constant when \( t \) reaches a certain value which they agree to place at about 3 seconds?
The answer seems to be as follows: First, as eye movements increase with fixation time, experimental thresholds will yield too high values when \( t \) reaches values of several seconds. And secondly, as \( \theta t \) increases with \( t \), these authors conclude that we have before a temporal summation phenomenon, the "memory" of the responsible neuron decreasing as \( t \) increases, and so they are led to state that there is a limit beyond which the neuron needs a constant input of new energy, that input being just sufficient to compensate the loss of energy caused by the weakness of the neuron's "memory."

It is surprising that the parabolic shape of the curves \( bt = f(t) \) has not long since incited physiologists to reconsider the above interpretation; the more so since this type of curve is found also in animals such as \( Mya \), which lacks eyes, and in nerve response to electrical stimulation (Lapicque). Recently, Segal proved that cell memory, being a passive property, cannot explain this type of curve. Indeed if the classical interpretation were true, such a summation should yield a curve of experimental type in which the energy loss involved by limited cell memory, unnoticeable at first, would become more and more important until, at the end of the "summation time," the curve would become a straight line. Now this classical interpretation applies only to concave curves, but experiments have always yielded convex curves (Fig. 4).

We shall eliminate this contradiction if we give up the hypothesis of temporal summation and analyze the phenomenon from the quantic and statistical point of view.

Threshold Brightness in Relation to Size of Tested Areas

Whatever the inner mechanism of liminal excitation, the quantic structure of light and the random distribution of quanta in weak flashes involve necessarily a certain relationship between threshold brightness \( b \) on the one hand...
and size $S$ of test area and stimulation time $t$ on the other. Therefore, if the experiments yield numerical results that are the same as those predicted by the quantic and statistical theory, there should be no doubt whatever that the peripheral mechanism of liminal excitation is the same as that involved in this theory.

Table I shows corresponding values of $bt$ and $t$, relative to test areas subtending visual angles of respectively $2'$, $16'$, $1^\circ$, and $3^\circ$ (Graham and Margaria).

<table>
<thead>
<tr>
<th>Stimulus time (milliseconds)</th>
<th>$2'$</th>
<th>$16'$</th>
<th>$1^\circ$</th>
<th>$3^\circ$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.31</td>
<td>9.34</td>
<td>0.563</td>
<td>0.178</td>
<td></td>
</tr>
<tr>
<td>0.63</td>
<td>9.55</td>
<td>0.589</td>
<td>0.178</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>9.34</td>
<td>0.603</td>
<td>0.187</td>
<td></td>
</tr>
<tr>
<td>1.25</td>
<td>9.55</td>
<td>0.589</td>
<td>0.224</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>9.78</td>
<td>0.646</td>
<td>0.219</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>9.78</td>
<td>0.646</td>
<td>0.219</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>9.78</td>
<td>0.646</td>
<td>0.219</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>32</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>64</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>80</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>128</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>160</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>256</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>320</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>500</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>640</td>
<td>9.55</td>
<td>0.677</td>
<td>0.258</td>
<td></td>
</tr>
</tbody>
</table>

Let us now consider the fourth line of this table. We notice that here $bt$ is still constant for each of the four columns. Piper's law applies quite well between 1 and $3^\circ$, but Ricco's law seems to apply only between $16'$ and $1^\circ$; and between $2'$ and $16'$, neither applies. This is why we thought it necessary to continue part of Graham and Margaria's investigations.

Our subjects were M. R., a young man of 17, and F. A., a young girl of 23. Both had normal vision. Each series of runs was preceded by 50 minutes' adaptation in complete darkness. The physical arrangement may be seen in Fig. 5. The light source is a tungsten filament lamp run on a constant current obtained from storage...
It sends part of its flux on a dry disc photocell which is connected with a microammeter; thus continuous intensity control is secured. Another part of the luminous flux enters a glass bar, 11 mm. in diameter, the two bases of which are rough. When it comes out of this bar, the luminous flux goes through a slit, the opening of which may be varied from 0 to 10 mm. by means of a micrometrical screw. We used only openings between 1 and 5 mm., for the calibration of the apparatus, operated by means of a dry disc photocell and a galvanometer showed that outside these limits the brightness of the observed field is no longer proportional to the opening of the screw-driven slit. The diffuse light pencil thus produced goes through a second slit per-

