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TEMPORAL AND SPATIAL SUMMATION IN HUMAN VISION AT DIFFERENT BACKGROUND INTENSITIES

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The present experiments were undertaken as part of an investigation of the suggestion made by Rose (1942, 1948) and de Vries (1943) that human visual performance is limited by the inevitable fluctuations in the numbers of quanta absorbed in the retina. In a previous paper (Barlow, 1957) it was shown that this idea (modified by assuming that there is also a weak intrinsic source of noise) leads to theoretical curves which fit experimental determinations of increment threshold made with a short duration small area test stimulus superimposed upon a large uniform adapting field. It was also shown that big changes in the amount of temporal and spatial summation occur when the background intensity is changed, with the result that when thresholds are determined with a long duration large area test stimulus the experimental points deviate from the appropriate theoretical curve and tend to obey the Weber law instead.

In following up this finding there were two objectives. The quantum fluctuation hypothesis predicts that the increment threshold intensity should be inversely proportional to the square root of the area and duration of the stimulus, and the first object was to find whether the occurrence of these laws fitted in with the hypothesis: the results show that the predicted laws of summation do hold over certain ranges, but when they hold the actual values of the thresholds are higher than the theory predicts. The second objective was to determine the parameters α and τ which were introduced in the previous paper; these are the area and time over which quanta absorbed from the background light are liable to be confused with those absorbed from a short duration small area stimulus light, and here the results obtained are disappointing, for one can only derive lower limits to these quantities. On the other hand, the results do show up the complicated interrelations between temporal and spatial summation and background intensity; tentative explanations of these effects, and of the failure to perform up to the quantal fluctuation limit, are put forward.

METHODS

The apparatus and its calibration have been described in the previous paper. It provided a background or adapting field of 13° diameter which was centred $6^\circ 30'$ from the fovea in the inferior nasal quadrant of the visual field of the subject's right eye. The stimulus, or test flash, was added to the centre of the background field, and consisted of a disk subtending from $6'$ to $5\cdot9^\circ$ at the subject's eye. Its duration varied from 7 to 1000 msec and was measured with photocell and oscilloscope. The intensity of the background was controlled by neutral filters, and that of the stimulus by neutral filters and a wedge which was adjusted by the subject. In all the experiments reported here an Ilford 603 (blue-green) filter was placed in both the background and stimulus pathways. The light passing this filter had a peak energy at $497\text{ m}\mu$ and quantities of light are expressed as the number of quanta of wave-length $507\text{ m}\mu$ (quanta/sec. degrees² for intensities) which would have had the same scotopic luminosity as the light in question. The light entered the eye through an artificial pupil 2 mm in diameter.

The same two subjects were used as in the previous experiments, and the same technique for determining threshold; the subject adjusted the wedge, with the stimulus repeating automatically at about 1 per 3 sec, until he considered that it was usually just visible. This seemed to correspond approximately to the '80% seen' intensity of frequency of seeing curves. The usual procedure was to determine a threshold at each area or duration of stimulus, then change to the next area or duration in the series; having completed the series in one order, it would then be repeated in reverse order. Each experimental run was preceded by a period of dark adaptation, and whenever the background intensity was changed the subject was allowed a few minutes to adapt to it.

RESULTS

Fig. 1 shows the over-all change in combined spatial and temporal summation for a range of background intensities from zero to 10^9 quanta/sec. degrees², using the fixation point so that the test stimuli were centred $6^\circ 30'$ from the fovea. The measure of summation that was used was the ratio of the threshold *quantity* of light for a short duration small area stimulus to the threshold *intensity* using the longest duration and largest area available; this quantity represents a solid angle multiplied by a duration, and its logarithm is plotted as ordinate. The results for both subjects are shown, and each point is the mean of the log. of up to four estimates of the ratio; the pair of thresholds required for a single estimate were determined within a few minutes of each other, but the different estimates were made over a period of several months. It will be seen that the amount of summation decreases continuously as the background intensity is raised over the whole of this range. At low intensities B.N. shows rather less summation than H.B., but this difference disappears at high intensities. The straight line drawn in the figure has a slope of $-0\cdot25$, and therefore represents the law

$$\Delta I/\Delta N \propto I^{\frac{1}{4}},$$

where ΔI is threshold intensity, ΔN threshold quantity, and I the background intensity. This is an empirical finding with no theoretical basis, and it may depend to some extent on the stimulus conditions used.

