

COMPARATIVE STUDIES ON THE PERIPHERAL AND CENTRAL RETINA

IV. TEMPORAL SUMMATION OF SUBLIMINAL VISUAL STIMULI AND THE TIME COURSE OF THE EXCITATORY AFTER-EFFECT

RAGNAR GRANIT AND WILLIAM A. DAVIS

*From the Eldridge Reeves Johnson Foundation for Medical Physics, University of
Pennsylvania*

Received for publication June 12, 1931

Bloch (1885) discovered that for short flashes of light the product of intensity, i , and time of exposure, t , are constant at the threshold and the observation has since been repeatedly confirmed. Although the simple formula $it = c$ seems to be a fairly good approximation for times between 2 and about 30σ (Piéron, 1920a, b; Blondel and Rey, 1912; and Reeves, 1918), for longer times of exposure the relation may assume the form $it = a + bt$ (Blondel and Rey). Braunstein (1923) found $it = c$: only within about 10σ and only with small areas. For very short times the relation breaks down. The obvious analogy between Bloch's rule and the Bunsen-Roscoe law, according to which the effect in photochemical reactions is directly proportional to the product of time of exposure and light absorbed, has led to interesting attempts to correlate the two particularly by Hecht, although as that author has pointed out (1929) there is evidence to show that such correlations in so far as the vertebrate retina is concerned are necessarily somewhat schematic.

Adrian and Matthews (1927) working on the excised eel's eye and using the latent period of the discharge in the optic nerve as an index of the intensity of the physiological process found that with supraliminal stimuli the product $i \times t$ was integrated just as in the experiments on the eye reported above. In a later paper (1928) they were also able to show that this index, the latent period, was influenced by synaptic processes in the retina. It was, as a matter of fact, by measuring the latent period that they discovered spatial summation between separated stimuli and proved that the interchangeability between area and intensity was due mainly, if not altogether, to synaptic interaction. In the light of this finding, it is now possible to understand the fact which they pointed out in their second paper, that area, a , stimulated also influenced the result so that approximately corresponding latencies were given by equal energies, defined

as equal products of $i \times t \times a$.¹ It would seem therefore as if part at least of the integration were synaptic in origin and the latent period were partly, or perhaps mainly, the time taken by the stimulus to attain neurone threshold. (See the recent important work of Eccles and Sherrington, 1931; Eccles, 1931.) In this connection it is interesting to note that Piéron has found in the human eye that the smallest quantities of energy necessary for threshold stimuli are obtained with relatively large areas stimulated for short times (about 10σ).

Previous papers in this series (Granit, 1930; Granit and Harper, 1930) show that with supraliminal stimuli spatial summation between separated areas occurs also in the human eye with sensory phenomena as indicators. In the present paper our main problem is to determine whether there is evidence for synaptic summation of two *successive* subliminal stimuli. It is evident that the reflex concept of temporal summation implies that, to use Sherrington's words, mere duration of a stimulus becomes equivalent to intensity ("addition latente," Sherrington, 1924-25). A relation of this general type is Bloch's rule, as well as the formula given by Blondel and Rey. From Richet and Bréguet's (1880) and Rutenburg's (1914) work we know that subliminals actually do sum in the human eye.

METHOD. Our method is taken from experiments on summation of successive subliminal stimuli in the spinal flexion reflex by Eccles and Sherrington (1930) which have been modified to fit the demands of a visual problem. The principle underlying this method is the use of a second subliminal as a test of the after-effect left by a subliminal predecessor. Eccles and Sherrington sent two electric shocks at various measurable intervals into two nerves of the limb and recorded isometrically the amount of reflex contraction elicited by the second shock in consequence of its acting upon the after-effect of the first. As a matter of course neither of them caused any contraction alone. As used for the present work in vision it means that a second subliminal flash will have to be adjusted so as just to be able to raise the after-effect of a preceding invisible flash above the threshold. It is then evident that the intensity necessary for the second subliminal, with various intervals between the two, must depend upon the amount of excitatory remainder left by the first. The higher the level of the excitatory after-effect, the less has to be added to it in order to make it visible. In this way it should be possible to map out the time course of a subliminal excitatory state just as was done by

¹ Adrian and Matthews did not rediscuss their earlier findings in the light of the important results brought forth in their third paper, which definitely excluded certain alternative explanations suggested in the discussion attached to the second paper. This probably explains why their proof that synaptic factors are involved in the latent period variations as well as in the retinal action current has escaped attention.

