Retinal Induction Caused by Direct Electric Currents of Various Forms

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INTRODUCTION

A sensation of flickering phosphenes is aroused by an alternating current which is applied to the eye. With this sensation as an index, Motokawa and his co-workers1-3) determined the strength-frequency curve with several minima. They explained the minima of the curve as due to the result that the retinal receptors with varying time constants were selectively stimulated by alternating currents of varying frequencies. This explanation was supported by the fact that the same kind of retinal induction as caused by colored light4) could be induced by an alternating current of a frequency suitably chosen.5-11

In the previous paper,7) it was found that retinal receptors were selectively stimulated by condenser discharges (C.D.), exponentially increasing currents (E.I.C.) and rectangular pulses (R.P.) of varying time constants or durations. In the present experiment, it was attempted to study the selectively stimulating actions of C.D., E.I.C. and R.P. of varying time constants or durations upon the retinal receptors, using the principle of retinal induction and its neutralization.

EXPERIMENTAL

Method

Motokawa’s method consists in measuring the electrical excitability of the retina with a constant current of 0.1 second, taking the least perceptible phosphenne as an index, following a conditioning stimulus applied to the dark-adapted eye.

When red, yellow, green and blue lights are used for conditioning, the electrical excitability reaches a maximum 1, 1.5, 2 and 3 seconds respectively after termination of the conditioning light.
Percentage increases of electrical excitability are expressed in terms of $\zeta$ which is defined by the formula: $\zeta = 100 \left( \frac{E - E_o}{E_o} \right)$, where $E$ and $E_o$ represent electrical excitabilities determined with and without the conditioning stimulus, respectively. The test current was applied to the human eye through a pair of silver electrodes of $2 \times 1.5 \text{ cm}^2$ in size, the cathode placed on the forehead slightly above the eyebrow and the anode on the homolateral temple of the subject. The contact of the electrodes with skin is secured by the use of warmed electrode paste containing NaCl in high concentration. The polarization at the electrode is almost negligible against the polarization at the skin because of the high salt concentration in the conducting medium and the large area of the electrode.

It depends solely upon the procedure to determine threshold values whether reproducible data of $\zeta$-values are obtained or not. It is absolutely necessary to use the comparing procedure, as it is called, in order to obtain reliable values of threshold. The procedure is as follows: The voltage is reduced step by step from a level high enough to elicit a distinct phosphene. When the subject can no longer discriminate an electric phosphene from the background of intrinsic light, he demands a comparing procedure. The procedure consists of delivering at an interval of several seconds two electric stimuli, one of which is the stimulus in question and the other one far below the threshold. The two stimuli to be compared with each other are given in a randomized order. The subject is requested to answer the question which the stronger stimulus is, and informed every time whether his answer is right or wrong. When a right answer is obtained, the stimulating voltage is further reduced. When the answer is wrong, further trials with the same voltage are made to see if the discrimination will fail 2 times in 3 trials. If this is the case, the latest value of voltage is adopted as a threshold. Near the threshold the voltage is graded in steps of about 1%, because a trained subject can discriminate a difference of about 1%. Thus, we have reached a threshold, but this is not always the only threshold which can be determined with our procedure: A further trial with a stimulating voltage 5% lower than the threshold just reached may cause a curious phenomenon that the subject now easily succeeds in discrimination. This is not due to an accidental fluctuation of the phosphene sensitivity of the subject, because this change is reproducible. In this way we can get the second threshold and sometimes the third. In order to obtain the lowest threshold, it is economical of time to skip over higher apparent thresholds by grading the stimulating voltage in gross steps. At the transition stage from the first threshold to the second, a curious phenomenon can take place, that the subject sees a phosphene in response to a weaker stimulus rather than to a stronger one.
When the voltage is reduced further and approaches the second threshold, the subject feels a phosphene only in response to a stronger stimulus. This paradoxic phenomenon makes us foresee the existence of the second threshold, although its physiological mechanism is not clear. In our experiments, such a stimulating procedure is repeated 20 to 40 times in order to obtain one value of threshold.

Trials are made at an interval of about 10 to 15 seconds, and about 20 values of threshold are determined in one session.

The accuracy of our measurements is such that a difference greater than two in $\xi$-values is usually significant.

A circular disc of ground glass of 1° in visual angle illuminated from behind with spectral light from a spectroscope served as a target. The patch was always fixed centrally by the left eye, where a minute point of red light served as a fixation mark. The wave-lengths of spectral lights were calibrated in comparison with the line spectra from a sodium and a cadmium lamp. As a light source for the spectroscope, an automobile headlight lamp was used. The intensity of spectral light was roughly adjusted to the equal energy by controlling the width of the entrance slit of the collimator. The intensity of white light used was always fixed at 70 lux.