One other feature of Fig. 1 is worth comment. Stiles's evidence (1939, and personal communication) suggests that cones (the π_4 mechanism) are probably the receptors subserving threshold at field intensities above 10^6 or 10^7 quanta/sec.degrees² under the conditions of these experiments, and this conclusion is consistent with some observations of the relative effectiveness of background lights of different colours in raising the threshold of the superimposed stimulus. Below this intensity rods must be operating, so that the first five pairs of points, up to and including the pair at $\log I = 5.7$, depend upon the rod mechanism, whereas the remaining three probably depend on the cones. There is no break in the curve at this point (though there might be with

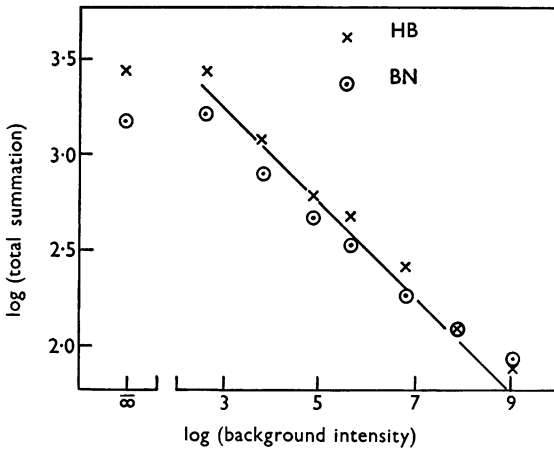


Fig. 1. The effect of background intensity on the amount of combined spatial and temporal summation up to 1 sec and 19 degrees². The measure of total summation whose logarithm is plotted as ordinate is the ratio of threshold *quantity* of light (for 7.6 msec, 0.0077 degrees². stimulus) to threshold *intensity* (for 935 msec, 19 degrees² stimulus).

different colours for stimulus and background lights), but the present result is sufficient to prove that the decrease in summation with increase in background intensity applies to the cone mechanisms as well as to the rod mechanisms.

If the product of solid angle and time, whose logarithm is plotted in Fig. 1, is to be free of arbitrary dependence upon particular conditions, the threshold *quantity* of light must be measured with a stimulus of area and duration within the ranges where complete temporal and spatial summation occur (Bunsen-Roscoe and Ricco ranges), and the threshold *intensity* with a stimulus of area and duration large enough for summation to have ceased. If these conditions are not met, the ratio of thresholds will depend upon the actual area and durations of stimuli used. For Fig. 1 the threshold quantities were estimated using a flash of 0.0077 degrees² (6' diameter) and 7.6 msec duration; these cannot be assumed to lie within the ranges of complete summation,

especially at high background brightnesses. Likewise it is uncertain that all summation has ceased for the stimulus of 19 degrees² (4.9° diameter) and 1 sec duration, used for measuring threshold intensity. For this reason thresholds were determined at intermediate durations and areas at the various background intensities on one subject. It was hoped that these results would also show whether the changes in total summation involved changes in both temporal and spatial summation, and whether the changes took place in the upper limits of complete summation (Bunsen-Roscoe and Ricco ranges), or whether the amounts, or ranges, of partial summation were involved.

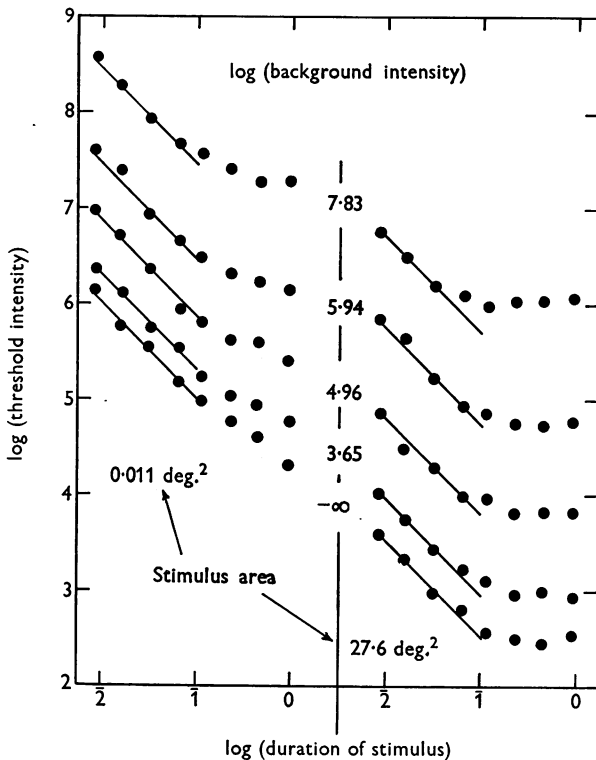


Fig. 2. Temporal summation. Log (increment threshold intensity) plotted against log (duration) for a small (0.011 degrees²) and a large (27.6 degrees²) area of stimulus at five different background intensities. The straight lines have slope -1 and are continued up to 0.1 sec. Intensities in quanta [507 m μ]/sec.degrees²; durations in sec.