Eccles and Sherrington for the reflex centre. In their work the time course of the central excitatory state left by a subliminal stimulus proved to be a very complex process with maxima and minima at unexpected intervals between the two shocks. This, they inferred, was at least in part due to the fact that electric stimulation is inadequate in that it samples a number of fibres of mixed inhibitory and excitatory character. In this respect the eye would probably be a more satisfactory type of centre, provided the excitatory remainder can be proved to have a synaptic component.

Time and intensity, as stated above, are interchangeable for short flashes, at the threshold. It should therefore be possible by varying either factor to determine the quantity ($q = it$) of light necessary for the second flash in order that it may raise the first above the threshold. Since it is technically far more convenient to vary the duration of the second flash than its intensity, this was the procedure adopted in most of our experiments. The work was however concluded by running six control series in which the intensity of flash 2 was varied by means of thin gelatine Wratten filters covering the opening through which passed the light of the second flash. In all the last experiments the procedure consisted in 1, making flash 1 subliminal by putting in neutral tint Wratten filters with a final adjustment made by shifting the position of the lamp; 2, running flashes 1 and 2 with various dark intervals and for each interval finding the angular opening of 2 or the filter necessary for raising the after-effect of 1 above the threshold. Two important precautions in such experiments are to restrict the fixation time to a certain number of successive trials and to have the flashes controlled by the experimenter and signalled by the observer.

The apparatus employed was as follows: In a heavy circular metal disc a 180° slot was cut out as shown in figure 1. Concentric light metal sectors of different widths were used for varying the size of the openings 1 and 2 as well as the dark interval between them. To the axis of the disc was geared another disc—not shown in figure 1—with an opening adjusted so as to expose 1 and 2 in their proper sequence approximately every 1.8 second, when the heavy disc rotated at a speed of 6.16 RPS. The speed of the motor was controlled with the aid of a Weston electric tachometer connected to a voltmeter which gave a needle excursion of about $1\frac{1}{2}$ divisions for 1 per cent alteration in speed, whereas the experimental values were determinable to only about 10 per cent. By means of a sliding rheostat, excursions of the needle were continuously compensated for. In most experiments flash 1 was kept constant at 25° of angular opening, corresponding to 11.3σ and flash 2 was varied up to the same limit, which is the range within which the relation $it = c$ holds. In a few series the motor was run at half its ordinary speed in order to obtain longer intervals between the flashes. This was compensated for by making flash 1 correspond to $12\frac{1}{2}^\circ$ so as always to have the first flash lasting 11.3σ .

RESULTS. The dark adapted periphery gives the most satisfactory conditions with regard to stability of threshold which is naturally a chief

difficulty and necessitates repeated controls with flash 1 alone. No stability is obtained in less than about an hour's dark adaptation.

In figure 2 *B*, *C*, *D* and *E* relate the interval in σ between the flashes, plotted as abscissae and the duration of the second flash in σ plotted as ordinates. *B* and *C* were obtained with an area of 1° , *D* and *E* with an area of $2\frac{1}{2}^\circ$ of visual angle. Each of these curves is the average of several experiments on the same observer. The differences between *B* and *C* and between *D* and *E* will be discussed in the next paragraph. In curve *A* the ordinates represent the duration of the second flash given as per cent of the duration of the first, the values for the curve being obtained by averaging the data of the other four curves. In the case of these four the ordinates are plotted from above downwards inasmuch as they represent the actual readings. Hence at the ordinate representing 11.3σ the stimulus is the one necessary for the threshold and the difference between the zero ordinate and any point on the curves shows how much excitation had to be added in order to reach the threshold. The difference between any point on the curve and the 11.3σ ordinate indicates the relative level of the excitatory state left by the first flash. The simple assumption has been made that flash 2 adds onto the remainder of flash 1. The value $11.3 - y$ is therefore defined as the level of excitatory remainder, y being the experimentally determined duration of flash 2. Another fairly simple definition of the level of the excitatory remainder would be to express it as an inverse function of the amount of light in the second flash, but such a procedure would only tend to smooth out significant differences in the actual readings without adding to the ease of interpreting the data.