The circuits for producing condenser discharges (C.D.), exponentially increasing currents (E.I.C.) and rectangular pulses (R.P.) which were used as conditioning stimuli, were almost the same as those used by Kurosawa.7)

As was shown in the previous paper, the supernormality of the electrical excitability following a conditioning stimulus is most marked when the intensity of the conditioning electric stimulus is made equal to the threshold intensity. The intensity of the conditioning electric stimuli used was made about 10% below the threshold, lest the phosphene caused by the test stimulus should be confused with that caused by the conditioning stimulus when the interval between the two stimuli was short. The duration of an exponentially increasing conditioning stimulus was fixed at 0.5 seconds.

The other procedures will be described together with the results.

Results

As was shown by Motokawa8), the curves of the electrical excitability of the eye as tested by a constant current pulse of 0.1 second reach a maximum 1, 1.5, 2 and 3 seconds respectively after the end of illumination when red, yellow, green and blue lights are used for pre-illumination. The curve for purplish light shows two maxima at 1 and 3 seconds. When
white light is presented after any colored light, the location of the maximum in the excitability curve as determined after removal of the white light does not coincide with that for the colored light alone, but with that for the complementary color. Examples are illustrated in A1, B1, C1 and D1 of Fig. 1. The curve connecting solid circles is the excitability curve for white light alone in each case. The curve for the successive stimuli, green and white, is decidedly higher than the curve for white light alone, and has two maxima at 1 and 3 seconds (Fig. C1). A curve of such form can be obtained by purplish light, the complementary to green, as mentioned above. Similarly, the other curves for the combined stimuli are complementary in character to the curve which would be obtained for the colored light alone. This phenomenon was termed "retinal induction" by Motokawa.4)

In the following it will be shown that retinal induction can be produced, using an electric stimulus of suitable form and time constant instead of colored light. The curve connecting empty circles in Fig. 1 A2 shows the result of retinal induction obtained by a C.D. of time constant of 2 msec. (condenser capacity 0.1 μF) which was shown by Kurosawa to be equivalent to red light. The maximum of the curve lies at about 2 seconds,
showing an effect equivalent to that of red light used as inducing light (compare A₂ and A₁).

Similarly, the curve connecting empty circles in Fig. 1 A₃ represents the example of the retinal induction, where the eye was first stimulated by a R.P. of 2.2 msec. in duration and then by the white light. This excitability curve shows almost the same shape as the curve obtained by the successive stimuli, red and white lights. Accordingly, the R.P. of 2.2 msec. in duration can be used as a substitute for red light in experiments of retinal induction. This is in agreement with Kurosawa's finding that a R.P. of 2.2 msec. alone causes an excitability curve having a maximum at 1 second.

The next experiments B₂ and B₈ demonstrate that a C.D. of time constant 80 msec. (condenser capacity 4 μF) and a R.P. of 22 msec. in duration may be correlated to yellow light. When these conditioning stimuli are presented prior to white light, each curve determined after removal of white light has a maximum at 3 seconds just like the curve in B₁ (see curves connecting triangles in B₂ and B₃). The curves connecting semi-solid circles (C₂ and C₈) represent the excitability curves, obtained with a C.D. of time constant 320 msec. (condenser capacity 16 μF) and with an E.I.C. of time constant 26 msec. (condenser capacity 10 μF) used for induction. Both curves resemble the excitability curve for purplish light alone, having crest times at 1 and 3 seconds. Another example is shown in D₂ of Fig. 1. The curve connecting squares shows the excitability curve obtained with an E.I.C. of time constant 80 msec. (condenser capacity 32 μF) as the inducing stimulus. The excitability curve has a maximum at 1.5 seconds and thus resembles the curve obtained by successive presentation of blue and white lights (D₁). From the facts stated above, it is evident that the conditioning electric stimuli have the same inducing effects as do colored lights.

The following experiment was undertaken in order to demonstrate the effects of intensity of inducing electric stimuli on ζ-values. The temporal sequence of procedure is shown in the inset of Fig. 2. A C.D. of time constant 80 msec., an E.I.C. of time constant 80 msec. and a R.P. of 22 msec. in duration were used as the inducing stimuli (see curves connecting circles, squares and triangles in Fig. 2 respectively).