Fig. 2 shows an experiment in which the increment threshold was measured for eight durations of test stimulus at five different background intensities (zero to 6.8×10^7 quanta/sec.degrees² entering the eye), using test spots having a small diameter (7.1'; left half of figure) or a large diameter (5.9°; right half of the figure). Each point is the average of two settings, the repeat

series being done in reverse order. The points at one background intensity were all done on the same day, and they belong to the same subject; the sets of points at different backgrounds were done at different sessions, but within a week of each other.

Consider first the set of determinations made with zero background and a small test spot (the bottom set of the left half of the figure). The duration was increased from 8.5 to 930 msec and this caused a drop in threshold intensity from 1.35×10^6 to 2.1×10^4 quanta/sec. degrees²; an increase of duration by a factor of 110 caused a decrease of threshold by a factor of 64, and the actual number of quanta required increased less than twofold from 130 to 220. Temporal summation is not quite complete up to 1 sec, and inspection of the intermediate points suggests that it starts to fail at about 0.1 sec. To aid comparison of the different sets of points a line of slope -1 has been drawn through the left-hand points of each set, ending at 0.1 sec. This line corresponds to complete summation (Bunsen-Roscoe law), and the actual law of summation followed can be judged by comparing the slope of the points with that of the line; $-\frac{1}{2}$ would indicate square root law summation; 0, zero summation. In the case of a stimulus of small area with no background illumination one can say that temporal summation is complete up to 0.1 sec, and nearly complete up to 1 sec. In contrast, consider the determinations made with a large stimulus superimposed on a background of high intensity (top set of right half of figure). It will be seen that complete summation stops at about 30 msec, and that there is hardly any summation at all beyond this point, so that here the increase of stimulus duration by 110 times only caused a 5 times decrease of threshold intensity, and the actual number of quanta required increased from 1.4×10^6 to 3.2×10^7 quanta, an increase by more than 20 times.

Fig. 3 shows log. increment threshold plotted against log. area of stimulus at five different background intensities and two durations of stimulus. The determinations at each background intensity were done in the same session as those at the same intensity in Fig. 2. The line of slope -1 indicates complete spatial summation (Ricco's Law), and it has been drawn up to 0.4 degrees². The actual amount of spatial summation can be judged from the slope of the sets of points. The display of spatial summation in Fig. 3 is similar to the display of temporal summation in Fig. 2, and it will be seen that the results are also analogous.

The general features of the complicated interrelations which these figures reveal are as follows. Temporal summation varies from complete (Bunsen-Roscoe Law valid) to zero (threshold intensity independent of duration) and the factors which reduce it (i.e. lessen the downward slope of the points) are (i) increase of stimulus duration, (ii) increase of stimulus area, and (iii) increase of background intensity. Exactly the same factors decrease the amount of spatial summation, though this never quite comes down to zero, and in

consequence the lowest threshold intensities here recorded are higher than the values found with larger stimuli (e.g. Denton & Pirenne, 1954). Looking at the points where the degree of summation changes one sees that the upper limit of complete temporal summation is about 0.1 sec, and the range is probably slightly curtailed by increasing the background intensity: this effect is more pronounced with large area stimuli, when the upper limit comes down to about 0.03 sec. The upper limit of complete spatial summation (Ricco's Law valid) is about 0.4 degrees² with short durations at low backgrounds, but