The actual level of the excitatory state varies from individual to individual and from experiment to experiment, extremes being shown by comparing *B* with *C* and *D* with *E*. This is chiefly because of the difficulty involved in knowing precisely how far below the threshold the first subliminal happens to be. But there are also variations from day to day which cannot be accounted for and which appeared in spite of the fact that the adaptation to the dark room was started from a constant level, obtained from light-adapting to a bright screen during 5 minutes. However the time course of the process appears always to be in a general way similar, as is well shown by the average curve *A*. It first drops rapidly to a fairly steady level which with different observers runs out to between $25-40\sigma$. Then follows a slower fall and at about 130σ it is necessary to have the second flash of nearly the same strength as the first. This duration of flash 2 obviously sets a limit to the experiment. When the interval between the two subliminals was increased to $130-140\sigma$, which were the longest intervals that could be obtained with our apparatus, it was sometimes impossible to obtain summation to threshold value. However, at these long intervals the probability of eye movements interfering must be

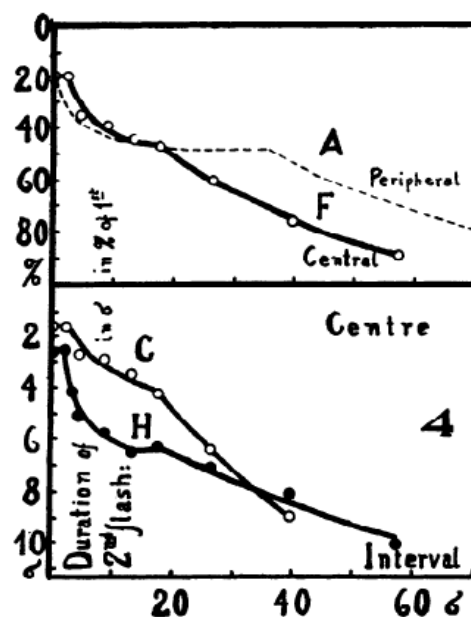
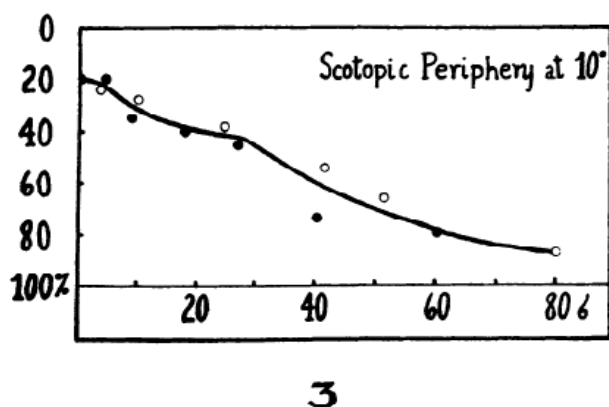
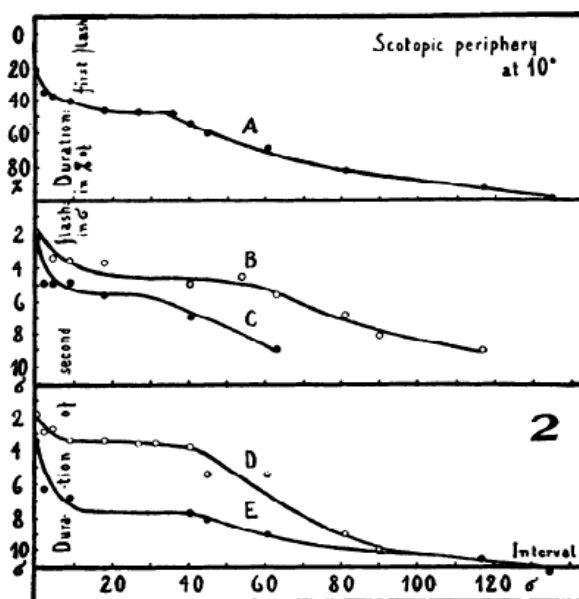
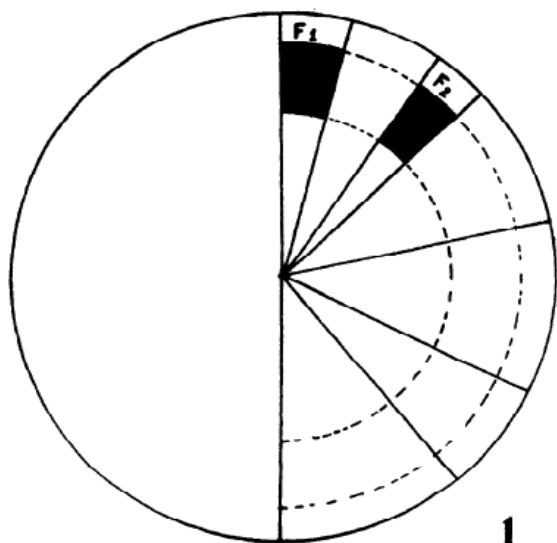