Fig. 5. Apparatus. $B_1, B_2$, glass bars; $C$, dry photocell; $D$, diagram; $F$, colored filter; $FP$, fixation point; $L$, light source; $M$, microammeter; $P$, prism; $S_1, S_2$, slits. $Sc$, screens; $T$, neutral glass filter (Tscherning type); $TD$, turning disc.

pendicular to the first, the opening of which may be 1, 2, or 5 mm. Then the light pencil enters a second glass bar, identical with the first one, at the end of which a total reflecting prism projects the diffuse light on the test field. The area of the latter may be varied by means of diaphragms 2, 3, or 5 mm. in diameter.

The test field is masked to the observer by an ebonite disc which turns round at a constant speed so that the field becomes visible every 9 seconds, during a time which depends on the opening of an adjustable sector of the disc. According to the length of the stimulation time thus determined, the shape of stimulus varies. Indeed, it is sinusoidal for very short stimuli and its plateau becomes longer and longer as the stimulation time increases. If the threshold is determined by nothing but the number of quanta absorbed by the retinal test area during the stimulation time $t$, as it is
involved by the quantic and statistical theory of excitation, it must be independent of the shape of the stimulus. Experience showed that this is indeed the case. Between the test field and the subject's eye is placed a blue filter which has its transmission maximum at 479 μm; in red light its transmission is poor (Fig. 6). If necessary, a neutral glass filter (Tscherning type) is used to decrease light intensity.

The subject's chin rests on a support and a screen protects his left eye from any stimulation. When beginning a run, the subject is told to close his eyes and 2 or 3 seconds before the occurrence of the flash he is told to open them. Then he fixates a small red point, the brightness of which is the faintest possible (about 2 to 3 times the threshold in continuous foveal vision) and he closes his eyes again when he has "seen." When the flash is not seen by the subject, the operator tells him to close his eyes again, and so on. Each run is made up of 20 flashes of equal intensity; 6 runs of decreasing intensity are generally sufficient to determine threshold intensity. When

an observer records any fatigue or when he feels disturbed by phosphenes he closes his eyes for a while, and the run is resumed some minutes later.

Thus we reduce undue fatigue as much as possible, fixation not needing to be continuous. On the other hand, this method eliminates another source of error, scarcely investigated; viz., rapid adaptation to liminal or very faint stimuli. Indeed, when, in peripheral vision, a just perceptible continuous stimulus is given, about 3 seconds later this stimulus is no longer "seen," that is to say, it has become subliminal. But after closing his eyes for a while, the subject "sees" it again, and so on.

When we began our investigations, we asked the subject to wear before one eye an artificial pupil and a lens correcting for accommodation. We have, however, observed that the above arrangement is a source of trouble for the subject and leads to confusion of the results much more serious than the one we observed later, when we gave up the artificial pupil and the correcting lens. Indeed, when the observer is adapted to complete darkness and the stimuli are at most twice the threshold stimulus, we are sure to exclude every chance of pupil contraction and the pupil will permanently maintain its maximum diameter.

The retinal region we investigated is region IV (near periphery) and our test area

FIG. 6. Optic density of filters used in our experiments.

Optic density

Blue filter

Red filter

100 300 600 700 μm
was situated 15° temporally on the horizontal axis of the right eye. By varying the distance between the observer's eye and the test field and by varying the diameter of the latter, we have obtained circular retinal test areas varying from 2'12" to 31'36"