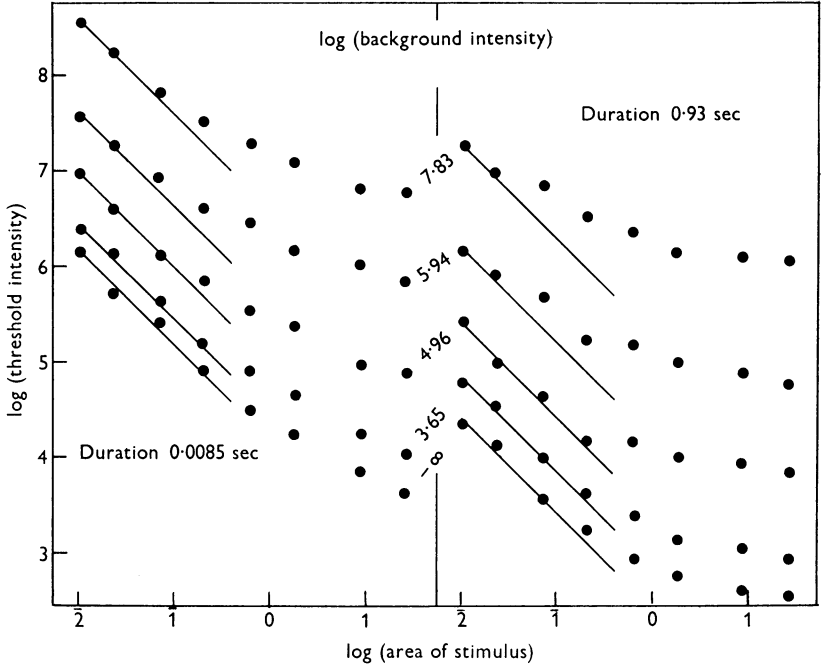


Fig. 3. Spatial summation. Log (increment threshold intensity) plotted against log (area) for a short (8.5 msec) and long (930 msec) duration of stimulus at five different background intensities. The straight lines have slope -1 and are continued to 0.4 degrees². Intensities in quanta (507 $m\mu$)/sec. degrees²; areas in degrees².

it is reduced to about 0.1 degrees² by raising the background intensity: increasing the duration of the stimulus reduces it still further to a value of about 0.025 degrees². Beyond the ranges of complete temporal and spatial summation there are ranges of partial summation which, within a variable range, approximate to the square-root laws predicted by the quantum fluctuation hypothesis. The upper limits of partial summation have not been reached under all conditions, but it can be seen that these ranges too are curtailed by the factors which reduce the ranges of complete summation—increase of stimulus area and duration, and background intensity.

The two sets of curves of Fig. 2 were obtained using the largest and the smallest values for the area of the test stimulus. It would obviously be possible to obtain similar curves for intermediate sizes of the stimulus, and similarly one could use intermediate stimulus durations to get curves of spatial summation like those of Fig. 3. Complete sets of thresholds at all combinations of stimulus area and duration have been determined at two background intensities, and these show that curves of temporal and spatial summation at intermediate values of area and duration lie between those taken at the extreme values which are shown in Figs. 2 and 3. No special features appear to be associated with particular durations or areas of test stimulus.

These complicated phenomena become more coherent if it is pointed out that the three factors which hinder further summation—increase of area or duration of the stimulus, or increase of the background intensity—all decrease the ratio $\Delta I/I$ at threshold. Hence as $\Delta I/I$ is reduced it becomes less susceptible to further lowering by increase of the area or duration of the stimulus.

DISCUSSION

Previous results

Figs. 2 and 3 show that temporal and spatial summation in human vision are complex, interrelated phenomena which are not adequately described by the simple empirical laws (Bunsen-Roscoe, Ricco, and Piper) except within certain rather narrow ranges. The shortcomings of these laws are fairly widely known, and the conditions under which they are valid are discussed by Graham & Margaria (1935) and Graham, Brown & Mote (1939). The interrelations between temporal summation and spatial summation do not, however, appear to have been sufficiently appreciated, though they have been reported in the literature. Piéron (1920) stated that there were reciprocal relations between the duration of the stimulus and the amount of spatial summation, and between the area of the stimulus and the amount of temporal summation. Graham & Margaria (1935) studied this effect and showed that the area of the test stimulus had a big effect on temporal summation. Their curves show clearly that the limit of complete temporal summation (Bunsen-Roscoe Law) is reached earlier with a large than with a small stimulus area, and that the reduction of threshold intensity brought about by increasing the duration of stimulus from under 1 msec to over 0.5 sec is greater when stimulus area is small than when it is large. Baumgardt (1947) obtained similar results, and Graham and Margaria's main conclusions are confirmed by the present findings, but there are some discrepancies. They found deviations from the Bunsen-Roscoe Law at durations as short as 2 msec, whereas deviations do not appear in the present results until just below 0.1 sec. Furthermore, they found a large range of partial summation for the large stimulus,

and only a small range for the small stimulus, whereas the reverse is true in the present results. The reason for these discrepancies is not clear, but they might result, in part at least, from the fact that they were using a retinal region 15° from the fovea, as against 7° in this paper. If this is the correct explanation, the retina closer to the fovea must be considerably more efficient at temporal summation than the more distant periphery.

The fact that an increase in the intensity of a background reduces the degree of spatial and temporal summation for a test flash superimposed upon it was shown by Stiles & Crawford (1934). Graham & Kemp (1938) showed the effect on temporal summation in rather greater detail, and Blackwell (1946) showed the effect on spatial summation in a very thorough study, but the interpretation of his findings is complicated by the use of a free-roaming eye so that the image of the test area could fall on any retinal region. Willmer (1954) showed that the apparent brightness of a small, foveally viewed, test patch was increased more by increasing its area at low intensities than at high intensities, which appears to be due to a change in the amount of spatial summation. The observations of Van der Brink & Bouman (1954) and Gregory (1955) also indicate changes of summation with intensity.