Fig. 1. Shows the rotating disc with its semicircular slot covered by a number of opaque sectors. F_1 and F_2 (black) are the adjustable openings through which passes the lightbeam. The disc rotates counter-clockwise. The size and location of F_1 is kept constant, F_2 is varied as described in the text.

Fig. 2. Experiments with observer I in the dark-adapted periphery at 10° . The subliminal flash is at about 6.6×10^{-5} millilambert. For description, see text.

Fig. 3. Experiments with observer II in the dark-adapted periphery at 10° . Black dots refer to a variation in duration of flash 2, the subliminal flash 1 being at about 1.0×10^{-4} ml. Open circles refer to a variation in intensity of flash 2, the subliminal flash 1 being at about 2.4×10^{-3} ml.

Fig. 4. Experiments with observer I in central vision, the eye adapted to about 0.03 ml. C and H are obtained with an area of 3° and 1° respectively. The subliminal flash is at about 0.021 ml., the background at the same brightness diminished by a just perceptible difference. For description, see text.

considerable. It is somewhat surprising to find that Rutenburg (1914) reports summation of two subliminals at 1300σ apart, which led us to expose our flashes only every 1.8 second. Rutenburg, in trying to determine the quantity, q , at the threshold, incidentally noted that with low intensities q decreased. This was then found to be a feature of his apparatus making the stimuli appear at shorter intervals when the intensity was diminished. The effect, as stated, could be traced up to 1.3 seconds, but it may be questioned whether he kept the number of trials constant. The duration of the flashes may also influence the time course of the excitatory remainder, particularly at long intervals where eye movements must make the probability of losing or catching a flash a function of the time it lasts.

A comparison of B and C with D and E shows that within limits the area stimulated is of little if any significance and the same result was obtained with central fixation (fig. 4) and areas related as 1:9. This does not mean that the effect of area is lacking at the threshold, for it has been well known since the publication of Ricco's work (1877) that the effect of area is considerable in compensating for low intensity of stimulation. But due to the fact that the total quantity ($i \times t \times a$) always is brought to just below threshold value and to the necessity of a constant index such as the threshold the spatial effect is already accounted for in adjusting the intensity for the first flash. The fact that the area stimulated does not materially alter the general relations found does, however, suggest that lateral diffusion of photo-chemical products hardly enters as an important factor.

Figure 3 shows that similar results are, within limits, obtained in those experiments in which the intensity of flash 2 is varied instead of its durations. The dots represent a variation in duration of the flash, the circles a variation of intensity. In these latter experiments the two flashes were of equal and very short duration (0.6σ) and the intensity of the second was varied by means of filters as has already been described.

Rapid local adaptation in the periphery makes it extremely difficult to apply our rather sensitive method to peripheral vision with a bright background. In central vision on the other hand it was found difficult to work with an absolutely black background and impossible to do so if the eye was kept dark adapted. In this latter case the fixation tends to shift to a more sensitive paracentral spot as was recognized long ago by Simon (1904). However in spite of the fact that he demonstrated unconscious deviations of considerable amplitude from the middle of the fovea, a number of workers still continue to report on the behaviour of the fovea in dark adaptation without controlling such eye movements. Because of these facts a background of about 0.02 ml. was chosen for the fovea. The results are shown in figure 4, the average curve F being plotted above the

individual averages C and H and together with the corresponding peripheral curve A of figure 2. The comparison, for reasons just stated, does not refer to identical conditions of background for A and F and only serves to emphasize the general similarity of the two. It will be seen that the actual time relations of the corresponding phases are somewhat different. A characteristic feature of the foveal curves is that the level of the excitatory remainder does not begin to drop until after $2-4\sigma$. This is sometimes noticeable in the periphery as well, where a similar short plateau is given by observer II (fig. 3). As a rule however this phenomenon is characteristic of the fovea.