TABLE II

<table>
<thead>
<tr>
<th>Diameter of test area</th>
<th>2'12&quot;</th>
<th>3'30&quot;</th>
<th>5'33&quot;</th>
<th>8'51&quot;</th>
<th>12'30&quot;</th>
<th>14'</th>
<th>19'31&quot;</th>
<th>31'30&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative values of (S)</td>
<td>(b) (arbitrary units)</td>
<td>1</td>
<td>2.33</td>
<td>6.35</td>
<td>14.8</td>
<td>32.2</td>
<td>40.3</td>
<td>82.1</td>
</tr>
<tr>
<td>Observer M. R.</td>
<td>150</td>
<td>102</td>
<td>45</td>
<td>20.8</td>
<td>7.71</td>
<td>7.97</td>
<td>3.11</td>
<td>1.20</td>
</tr>
<tr>
<td>Observer F. A.</td>
<td>163</td>
<td>61.2</td>
<td>26.6</td>
<td>11.4</td>
<td>5.06</td>
<td>4.86</td>
<td>2.30</td>
<td>0.71</td>
</tr>
<tr>
<td>(b \times S) (relative values)</td>
<td>Observer M. R.</td>
<td>1</td>
<td>1.03</td>
<td>1.14</td>
<td>1.23</td>
<td>1</td>
<td>1.29</td>
<td>1.02</td>
</tr>
<tr>
<td>Observer F. A.</td>
<td>1</td>
<td>0.95</td>
<td>1.04</td>
<td>1.04</td>
<td>1</td>
<td>1.20</td>
<td>1.16</td>
<td>0.99</td>
</tr>
<tr>
<td>Mean values</td>
<td>1</td>
<td>0.99</td>
<td>1.09</td>
<td>1.14</td>
<td>1</td>
<td>1.25</td>
<td>1.08</td>
<td>0.94</td>
</tr>
<tr>
<td>Coefficient (x) (mean values) computed from the relation (b \times S = constant)</td>
<td>1.01</td>
<td>0.95</td>
<td>0.96</td>
<td>1.00</td>
<td>0.94</td>
<td>0.98</td>
<td>1.01</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 7. \(\circ\), threshold brightness for extremely red light (cones). \(\times\), threshold brightness for the blue light (rods).

in diameter. We are now pursuing the same investigations with another apparatus, allowing for visual angles up to 8°.

Table II shows the relation between the threshold brightness \(b\) and the visual angles subtended by the test areas; Fig. 7 shows the average values for two
observers. It should be noted that the observed values correspond closely with a curve the analytical expression of which is: \( bS = \text{constant} \). This is precisely Ricco's law and it is now demonstrated that it applies continuously from 2'12" to 31'36" and, perhaps, further on.

It was necessary to make sure that the thresholds measured by this method were independent of the stimulation time \( t \). We proceeded to study this by seeking experimentally the value \( \tau \) which is the point from which \( bt \) begins to increase. By using stimulations lasting noticeably less than \( \tau \) (in fact we used \( t \approx 8.3 \) milliseconds for areas of 14' or more in diameter and \( t = 20 \) milliseconds for smaller areas), we made sure that the threshold values we had obtained were indeed independent of \( t \).

**The Spatial Law of Threshold in Peripheral Cone Vision**

The relationship between threshold in peripheral cone vision and tested retinal area has been studied by Piéron, whose results did not allow him to formulate any law. The quantic and statistical theory of visual excitation enables us to predict this law. To do so, we have but to look up the histology of the retina.

In region IV, the number of cones per area unit is about \( 1/30 \) of the number of rods (Østerberg). In this region, the number of rods belonging to the same ganglion cell is about sixty and there are also two cones linked to the same cluster of rods.

Our quasi-independent unit includes thus either one cone only or two cones contained in the same cluster. When there is a certain number of clusters stimulated by extremely red light, Piper's law must apply (see p. 274).

We measured the threshold for extremely red light for areas of 12'30" to 31'36" in diameter. Before the runs were made, there was a period of dark adaptation, 20 minutes long.

Fig. 6 shows the course of the photometric density of the red filter used, in relation to wavelength. From this graph we can see that every light of 679 \( \mu \) wavelength or less is practically absorbed by this filter and that the light it does transmit is chiefly composed of radiations the wavelengths of which are superior to 700 \( \mu \). It should be noted here that the energy distribution of our light source has its maximum far beyond 700 \( \mu \); so we are sure that our stimulus contains much less short wavelength energy than it would seem from the graph of Fig. 6. Rod visibility curves (Hecht and Williams) allow us to show by computation that, in such conditions, only the cones must have been stimulated.