The effect of background luminance on summation must be closely related to the changes in summation during dark-adaptation which have been found by Craik & Vernon (1941), Arden & Weale (1954), and Rushton & Cohen (1954), though Wald (1938) failed to observe any such effect. Another observation which may be related is that of Beitel (1934, 1936), who observed the effect of one spot upon the threshold for another placed near it, and found the threshold lowered (summation) if it was at a low intensity, and raised (inhibition) if it was brighter. This was probably early evidence of that complexity of retinal organization, foreseen by Baumgardt & Segal (1947) and since (Kuffler, 1953; Barlow, 1953) shown clearly in electrophysiological preparations, which makes the interpretation of psychophysical experiments in terms of summation alone inadequate.

In the present paper a retinal locus $6^\circ 30'$ from the fovea was used. This is not ideal for the study of spatial summation because the sensitivity of the retina is not uniform here. Pirenne & Marriott (1954) showed that the threshold for a small stimulus drops by 0.5 log units on moving from $3^\circ 30'$ to $9^\circ 30'$ from the fovea, the limits reached by the largest test spot used here. Pirenne & Marriott (1954) also compared the threshold for the two halves of a circular test field 11.3° in diameter centred 7° from the fovea, and found the threshold for the peripheral half only 0.21 log. units lower; for a 6° spot the difference would presumably be less, and the degree of non-homogeneity this indicates is probably not enough to obscure the results of the present paper. The main contribution of these results is to show up the interrelations between temporal summation, spatial summation, and background intensity, in a single retinal region.

Area and time

α and τ were defined (Barlow, 1957) as the area and time over which quanta absorbed from the background were liable to be confused with quanta absorbed from a short duration small area stimulus, and the present observations were made in the hope of obtaining values for them. It was thought at first that the product of area and time which is plotted in Fig. 1 could be identified with the product of α and τ . The argument for doing so is that threshold depends on the *quantity* of light exceeding a certain value, and that stimulus and background lights must be treated alike by the unit which ultimately responds to this quantity. Fig. 1 may be thought of as showing the factor by which the *intensity* of a long duration large area stimulus must be multiplied to obtain this *quantity*, and it should therefore be equal to $\alpha\tau$, the factor by which the background *intensity* must be multiplied to obtain the *quantity* of light, which is liable to be confused with the stimulus. This argument would be acceptable in the case of many simple physical systems, but in the case of the eye it is seen to be fallacious as soon as one considers the complexity of organization of the retinal units. The surround of a receptive field tends to inhibit the central zone so that when light is delivered to both synchronously it is less effective than when it falls on the centre alone (Kuffler, 1953; Barlow, 1953): now it is clear that light from the stimulus falling in this surround will *not* sum with light falling in the central zone, but it is possible that *fluctuations* in the number of quanta absorbed from the background *will* contribute to the noise from which the stimulus is to be distinguished.

It does not seem possible to get definite values of α and τ from these results and the best that can be done is to take the upper limits to the Ricco and Bunsen-Roscoe ranges as lower limits to their values. One can extend a stimulus up to these limits without raising the threshold number of quanta required, and when it has these values the number of quanta from the background contributing to the noise cannot be less than the number absorbed in that area and time. There are, however, many possible reasons for the true values of α and τ lying beyond the ranges of complete spatial and temporal summation, so that one cannot decide their true values from these experiments, nor can one tell whether they change with background intensity.

Quantum fluctuation hypothesis

In counting the quanta absorbed from the stimulus a certain number of quanta coming from the background will inevitably be counted with them, and according to the hypothesis to be tested the threshold corresponds to the limit set by the fluctuations in this number. The limit will be lower if this number is reduced, but at the same time the maximum possible number of quanta from the stimulus must be collected. Using stimuli which are sharply

delimited in space and time (as in the present experiments) the best performance will clearly be obtained by 'sampling' the numbers of quanta absorbed over areas and durations matched to the area (A) and duration (T) of the stimulus. When A and T are increased, the 'sampling' area and time must also be increased, and the average number of quanta counted from the background will then be increased in direct proportion to the area and duration of the stimulus. The actual numbers absorbed on particular occasions will be distributed according to the Poisson distribution, to which an approximation is given by a normal distribution of standard deviation equal to the square root of the average number of quanta absorbed. Hence, if the threshold response is of constant reliability, $\Delta N \propto A^{\frac{1}{2}}T^{\frac{1}{2}}I^{\frac{1}{2}}$, where ΔN is the incremental quantity of light; or $\Delta I \propto A^{-\frac{1}{2}}T^{-\frac{1}{2}}I^{\frac{1}{2}}$, where ΔI is incremental intensity. The dependence on intensity is actually described better if $I + X$ is substituted for I (Barlow, 1957), where X is an intrinsic source of noise represented as 'dark light'. The expected law then becomes

$$\Delta I \propto A^{-\frac{1}{2}}T^{-\frac{1}{2}}(I + X)^{\frac{1}{2}} \quad (1)$$

