The Relation between the Magnitude of Cone Processes and the Duration of Illumination in the Human Fovea

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INTRODUCTION

It is a well-known fact that the product of intensity I and duration t of light is constant for just visible brief flashes of light. However the above-mentioned Bunsen-Roscocoe law does not hold any more when the duration of light exceeds a certain critical value.

Much work has been done by a number of investigators¹⁻⁸⁾ on the relation between intensity and duration of light just effective to produce a visual effect.

Graham and Margaria⁶⁾ working in the peripheral areas of the human retina, found that as the duration of light increases, a transition can be seen from the relation $I t = \text{constant}$ to the relation $I = \text{constant}$. This means that the effect of light on the retina becomes constant independent of duration, when the latter is longer than a certain critical value.

Karn⁷⁾ obtained results similar to those by Graham and Margaria at the fovea, too. A similar relation was found by Hartline⁵⁾ in the Limulus eye, taking action potentials of a single optic nerve fiber as an index.

In the present experiment, the electrical excitability of the retina following a photic stimulus was investigated as a function of intensity and duration of the light used, because it has been shown by Motokawa and his associates that measurements of electrical excitability provide serviceable means for analysis of visual function.

EXPERIMENTAL

Method

Following exposure to light, the electrical excitability of the dark-adapted eye increases temporarily above normal.

The crest time of supernormality depends upon the wave-length of

the light used, and the degree of supernormality increases with its intensity. Therefore, increases in electrical sensitivity were measured, using photic stimuli of various intensities and durations. The details of the apparatus and the procedure to determine electrical excitability are given in Motokawa's papers⁹⁻¹⁰). So only important points will be mentioned here.

After a preliminary dark adaptation for about 20 minutes, experiments were carried out. The index of excitation was the least perceptible electrical phosphene. Stimulating currents, single constant current pulses of 100 msec. were applied to the eye through a pair of silver electrodes, placed one on the forehead slightly above the eyebrow, and the other on the homolateral temple of the subject.

First, the threshold voltage for a dark-adapted eye was measured in such a way that, starting with a voltage sufficient to cause a distinct light sensation, the stimulating voltage was lowered step by step until finally, the subject could no longer distinguish the stimulus from one far below the threshold. By repeating this procedure, the reference threshold was determined.

Then the excitability after an illumination was determined in a similar manner, fixing the interval between the end of illumination and the electrical stimulus at 1, 1.5, 2, or 3 seconds.

The effect of light was expressed in terms of ζ which was defined by the formula $\zeta = 100 (E - E_0) / E_0$, where E represents the electrical excitability after an illumination, and E_0 that at the resting level.

An opaque glass disc. of 1 cm. in diameter was illuminated from behind by white light or spectral light, and viewed from a distance of 45 cm. so that the visual angle subtended by the disc at the eye was $1^\circ 30'$. The target was always fixated centrally. In order to vary the duration of illumination from 40 msec. to 500 msec. a sector having a variable slit was moved like a pendulum in front of the target.

Duration of illumination corresponding to each width of the slit was calibrated with a photocell and a cathode-ray oscilloscope.

The spectrum used in this experiment was an equal-energy spectrum, whose intensity was 350 times as high as the threshold intensity for the red light of 650 $m\mu$ of visual angle 2° at the dark-adapted fovea.

The intensity of the light stimulus was controlled by a neutral wedge.

Results

Examples of ζ -time curves obtained at the fovea are illustrated in Fig. 1. In this experiment, a flash of spectral light 40 msec. in duration was delivered, and the excitability at various times after the flash was measured. The data refer to red (650 $m\mu$), yellow (585 $m\mu$), green 530 $m\mu$) and blue (470 $m\mu$) lights.

Fig. 1. ζ -time curves obtained at fovea with preilluminating spectral lights of 40 msec. and different wavelengths. Ordinates: percentage increases of electrical excitability caused by a flash of light above resting level, Abscissas: time in sec. after end of preillumination.

As can be seen in the figure, the curve has its crest at about 1 sec. for red light, at about 1.5 sec. for the yellow light, at about 2 sec. for the green light and at about 3 sec. for the blue light. According to the analysis by Motokawa¹⁵⁻¹⁶⁾, the crest times 1, 1.5, 2 and 3 seconds are characteristic of the red, yellow, green and blue processes respectively, and the magnitudes of the maximal ζ -values are in proportion to the logarithms of the intensities of the lights used.

The relation between the magnitude of each color process and the duration of the light stimulus is represented in Fig. 2, in which the maximal ζ -values of each process are plotted as ordinates against the logarithms of durations as abscissae.

As can be seen in this figure, each process increases in magnitude as

Fig. 2. Dependence of magnitudes of cone processes (maximal ζ -values) upon log durations of preillumination at fovea.

the duration is lengthened, and reaches the highest level at about 200 msec. The critical duration at which the magnitude of response reaches the highest level may be called "saturation time".

It is to be noted that the saturation time is independent of wave lengths. This finding may be interpreted in such a manner that the saturation time would be determined by the total amount of energy absorbed, because the light used in the above experiments came from an equal-energy spectrum.

At the critical duration the product of light intensity and its duration would reach a certain critical value, so that the effect of light becomes maximal. The fact that the response remains constant above the critical duration would correspond to the relation $I = \text{const.}$, which has been found by the previous investigators.