The important fact should be noted that every stimulation leading to a sensation was recorded by both subjects as "red light." Therefore we may state that in peripheral vision of extremely red light the photochromatic interval is null.
Fig. 7 shows our average results and Table III the individual results obtained from each observer. The measured values correspond remarkably well with a curve $b\sqrt{S} = \text{constant}$. This is Piper's law. We have not been able to study areas smaller than $12'30''$ in diameter because of the insufficient luminosity of our source; a new apparatus is now being constructed, which will allow us to study very small areas, as well as areas several degrees in diameter.

The measurement of $\tau$, in the case of peripheral cone vision, provides another important piece of information. Between $12'30''$ and $31'36''$ $\tau$ has been found to be practically constant, while in rod vision and for the same scale of diameters it varies from about 25 milliseconds to about 10 milliseconds. Now 120 milliseconds is precisely the value of $\tau$ which we found for the smallest area ($2'12''$ in diameter) stimulated by blue light. This also proves that the liminal excitation of peripheral cones does take place because of the absorption of 2 quanta by a single cone or by two cones included in the same cluster of rods.

### Table III

<table>
<thead>
<tr>
<th>Diameter of test area</th>
<th>$12'30''$</th>
<th>$19'31''$</th>
<th>$31'30''$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative values of $S$</td>
<td>1</td>
<td>2.53</td>
<td>6.35</td>
</tr>
<tr>
<td>Relative values of $\sqrt{S}$</td>
<td>1</td>
<td>1.58</td>
<td>2.52</td>
</tr>
<tr>
<td>$b$ (arbitrary units)</td>
<td>Observer M. R. 400</td>
<td>225</td>
<td>186</td>
</tr>
<tr>
<td></td>
<td>Observer F. A. 143</td>
<td>98</td>
<td>47.4</td>
</tr>
<tr>
<td>$b \times \sqrt{S}$ (relative values)</td>
<td>Observer M. R. 1</td>
<td>0.90</td>
<td>1.17</td>
</tr>
<tr>
<td></td>
<td>Observer F. A. 1</td>
<td>1.08</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>Mean values 1</td>
<td>0.99</td>
<td>1.00</td>
</tr>
<tr>
<td>Coefficient $x$ (mean values) computed from the relation $b \times S^2 = \text{constant}$</td>
<td>-</td>
<td>0.51</td>
<td>0.50</td>
</tr>
</tbody>
</table>

### Liminal Brightness in Relation to Stimulation Time

Let us now compute the course and the numerical values of $bt$ for a given retinal area. For this purpose it is sufficient to know the probability that, among $N$ quanta absorbed during the stimulation time $t$, two at least are separated by a time interval less than or at most equal to $\tau$. The problem becomes one of computing the probability $P_{n,t,r}$ that among $N$ points, chosen at random on a segment $t$ of a straight line, two at least are separated by an interval less than or at most equal to $\tau$. We owe to Paul Lévy the generalized solution of this problem; a particular solution is:

$$P_{n,t,r} = 1 - \left[ 1 - \frac{(N - 1)\tau}{t} \right]^m$$
When \( P_{n, \tau} = 0.5 \) — threshold condition — we may compute \( N \). But as \( N \) is the mean number of quanta, we must take into account Poisson's law of small numbers. Indeed, when we consider a single flash, the number \( q \) of quanta actually absorbed may be less than, equal to, or more than \( N \). We must therefore write:

\[
P_{n, \tau} = 1 - 
\sum_{q=0}^{\infty} C_{q, N} \left[ 1 - \left( \frac{q - 1}{\tau} \right) \right]^n,
\]

where the \( C_{q, n} \) (Poisson's coefficients) express the probability that \( q \) quanta will be absorbed. Thus we may compute the ratio \( bt/br \) for any value of \( t \).

When \( t \leq \tau \), the mean liminal flux carries less than two quanta. It seems convenient to take as the threshold condition 60 per cent positive answers. In this case, the mean liminal flux amounts almost exactly to two quanta (actually a two quantum flux corresponds to 59.4 per cent of positive answers).