The results shown in Figs. 2 and 3 do not fit this equation. It is true that increment threshold is in fact roughly proportional to $A^{-\frac{1}{2}}$ over a moderate range which varies in position with background intensity and stimulus duration. This is the range for which Piper's law holds, and it would be represented on this double logarithmic plot by a line of slope -0.5 . Similarly, there is a rather short range in Fig. 2, where increment threshold is proportional to $T^{-\frac{1}{2}}$. The validity of such square-root laws might be taken as some evidence for the quantum fluctuation hypothesis, but there is a serious objection. The law $\Delta I \propto (I + X)^{\frac{1}{2}}$ holds for small area short duration stimuli, and it fits (approximately) the left-hand points of Figs. 2 or 3. It will obviously only continue to hold for as long as these curves continue downwards parallel to each other; but, as has been pointed out, the laws of complete temporal and spatial summation break down at smaller areas and times when the background intensity is raised. It follows that the law $\Delta I \propto (I + X)^{\frac{1}{2}}$ does not hold beyond the ranges of complete summation, and it is only here that the $A^{-\frac{1}{2}}$ and $T^{-\frac{1}{2}}$ laws begin to hold. Equation 1 does not, therefore, hold for all three variables over any range of A , T and I .

In summary, then, square-root laws are found as predicted by the quantum fluctuation hypothesis, but the range for areas is variable, and the range for times short; furthermore, for values of A and T where $\Delta I \propto A^{-\frac{1}{2}}$ and $T^{-\frac{1}{2}}$, $\Delta I \propto (I + X)^{\frac{1}{2}}$ is untrue, and conversely for values of A and I where $\Delta I \propto (I + X)^{\frac{1}{2}}$ holds, $\Delta I \propto A^{-\frac{1}{2}}$ and $T^{-\frac{1}{2}}$ do not.

Since equation 1 is wrong, one or both parts of the hypothesis from which it is derived must be wrong: either a subject's responses are not of equal reliability under different conditions, or they are not limited solely by quantal

fluctuations, or neither is true. The first possibility appears unlikely to be sufficient to account for the major deviations because (a) false positive responses do not occur noticeably less often where the deviations are greatest (b) deliberate attempts to affect the reliability of response have rather a small effect on the absolute threshold (Barlow, 1956). Furthermore, the slope of frequency of seeing curves is related to reliability of response, but this does not seem to vary greatly within the range of conditions covered here (see Blackwell 1946), though it does under some conditions (see Denton & Pirenne, 1954; Crawford & Pirenne, 1954). Other factors must, therefore, reduce efficiency of vision below the quantal fluctuation limit, and the present results show the conditions where the efficiency is greatest, and what factors decrease it. In the retinal region $6^{\circ} 30'$ from the fovea efficiency is highest for a stimulus about $40'-45'$ in diameter (0.4 degrees²) and about 0.1 sec duration, superimposed on a background of low intensity. Efficiency falls off when the added stimulus is changed in area or duration to values lying outside the Piper and $T^{\frac{1}{2}}$ ranges, and when the background intensity is raised. The following tentative explanations for these losses of efficiency are suggested.

Mismatching loss

Work on single retinal units in the frog (Hartline, 1940; Barlow, 1953) has indicated that the response depends on the total quantity of light falling in the central zone of the receptive field, and it is natural to suppose that fluctuations in the background light in an area at least as large as this will interfere with the detection of incremental stimuli. Hence when a stimulus is smaller than this area an unnecessarily large number of quanta from the background must be summed with it, thus raising the threshold above the optimum that would be attainable with a receptive field matching the stimulus. For a fixed size of receptive field efficiency will be highest for a test spot which exactly fills it, and will fall off when the spot is reduced in size. In a similar way, efficiency might be expected to drop off when the duration of a stimulus is decreased below the summation time (upper limit of Bunsen-Roscoe range). Whether there is also a loss when the stimulus is larger or longer than the summation time will depend upon other factors, such as the extent of the 'transmission' or 'screening' loss (see below).

Lateral inhibition loss

In the cat (Kuffler, 1953) and frog (Barlow, 1953) it has been shown that the annular surround of a receptive field acts in opposition to the central zone. This can lead to the paradoxical situation where a large stimulus spot evokes a weaker discharge than a smaller one. More recently (Barlow, FitzHugh & Kuffler, 1957) it has been shown that this lateral inhibition occurs when the retina is light-adapted and the stimuli are superimposed on a steady

background, but does not occur when the background is turned off and the retina dark-adapted. Furthermore, even in light-adaptation, the inhibitory effect is less pronounced when brief stimuli are used. Thus the conditions (raising background intensity and increasing stimulus duration) which diminish spatial summation in human experiments are the conditions which accentuate lateral inhibition in animal experiments. The gap between the quantum fluctuation limit and the actual performance with long large stimuli might thus be attributed to lateral inhibition.