As is shown in Fig. 2, ζ-values rise as the intensity of the inducing electric stimulus increases, and attain maxima at an intensity equal to the threshold one. In the intensity range above the threshold intensity, the curve decreases gradually as the intensity of the inducing stimuli increases.

This relation is common to the stimuli of any kind. It is worthy of attention that the retinal induction takes place most strongly when the
The phenomenon of retinal induction stated above was further confirmed by the next experiment based on another principle.

As was shown in the preceding paper by Motokawa\(^{10}\), no retinal induction takes place when another colored light complementary to the inducing one is interposed between this and the subsequent white light. It is because that the after-effect of the inducing light is extinguished by the action of the colored light complementary to it. This phenomenon was designated "neutralization of retinal induction". In the next experiment, an electric stimulus of properly chosen time constant or duration was interposed at varying intervals between the preceding colored and the subsequent white lights. Retinal induction is expressed quantitatively by "contrast effect". The contrast effect is defined as the difference between the maximal ordinate of excitability curve obtained by the procedure of retinal induction and the corresponding ordinate of the control curve for white light alone. In Fig. 3, the values of contrast effect are plotted as ordinates against the intervals between the inducing colored light and the neutralizing electric stimulus. The curves marked by crosses and solid circles represent control experiments, in which no neutralizing electric stimulus was used. The white test light was presented at varying intervals from the inducing colored light. In these control experiments, the contrast effect remained almost unchanged for a period of about 15 seconds.

Next, an E.I.C. of time constant 80 msec. which had been shown to be equivalent to blue light was applied to the eye at varying intervals after
Fig. 3. Neutralizing effect of electric stimuli upon retinal induction caused by colored lights. Neutralizing electric stimuli were applied to the eye at varying intervals after exposure to inducing colored lights. The interval between inducing light and white light was fixed at 15 seconds. Ordinates: contrast effects.

removal of yellow inducing light, the interval between the inducing light and the white test-light being fixed at 15 seconds. The intensity of the neutralizing electric stimulus was equal to the threshold intensity. In this case, the contrast effect decreased as the interval between the inducing photic stimulus and the neutralizing electric stimulus increased, and was reduced to zero at 5 seconds (see full curve connecting squares in Fig. 3 A). As was shown by Motokawa, the retinal induction caused by any colored light is more liable to neutralization as the time elapses since its creation. Therefore, the more retarded its presentation, the more effective the neutralizing electric stimulus.

When the intensity of the neutralizing electric stimulus was about 2 times as high as the threshold intensity, it was found that the contrast effect was higher than in the former case, and that a complete neutralization took place at a longer interval (see broken curve connecting squares in
This means that the neutralizing effect of the electric stimulus above threshold is weaker than that of threshold strength, and we can understand this relation from the fact mentioned above that electric stimuli of any wave form have an optimal stimulating action upon the retinal receptors at an intensity equal to the threshold intensity.

In the experiments mentioned above, yellow light of 585 m\(\mu\) was used as inducing light. In the next experiments, blue light of 470 m\(\mu\) was used for induction, and as neutralizing electric stimuli two kinds of stimuli, C.D. and R.P. were used, the other procedure being the same as in the above experiments. The curve connecting empty circles and the curve connecting crosses enclosed by circles represent, respectively, the data obtained with a C.D. of threshold strength and another of an intensity 2 times as high as the threshold intensity. The time constant of the C.D. used was 80 msec, so as to be equivalent to yellow light. The stronger neutralizing stimulus has proved to be less effective in this experiment, too. The relation can be seen in the experiments carried out with R.P. as neutralizing stimuli. The solid curve marked by triangles refers to the threshold intensity, and the broken curve of the same mark to an intensity 2 times as high as the threshold intensity. The neutralizing action of the R.P. of threshold intensity is evidently stronger. In all the experiments of neutralization stated above, only the electric stimuli were used, which had been shown to be complementary to the inducing colored light. So, a systematic experiment was undertaken varying the wave form and time constant in a systematic manner. In the first place, we used C.D. of varying time constants as neutralizing electric stimuli. The data obtained in such neutralizing experiments are shown diagrammatically in Fig. 4. The interval between the inducing photic stimuli and the neutralizing electric stimuli was fixed at 6 seconds. This interval corresponds to the interval at which the contrast effect is reduced to zero at the threshold intensity.