Our results indicate that there are at least two factors which determine the level of the excitatory remainder as is illustrated by the two components of the curves—the fall to a plateau level and the subsequent sudden drop from this plateau. It is perhaps not mere coincidence that the break in the curve takes place at a time which corresponds approximately to that which constitutes the upper limit of the interval within which $i \times t = c$ has been found to hold. It is also worthy of note that Bloch's rule does not apply for very short exposures which cover the duration of the initial short plateau.

It is now desirable to attempt a direct determination as to whether subliminal stimuli reach the synapses and whether such stimuli are discharged laterally as is known to be the case with supraliminal ones. The method used has been to employ two semicircular test patches of 1° radius (fig. 1), 10 to 30 minutes of visual angle apart. By slightly rearranging the apparatus shown in figure 1 the two flashes have been made to stimulate the two separated semicircles. The flash applied to the one area is made subliminal and constant and the experiment consists in determining whether a similar subliminal second flash to the other area is capable of raising the remainder of flash 1 above the threshold. Care was taken that no light from one semicircle could spread over onto the other.

In spite of every possible precaution, however, the experiment was found to be too difficult to be very reliable. A great deal of time was devoted to it until we finally became convinced that the two flashes actually do sum in the dark adapted periphery at 10° and that it makes little difference whether the flashes come simultaneously or are separated by a few σ . The possibility of spread owing to imperfections in the optical system of the eye is a factor which must be considered. Whether it can explain the result or not is a question for which no definite answer can be given at this time although it must be emphasized that the defects of the optical system at oblique angles of incidence as low as 10° can hardly be serious. Aubert and Foerster (1865) performed an interesting experiment many years ago which sheds light on this problem. They projected an image of two light spots onto the retina of the excised eye of an albino

rabbit so that the images could be examined microscopically through the sclera. Thus they found that in moving the eyeball around its axis the two points appeared sharp and separated all over the retina, an observation which has recently been confirmed by Gross (1931). Aubert and Foerster concluded that the impairment of form discrimination in peripheral vision is chiefly due to properties of the retina. In a later paper in this series (Graham and Granit, 1931) it will be shown that in so far as purely physiological factors are concerned summation and its anatomical equivalent, the convergence of several frontal and lateral paths upon single neurones, offer a satisfactory explanation of the loss of visual acuity in the periphery. In our experiment it would seem as though the physiological factors are the more important because of the curious fact that the effect of separated areas upon one another could not be obtained with very long exposures even though the semicircles were separated only by a very thin black line.

As regards central vision a large number of tests were made with the faintly illuminated background of the previous experiments. The effect was however so small that it was thought statistical methods and a great number of observers would be necessary for a satisfactory treatment of the problem. We have therefore no definite results to report.

DISCUSSION. Temporal summation seems to be as fundamental a retinal property as the effects of spatial summation discussed in the previous communications. It is obtained in different parts of the retina and with different states of adaptation. Although it is probable that part of the effect is photochemical in nature, there is little reason to assume a photochemical after-effect lasting for 130σ and taking the complicated course indicated by our curves. As shown in the last section there is also some evidence to the effect that states of excitation which are subliminal to the final conscious interpretation reach the synapses and spread laterally. This then would be an important factor in determining the well known facilitating effect of area upon the threshold. Piéron (1929) and Graham and Goldman (1931) have recently come to the same conclusion.