Transmission or screening loss

The two preceding causes of loss of efficiency are based upon known physiological mechanisms, and may suffice to explain losses when the stimulus is too small and short, or too long and large. They do not explain why there is a progressive loss of efficiency, with all except short small stimuli, when the background intensity is increased. Gregory's (1956) suggestion that additional 'neural' noise is added to the system between the receptors and the visual centres might provide an explanation, but only if noise is added *after* the point at which sensory adaptation occurs: if the noise was added *before* adaptation, it would cause greatest loss of information with the weakest signals, that is at low intensities. An alternative proposal is derived from that put forward by Baumgardt (1953) to reconcile the slope of frequency of seeing curves at absolute threshold with his two-quanta explanation of spatial and temporal summation. He suggested that the absorption of two quanta within a certain area and time caused an impulse in the optic nerve, but that two or more such impulses were required to cause a sensation. The new feature of this idea is that the threshold decision is not made in a single step, but in stages; this feature fits easily into a signal noise theory of threshold. The original idea leading to equation 1 required that the absorption of every single quantum should be signalled to some central point where the threshold decision was taken. According to the new idea the retina would 'screen' messages from the receptors, and only signal centrally when something occurred with a moderately low prior probability if there was no stimulus. If one such signal corresponded to a very low prior probability, one would be sufficient to allow a 'seen' response to be given without danger of excessive false positives, and in this situation 'probability summation' alone could occur (see Pirenne, 1956). If, on the other hand, each signal corresponded to an event of high prior probability, the conditions would return closer to those assumed for equation 1. In this way the idea that impulses in the optic nerve occur moderately often without any incremental stimulus being applied, links the 'probability summation' hypothesis with explanations of temporal and spatial summation as signal/noise discriminations of constant reliability.

A screening mechanism of this type might explain a number of puzzling

aspects of visual function; for example, the failure of temporal and spatial summation when the intensity of the threshold increment becomes low relative to the background intensity (see p. 343), and the occurrence of Weber's law with long large stimuli (Barlow, 1957). Furthermore as well as explaining why efficiency drops when the background is increased, it may also show how the eye avoids overloading and maintains reasonable efficiency over such a very wide range of intensities. It should be noticed that explanations of loss of efficiency through screening are complementary to explanations in terms of specific physiological mechanisms, and do not conflict with them. For instance, lateral inhibition may be the means by which the screening level is raised when the background intensity is increased. At present, however, one can only suggest that Baumgardt's screening concepts might be a fruitful modification of the quantum fluctuation hypothesis.

In conclusion, then, the eye does not perform equally efficiently in the detection of test objects of different areas and durations superimposed on backgrounds of different intensities, and these variations of efficiency provide clues as to the physiological mechanisms of vision.

SUMMARY

1. Increment thresholds have been measured in a retinal region $6^{\circ} 30'$ from the fovea with test spots of varying sizes and durations superimposed on backgrounds of various intensities.

2. The total amount of summation (as measured by the ratio of lowest threshold quantity of light to lowest threshold intensity) decreases continuously as background intensity is raised: this decrease occurs in the photopic as well as the scotopic range.

3. The upper limit of complete temporal summation is decreased by increasing the area of the stimulus, and by increasing the background intensity.

4. The upper limit of complete spatial summation is decreased by increasing the duration of the stimulus, and by increasing the background intensity.

5. The increment threshold lies above the limit set by quantal fluctuations of the background light, except possibly for a single set of conditions: factors which might prevent attainment of the limit are suggested.

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REFERENCES

- ARDEN, G. B. & WEALE, R. A. (1954). Nervous mechanisms and dark-adaptation. *J. Physiol.* **125**, 417-426.
- BARLOW, H. B. (1953). Summation and inhibition in the frog's retina. *J. Physiol.* **119**, 69-88.
- BARLOW, H. B. (1956). Retinal noise and absolute threshold. *J. Opt. Soc. Amer.* **46**, 634-639.
- BARLOW, H. B. (1957). Increment thresholds at low intensities considered as signal/noise discriminations. *J. Physiol.* **136**, 469-488.
- BARLOW, H. B., FITZHUGH, R. & KUFFLER, S. W. (1957). Change of organization in the receptive fields of the cat's retina during dark adaptation. *J. Physiol.* **137**, 338-354.