Let us now consider the \( bt \) curve corresponding to the area 1° in diameter tested by Graham and Margaria (Fig. 8). If \( \tau \) is given a value of 3.2 milliseconds (its precise value does not appear from Graham and Margaria's exper-
iments but is included between 2.5 and 5 milliseconds), we may compute the theoretical curve by means of formula (1). It fits well with the general course of the experimental curve but we may distinguish in the latter three fragments of parabolic kind. There are two sharp upward movements: one at about 20 milliseconds, the other at about 200. Between 300 and 640 milliseconds it seems to resume its ordinary course, as becomes obvious when we compare the theoretical and the experimental curves. One might think that these two sharp upward movements are due to errors in measurement, but this does not seem to be the case, for they are, on the contrary, systematic.

Indeed, the upward movement that takes place at about \( t = 200 \) milliseconds may be found also in the curves corresponding to areas 2' and 16' in diameter; moreover, it is also to be found in the curve expressing the results obtained by Piéron (Figs. 8 and 9). We shall discuss these systematic deviations at the end of this paper.

**Ricco's Law, the Constant \( \tau \), and the Morphology of the Ganglion Cells**

The fact that Ricco's law is valid in the retinal region considered, up to visual angles of 1°, makes probable the existence of ganglion cells with ramifications spreading at least as far as 300 \( \mu \); such a distance corresponds to a visual angle of 1°. Indeed, the histology of the retina shows that region IV is specially rich in giant ganglion cells which are perhaps nothing but a kind of parasol cell (Polyak). These cells are actually morphological units and their ramifications spread often farther than 350 \( \mu \). On the other hand, these ramifications overlap those of the neighboring giant cells. The figure 300 \( \mu \), computed from Graham and Margaria's psychophysiological measurements, fits, therefore, very well with the histological facts. Such a giant cell would then be what, in rod vision, we have called a "quasi-independent unit;" it would be linked to every smaller ganglion cell contained in the area circumscribed by its ramifications.

We have been led to admit (Baumgardt) that the constant \( \tau \) is a characteristic of the largest ganglion cell existing in the tested area; it should be remembered that the larger the stimulated area, the smaller the constant \( \tau \). But as we have observed that \( \tau \) seems to decrease continuously when \( S \) increases, we must admit that there may be another explanation. Indeed, \( \tau \) might depend on the mean distance between the two rods absorbing one quantum each, for we are aware of the existence of damped subliminal action potentials called "not propagated" action potentials, which, however, spread over a distance of about 1 mm. (Katz; Hodgkin). Therefore we can understand that the smaller the course of subliminal action potential generated by the absorption of one quantum, the greater is \( \tau \), for in such a case, the damping effect is less important than when the distance between the absorbing rods is long. At any rate, the solution of this problem requires a serious investigation of the course of \( \tau \) in relation to \( S \).
Deviation between Experimental Time Law and Theoretical Time Law

We have seen that the curves obtained by Graham and Margaria are of the same type as those which theory leads us to expect. However, there remains a systematic deviation, which becomes more important as the stimulated area becomes smaller. Let us consider Fig. 8, which expresses the relation between $b_t$ and $t$. The tested area measures 1° in diameter and the value of $\tau$ is between 2.5 and 5 milliseconds. What is the reason for these deviations between experimental and theoretical curves?

![Figure 9](image)

We think that there are two reasons. First, the formula does not take into account the fact that the absorption of the two quanta may take place within the field of one of the many smaller ganglion cells existing in the stimulated area. Therefore, when $t$ is less than 20 milliseconds, the actual probability $P'$ is definitely greater than the computed probability $P$. Indeed, Fig. 9 shows that for 16° area $b_t$ is constant when $t$ is less than 20 milliseconds. Secondly, when $t$ increases, the mean number $N$ of absorbed quanta also increases and $q$, the number of quanta actually absorbed, more and more often is greater than 2. When, in a single test, the time interval between the absorption of the two first quanta is greater than $\tau$, there is no propagated action potential, but owing to the local excitation caused by the absorption of the first quantum, the
ganglion cell concerned must go through a relatively refractory state which prevents the raising of a propagated action potential even if the absorption of a third quantum follows the absorption of the second one within a time interval not longer than \( \tau \). It will therefore be necessary for the third quantum to follow the second one very closely or, perhaps, for a fourth one also to be absorbed. In any case, \( bT \) will then increase more rapidly than we should expect from the relation shown in equation (1).