In this figure, the curve connecting semi-solid circles refers to red inducing light (650 m\(\mu\)) and shows a complete neutralization over a range of time constant from 160 to 640 msec. Therefore, the C.D. with time constants in this range must have a neutralizing action equivalent to that of blue-green light, complementary to the inducing light. The curve connecting empty circles refers to green inducing light (530 m\(\mu\)) and shows a perfect neutralization at time constants around 25.6 msec. From this fact, the C.D. of these time constants must be equivalent to purplish light in neutralization. The curve connecting empty triangles represents the neutralizing action of C.D. upon the retinal induction caused by blue light (470 m\(\mu\)). Since a minimum of this curve is seen in a range of time constant of from 60 to 120 msec, the electric stimuli of these time constants must be equivalent to yellow light, complementary to blue. Although
Retinal Induction Caused by D.C.

Fig. 4. Neutralizing effects of C. D. upon retinal induction caused by colored lights.

The interval between inducing light and the neutralizing electric stimulus was fixed at 6 seconds in the experiments stated above, a similar experiment was carried out without any interval between the two. The result is represented by a broken curve marked by solid triangles.

The curve has a minimum over a time constant range from 60 to 120 msec. running parallel with the corresponding curve obtained at the interval of 6 seconds between the two stimuli. It is to be noted that the contrast effect is not reduced to zero even at the minimum. This shows again that retinal induction is more difficult to neutralize immediately after its creation than at later stages.

In the following experiment, E.I.C. of varying time constants were used for a neutralizing electric stimulus (see Fig. 5). As can be seen in this diagram, the retinal induction caused by red light was perfectly neutralized by electric stimuli of time constants from 2.3 to 23 msec. Thus, the E.I.C. of these time constants must be equivalent to blue-green light complementary to red light (see curve connecting semi-solid circles). As the retinal induction caused by yellow light is perfectly neutralized by electric stimuli of time constants ranging from 74 to 112 msec. as well, the electric stimuli of these time constants must be equivalent to blue light (see curve connecting squares).

Similar experiments were carried out with R.P. of varying durations (see Fig. 6).
Fig. 5. Neutralizing effects of E. I. C. upon retinal induction caused by colored lights.

Fig. 6. Neutralizing effects of R. P. upon retinal induction caused by colored lights.

**DISCUSSION**

Color processes are characterized by their own time constants. This relation manifests itself in various aspects of color sensations (Piéron)\(^9\), and in electrical excitability of the eye following illumination (Motokawa)\(^8\). The present investigation has added further evidence for this relation, showing selective actions of electric stimuli upon the retinal receptors.
depending upon the wave form and time constant of the stimulating currents.

As has been demonstrated above, the inducing and neutralizing actions of electric stimuli are strongest when they are of threshold strength. This may be supposed to have a close connection with the established fact that the selectivity of the stimulating current is highest at the threshold strength. As was shown by Motokawa\(^4\), no color induction whatsoever can be caused by white light which is supposed to stimulate uniformly all sorts of retinal receptors. When the conditioning electric stimulus used is too strong, the selectivity in its stimulating effect must be worse than at lower intensities. All kinds of retinal receptors would be stimulated more or less by such a strong electric stimulus, and this would lead to reduction of retinal induction. However, this interpretation encounters a difficulty which was found in Kurosawa's experiment. This author found that the supernormal electrical excitability caused by an electric stimulus was maximal when its intensity was equal to the threshold. If a too strong electric stimulus had a stimulating action upon all sorts of retinal receptors, so it would be expected that the supernormal electrical excitability caused by this stimulus should be high, because it is a general rule that stronger excitation is followed higher supernormality.

The mechanism of the phenomenon under consideration awaits elucidation by further experiments.

**Summary**

The curve showing the time course of electrical excitability of the eye determined after exposure to colored light and then to white light is materially different from the curve for white light alone, but closely similar to that for the complementary colored light alone. This phenomenon is termed "retinal induction".

1. In the present experiment it is shown that direct currents of suitable form and time constant may be used as a substitute for inducing colored light in the experiments of retinal induction.

2. Condenser discharges, exponentially increasing currents and rectangular pulses of various time constants and durations are used, and it is found that the inducing effect is maximal when they are of threshold strength, irrespective of the wave form and time constant.

3. Condenser discharges of small time constants show an inducing effect equivalent to that of lights of longer wave-lengths, while exponentially increasing currents of large time constants behave like blue light in retinal induction.

4. When light complementary to the inducing light is interposed
between this and the subsequent white light, no retinal induction can be found, and this phenomenon is termed "neutralization of retinal induction." It is shown that electric stimuli of suitable wave form and time constant can neutralize the retinal induction caused by colored light.

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References

2) Abe, Z., ibid., 1951, 54, 37.