All the previous papers in this series show that with supraliminal stimuli synaptic factors can be traced and in some cases measured with a considerable degree of accuracy throughout the range of sensory phenomena studied. It is now interesting to see that even subliminal stimuli yield results which could be explained only with difficulty and a number of arbitrary assumptions unless the obvious conclusion is drawn that the absolute sensory threshold is ultimately conditioned by processes in the neurones, i.e., is subjected to modifications by temporal and probably also by spatial summation. The process may take place at different levels in the retina, perhaps as early as in the receptor body or at the junction between receptor and bipolar cell. Inasmuch as the effect is apparently

identical with central summation as studied by Eccles and Sherrington and by Bremer (1930) with a somewhat similar method, the absence of secondary excitatory maxima, such as found in some of their curves, is worth noting. To account for the steady state of the excitatory remainder revealed by the plateau in our curves many suggestions may be proposed. In general they will fall into two categories dependent upon whether one prefers photochemical notions to current concepts regarding the process of central excitation, either assumption being able to account for the fact that time compensates for intensity. In view of the probability of lateral synaptic spread the authors are inclined to regard the plateau as a retardation in the removal of the excitatory remainder caused by delayed impulses over lateral channels (Forbes, 1922; Eccles and Sherrington, 1931).

SUMMARY

A flash of light lasting for 0.0113 second is adjusted to a strength just below the absolute threshold of vision. When this flash is followed by a second subliminal of still shorter duration it is found that the second flash sums with the after-effect of the first to give a visible effect. The shorter the interval between the flashes, the smaller the quantity (intensity \times duration) with which the second subliminal is capable of raising the after-effect of the first to threshold value. By measuring this quantity at various intervals between the flashes it has been possible to determine the level of the subliminal excitatory remainder as a function of time.

The authors wish to acknowledge their thanks to Dr. D. W. Bronk for valuable suggestions and to Mr. A. J. Rawson for technical assistance.

BIBLIOGRAPHY

- ADRIAN, E. D. AND R. MATTHEWS. 1927. *Journ. Physiol.*, lxiv, 279.
 1928. *Journ. Physiol.*, lxv, 273.
 AUBERT, H. 1865. *Physiologie der Netzhaut*. Breslau. p. 250.
 BLOCH, A. M. 1885. *C. R. Soc. biol.*, Series 8, ii, 493.
 BLONDEL, A. AND J. REY. 1912. *Trans. Ill. Eng. Soc.*, vii, 625.
 BRAUNSTEIN, E. P. 1923. *Zeitschr. f. Sinnesphysiol.*, lv, 185.
 BREMER, F. 1930. *C. R. Soc. Biol.*, ciii, 509.
 ECCLES, J. C. 1931. *Proc. Roy. Soc. B.*, cvii, 557.
 ECCLES, J. C. AND C. S. SHERRINGTON. 1930. *Journ. Physiol.*, lxix, 1.
 1931. *Proc. Roy. Soc.* cvii, 511, 535, 586, 597.
 FORBES, A. 1922. *Physiol. Rev.*, ii, 361.
 GRAHAM, C. H. AND N. GOLDMAN. 1931. *Amer. Journ. Psychol.*, (in press).
 GRAHAM, C. H. AND R. GRANIT, 1931. *This Journal*, xcvi, 664.
 GRANIT, R. 1930. *This Journal*, xciv, 41.
 GRANIT, R. AND P. HARPER. 1930. *This Journal*, xcv, 211.
 GROSS, K. 1931. *Zeitschr. f. Sinnesphysiol.*, lxii, 38.
 HECHT, S. 1929. *The foundations of experimental psychology*. Chapt. ii, 216.

- PIÉRON, H. 1920a. *C. R. Soc. Biol.*, lxxxiii, 1072.
1920b. *C. R. Acad. Sci.*, clxx, 525.
1929. *L'Annee Psychol.*, xxx, 87.
- RICCÒ, A. 1877. *Annali di Ottalm.*, vi, fasc. 3, 373.
- RICHET, Ch. AND A. BREGUET. 1880. *Arch. d. Physiol. et Pathol. norm.*, vii (2) 689.
- REEVES, P. 1918. *Astrophys. Journ.*, xlvii, 14.
- RUTENBURG, D. 1914. *Zeitschr. f. Sinnesphysiol.*, xlvii, 268.
- SIMON, R. 1904. *Zeitschr. f. Psychol. u. Physiol. d. Sinnesorg.*, xxxvi, 186.
- SHERRINGTON, C. S. 1924-25. *Proc. Roy. Soc. B.*, xcvi, 519.