The second upward movement (at about 200 milliseconds) may then be ascribed to the refractory state of the smallest ganglion cells. Indeed, inside a 16' area, there are about twenty clusters of rods, and the data of Graham and Margaria show that for smaller areas consisting of a part of a single cluster, there is at about 200 milliseconds a sudden upward movement of \( bT \) which may be explained by the above mechanism. It is not surprising to find the same phenomenon on the curve corresponding to the 16' area (see Fig. 9), and in Fig. 8 (1° area) we may observe it once more.

It seems that the quantic and statistical theory cannot by itself allow the prediction of these effects. Indeed these sudden upward movements are due to the fact that the more subliminal action potentials there are, the more the ganglion refractory state is reinforced; they are nervous phenomena. This mechanism which actually produces a nerve adaptation may give us a clue to the important problem of why, a long time before the mechanism of photochemical adaptation begins to come into play, the sensation level increases much more slowly than the brightness. The analysis of the measurements of differential threshold, made by König and Brodhun, shows that the sensation level increases approximately linearly with brightness when brightness is very faint; then it becomes proportional to the square root of the brightness, then proportional to its cubic root, and finally proportional to its logarithm. It is in this least range of brightness that the sensation level follows the mass action law, essential basis of any photochemical theory of vision. But when brightness increases still further, the logarithmic law must be replaced by another law which determines a slower increase of the sensation level; and finally, when the brightness has become such that each purple molecule just recombined is immediately decomposed again by a quantum, the sensation level will have reached its maximum.

We are far from being able to follow these mechanisms mathematically. But we believe that it is necessary to distinguish on the one hand the phenomena due to the quantic and random character of the stimulating light, and on the other hand, those due to nervous adaptation (retinal and no doubt, cortical too) and to photochemical adaptation. Thus, we may hope, thanks to mathematical analysis, to come to a new theory of vision lacking all speculative character and using no arbitrary parameters. Such a theory might advantageously replace the actual photochemical theories, which by means of a certain number of parameters carefully chosen have so far vainly tried to express by a single
formula what actually seems to be the result of several essentially different mechanisms.

SUMMARY

1. The photochemical theories of vision cannot provide a valid interpretation of the facts over the whole range of brightness. The fact that liminal excitation is increased by the absorption of a very small number of quanta, each absorbing rod receiving a single quantum, excludes the intervention of the mass action law which is the basis of all photochemical theories.

2. Owing to the quantic structure of light and to the random distribution of quanta in a faint light pencil, there must exist numerical relations between the threshold energy on the one hand and the size of the retinal area stimulated and the stimulation time on the other, whatever may be the inner mechanism of liminal excitation. When taking as a basis Van der Velden's experimental results, viz. that two quanta absorbed during a certain interval of time are sufficient to raise threshold excitation, the probability calculus enables us to compute the course of threshold energy in relation to the stimulation time and to the stimulated retinal area. No arbitrary parameter is needed to do so; the only constant to be used is found by experiment.

3. The quantic and statistical theory of visual excitation that we put forward in the present paper enables us to predict the validity of Ricco's law within what we call a "quasi-independent unit" and the validity of Piper's law within a test area made up of a certain number of such units. This theory does not correspond exactly with Piéron's law for foveal threshold in relation to the size of the stimulated area, but the deviation is probably due to an artefact; viz., the action of the micronystagmus.

4. Experiment proves that in region IV of the retina, 15° temporally from the fovea of the right eye of two observers, Ricco's law applies strictly in rod vision from 2'12" to 31'36" and, perhaps, further on.

5. In the same region, from 12'30" to 31'36", Piper's law applies strictly in cone vision of extremely red light.

6. In peripheral vision with extremely red light the photochromatic interval has been found to be null.

7. Our theoretical interpretation of the term "quasi-independent unit" fits well with the histological data of the retina.

8. Numerical deviations of the theoretic time law of threshold intensity from the empirical course may be due to the existence of a relative refractory period of the ganglion (or bipolar) cells. This mechanism would be a sort of instantaneous adaptation of nervous elements and would explain the fact that the sensation level increases very much slower than the brightness level, in a range of the brightness scale where the photochemical adaptation cannot account for this phenomenon.
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