- BAUMGARDT, E. & SEGAL, J. (1947). Facilitation et inhibition, paramètres de la fonction visuelle. *Année Psychol.* **43**, **44**, 54–102.
- BAUMGARDT, E. (1947). Sur la loi spatiale de la brillance liminaire en vision extrafovéale. *C.R. Acad. Sci., Paris*, **225**, 259–261.
- BAUMGARDT, E. (1953). Seuils visuels et quanta de lumière. Précisions. *Année Psychol.* **53**, 431–441.
- BEITEL, R. J., JR. (1934). Spatial summation of subliminal stimuli in the retina of the human eye. *J. gen. Psychol.* **10**, 311–327.
- BEITEL, R. J., JR. (1936). Inhibition of threshold excitation in the human eye. *J. gen. Psychol.* **14**, 31–61.
- BLACKWELL, H. R. (1946). Contrast thresholds of the human eye. *J. opt. Soc. Amer.* **36**, 624–643.
- CRAIK, K. J. W. & VERNON, M. D. (1941). The nature of dark adaptation. *Brit. J. Psychol.* **32**, 62–81.
- CRAWFORD, B. H. & PIRENNE, M. H. (1954). Steep frequency-of-seeing curves. *J. Physiol.* **126**, 404–411.
- DENTON, E. J. & PIRENNE, M. H. (1954). Absolute sensitivity and functional stability of the human eye. *J. Physiol.* **123**, 417–442.
- DE VRIES, H. (1943). The quantum character of light and its bearing upon the threshold of vision, the differential sensitivity and acuity of the eye. *Physica*, **10**, 553–564.
- GRAHAM, C. H., BROWN, R. H. & MOTE, F. A. (1939). The relation of size of stimulus and intensity in the human eye. I. Intensity thresholds for white light. *J. exp. Psychol.* **24**, 555–573.
- GRAHAM, C. H. & KEMP, E. H. (1938). Brightness discrimination as a function of the duration of the increment in intensity. *J. gen. Physiol.* **21**, 635–650.
- GRAHAM, C. H. & MARGARIA, R. (1935). Area and the intensity time relation in the peripheral retina. *Amer. J. Physiol.* **113**, 299–305.
- GREGORY, R. L. (1955). A note on summation time of the eye indicated by signal/noise discrimination. *Quart. J. exp. Psychol.* **7**, 147–148.
- GREGORY, R. L. (1956). An experimental treatment of vision as an information source and noisy channel. *Information Theory: third London Symposium*, pp. 287–299. Ed. C. Cherry. London: Butterworth.
- HARTLINE, H. K. (1940). The effects of spatial summation in the retina on the excitation of the fibres of the optic nerve. *Amer. J. Physiol.* **130**, 700–711.
- KUFFLER, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *J. Neurophysiol.* **16**, 37–68.
- PIÉRON, H. (1920). De la valeur de l'énergie liminaire en fonction de la surface rétinienne excitée pour la vision fovéale, et de l'influence réciproque de la durée et de la surface d'excitation sur la sommation spatiale ou temporelle pour la vision fovéale et périphérique. *C.R. Soc. Biol., Paris*, **83**, 1072.
- PIRENNE, M. H. (1956). Physiological mechanisms of vision and the quantum nature of light. *Biol. Rev.* **31**, 194–241.
- PIRENNE, M. H. & MARRIOTT, F. H. C. (1954). Quantum theories of the absolute threshold: influence of retinal position and area. *Optica Acta*, **3**, 151–155.
- ROSE, A. (1942). The relative sensitivities of television pick-up tubes, photographic film, and the human eye. *Proc. Inst. Radio Engrs, N.Y.*, **30**, 293–300.
- ROSE, A. (1948). The sensitivity performance of the human eye on an absolute scale. *J. opt. Soc. Amer.* **38**, 196–208.
- RUSHTON, W. A. H. & COHEN, R. D. (1954). Visual purple level and the course of dark-adaptation. *Nature, Lond.*, **173**, 301–302.
- STILES, W. S. (1939). The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc. Roy. Soc. B*, **127**, 64–105.
- STILES, W. S. & CRAWFORD, B. H. (1934). The liminal brightness increment for white light for different conditions of the foveal and parafoveal retina. *Proc. Roy. Soc. B*, **116**, 55–102.
- VAN DER BRINK, G. & BOUMAN, M. A. (1954). Variations of integrative actions in the retinal system: an adaptational phenomenon. *J. opt. Soc. Amer.* **44**, 616–620.
- WALD, G. (1938). Area and visual threshold. *J. gen. Physiol.* **21**, 269–287.
- WILLMER, E. N. (1954). Subjective brightness and size of field in the central fovea. *J. Physiol.* **123**, 315–323.