If the amount of energy absorbed were a determining factor, it might be expected that the saturation time would be shortened by increasing the intensity of light. Next experiment was performed to see if this would really be the case. In this experiment spectral lights of an intensity 10 times as strong as that used in the above-mentioned experiment.

The ζ -time curves are illustrated in Fig. 3. They are somewhat higher than those illustrated in Fig. 1, but their crest times are the same as those of the corresponding curves in the previous experiment, namely 1.0, 1.5, 2.0, and 3.0 sec. for red, yellow, green and blue light respectively.

Fig. 4, represents the relation between the magnitudes of the cone processes and the logarithms of durations of preillumination. The general character of the relation is very similar to that found with the weaker stimuli, although the maximal magnitudes of the cone processes are higher than those of Fig. 2. It is to be noted that the saturation time

Fig. 3. ζ -time curves for spectral lights 10 times as strong as those used in Fig. 1.

Fig. 4. Dependence of magnitudes of cone processes upon log-durations of preillumination at an intensity level higher than that used in Fig. 2.

is still 200 msec. despite the fact that the intensity used was 10 times as high as that used in the preceding experiment. This finding cannot be in line with the assumption made above that the saturation time would be determined by the total amount of energy absorbed, because the increase of light energy given to the retina has brought no shortening of saturation time.

It is now apparent that the principle of the constant energy does not hold, and that the data obtained in these experiments can not be explained in terms of photochemical reaction.

In the next series of experiments, white light was used as preilluminating light instead of spectral lights, the other experimental condition being the same as above.

A flash of white light 400 msec. in duration and of various intensities was given to the foveal center (visual angle $1^{\circ}30'$). The ζ -time curves

Fig. 5. ζ -time curves obtained at fovea with preilluminating white light of 40 msec. at various intensities.

obtained are shown in Fig. 5. The intensities used were 100, 1, 0.1, and 0.01 lux from the top downward. As can be seen in this figure, the curves consist of one elevation, having their maximum at about 2 sec. As the intensity of light is lowered, ζ -values decrease. Such curves for white light represent an envelop of the R, Y, G, and B processes⁹⁾¹⁵⁾¹⁶⁾ (Moto-kawa).

The relation between the maximal magnitudes of ζ and the duration of white light is shown in Fig. 6. As the duration of preillumination rises

Fig. 6. The relation between maximal ζ -values and log durations of preilluminating white light of various intensities.

ζ -values increase in proportion to the log of duration and attain a constant level at about 500 msec. It is to be noted that the saturation time is constant irrespective of light intensities. The relation is very similar to those obtained with spectral lights mentioned above, but it deserves attention that the saturation time for white light is definitely longer than that for spectral lights, the former is 200 msec., while the latter 500 msec. It seems that there is some qualitative difference between monochromatic lights and compound light like white light. The difference observed between the spectral and white lights cannot be due to the difference in brightness, because white light of very low brightness, e.g. that of intensity 0.1 lux yielded a saturation time of 500 msec., while the saturation time for the brightest spectral light, yellow was still 200 msec.

DISCUSSION

As the above experiments show, excitation of retinal receptors is always saturated at a constant duration of illumination independently of its wave length. This means that the so-called saturation time has no concern with the individual characters of the receptors involved.

As has been pointed out above, we can not explain this phenomenon

based upon the photochemical reaction following the Bunsen-Roscoe's law, because the saturation time remains constant even though the total amount of energy given to the retina is changed. Therefore it does not seem likely that the saturation of the effect of light occurs when the amount of light delivered to the retina has amounted to a certain constant value.

According to Wright¹²⁾, excitation of the retinal receptors seem to depend upon the balance between the decomposition and the resynthesis of the photochemical substances. If this supposition is correct it is possible that the saturation time depends upon not only the velocity of photolysis, but also that of resynthesis which proceeds during and after an illumination. However, we need not limit our discussion to the events of the receptor-cell level, for it is certain that neurophysiological phenomena occurring in the retinal network play an important role in retinal excitation caused by superthreshold stimuli, such as those used in our experiments. The consideration of neurophysiological phenomena is especially important in our case, because it is very likely that the site of attack of electrical stimuli is not the receptor-cells, but the retinal network. The marked difference between the saturation times of spectral lights and white light is most difficult to interpret.

A tentative explanation of this fact may be as follows: Some interaction occurs among different receptor systems, when they were excited concurrently by white light. The interaction would cause retardation of processes of excitation and recovery in individual systems, so that the saturation time becomes longer for white light than for monochromatic light which stimulates fewer kinds of receptor systems. It would however, be difficult to assume that there occurs such an interaction at the receptor-cell level.

We have, however, some grounds to assume such an interaction in the retinal network, because it is known that there are lateral connections among individual paths even at the fovea; Granit¹⁴⁾ suggested physiologically that there is some interaction among receptor systems at the fovea.

SUMMARY

By the method of electrostimulation, the relation between the magnitude of cone-processes and the duration of the light stimulus was investigated at the human fovea.

1. The magnitudes of cone processes increased almost proportional to the logarithm of the duration of light till a certain critical duration was attained beyond which the response remained constant. The critical duration was designated "saturation time".

2. The saturation time was 200 msec. remaining unaltered, no mat-

ter what the wave lengths and intensities of the spectral lights used might be.

3. The saturation time for white light was always 500 msec. regardless of its intensity.

4. The difference in saturation time between spectral and white lights was interpreted in terms of interaction among the receptor systems involved.

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