Suppression of Color Contrast and Retinal Induction by Mechanical Pressure Applied to the Eyeball

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(Received for publication, January 11, 1957)

INTRODUCTION

Color and brightness contrasts are familiar visual phenomena, but their mechanisms have long remained obscure. Motokawa\(^1\)-\(^4\) found a phenomenon which is very likely to represent a retinal process underlying contrast and other similar visual phenomena, and termed it retinal induction. This phenomenon can be found not only in the human eye, but also in mammalian retinas.\(^5\) Further it was shown that retinal induction was caused not only by colored light, but also by intermittent white light\(^6\) and by alternating currents.\(^7\)

Two kinds of retinal induction were distinguished by Motokawa; the induction effect remaining within a pre-illuminated retinal area after exposure to colored light is called direct induction, and the one set up around the retinal area pre-illuminated is called indirect induction. Direct or indirect induction usually remains unchanged for about 20 seconds, but is extinguished by a second exposure of the retina to a stimulus of complementary color. This phenomenon is called neutralization of retinal induction.

Motokawa and Ebe\(^8\) showed that a pre-established retinal induction could not be abolished by antidromic stimulation of the optic nerve, and Nakagawa and Kohata\(^9\) found that a pre-established retinal induction could not be abolished by illumination with white light of very high intensity.

In a previous paper\(^10\)-\(^11\) we studied the effect of a mechanical pressure applied to the eyeball upon the excitability of the eye and upon the super-normal electrical excitability caused by colored light. The present investigation represents an extension of the preceding one and deals with the effect of mechanical pressure upon retinal induction, and color contrast.
EXPERIMENTAL

Method

After a preliminary dark adaptation for about 20 minutes, experiments were carried out. The method used was essentially the same as that described in the previous papers.\(^4\)\(^{10}\)\(^{12}\) It consisted in measuring the electrical sensitivity of the dark-adapted eye after a brief illumination, taking the least perceptible electrical phosphene as an index.

Electrical thresholds were determined with the method of limits of ascending order. The stimulating voltage was raised, from a sub-threshold value, at first with gross steps and then with smaller steps of about a few per cent until some misty sensation was aroused by the test shock. The final determination of a threshold depended on a comparison procedure in which the effect of a stimulus was compared with that of a control stimulus of zero voltage.

In this way, electrical thresholds of the eye were measured with and without pre-illumination. The effect of illumination was expressed in terms of percentage increases of electrical excitability (reciprocals of threshold) above the resting level. The target used was 10.5 mm. in diameter or 2° in visual angle, and was illuminated from behind by spectral light or white light. The duration of illumination was 2 seconds, if not otherwise stated. The distance from the stimulating surface to the subject's eye was always 30 cm.

The method for applying mechanical pressure to the eyeball was described in detail in the preceding papers\(^{10}\)\(^{11}\) so that it seems unnecessary to repeat the same description here. In this apparatus the degree of pressure is expressed in grams. In the present experiment, the greatest pressure used was 200 g. and its duration was 2 seconds. It is to be noted that a pressure of 480 g. just stops the pulsation of the central retinal artery.

Results

1. Is retinal induction affected by repeated stimulation with strong white light?

The direct induction caused by a colored light within an illuminated retinal area is revealed by a subsequent white test light, because the curve of electrical excitability for the white test light is modified by the preceding colored light. The strength of induction is measured by the difference between the excitability curve for the pair of colored and white lights and that for the white light alone. Nakagawa and Kohata showed that retinal induction was not affected when a strong white light was interposed between the inducing colored light and the subsequent white test light. The question now arose whether or not a pre-established retinal induction was destroyed by repeated stimulation with strong white light. The inducing
colored light (R) used was red spectral light of 650 m\(\mu\), and the white test patch (Wh) was 10 lux and 1 mm. in diameter. The interposed white light (W) was much stronger than any of the inducing and the test lights. The result is shown in Fig. 1, in which a low curve marked by crosses represents the excitability curve for the white test light alone. As is indicated in the inset, in one experiment two white light stimuli were interposed between R and Wh, but the excitability curve obtained was found little different from the control curve obtained by the pair of R and Wh. In another experiments four white light stimuli were used, but no effect of the interposed white stimuli could be found upon the retinal induction; the latter, once started, can remain unchanged for a considerably long time, however strongly the retina is excited by white light. It is, however, curious that retinal induction is easily extinguished by subsequent

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**Fig. 1.** Experiments showing stability of retinal induction. In the interval between inducing red light (R) and white test light (Wh) 2 to 4 white stimuli (W) were interposed. Ordinates: Percentage increase of electrical excitability (\(\xi\)). Abscissae: Time after white test light (Wh). Temporal sequence of stimuli were shown in inset where \(S\) and \(t\) denote electrical test shock of 0.1 sec. and interval between Wh and respectively. All stimuli were applied to one and the same retinal area.
exposure of the retina to the weakest complementary color, as was shown by Motokawa\textsuperscript{10}).

In the following experiment a colored light of the same quality as the inducing light was interposed between the latter and the white test light in order to see whether or not the retinal induction caused by the inducing light was further strengthened. The result was negative; little change could be found in the curve of induction so long as the intensity of the interposed colored light was lower than that of the inducing light. An example is shown in Fig. 2. The inducing light, $R_1$, was a strong filtered light (630–670 m\textmu) of 200 lux in intensity and the interposed light, $R_2$, was red spectral light (650 m\textmu) of an intensity five times the foveal threshold. The curve marked by triangles represents the curve of induction obtained by the use of $R_2$ and Wh.

![Fig. 2. Further experiments showing stability of retinal induction. A light (R$_2$) of the same color as the inducing red light (R$_1$) was interposed between R$_1$ and Wh. Retinal induction caused by R$_1$ is little altered by R$_2$. Other explanation is as in Fig. 1.](image)

The chain curve connecting empty circles represents the curve obtained by the series of stimuli $R_1$, $R_2$ and Wh. The continuous curve marked by dots represents the one obtained by the stimulus sequence $R_1$ and Wh. It is obvious that these two curves coincide with each other.
within the limits of experimental error. The experiments mentioned above demonstrate a high stability of retinal induction. In contrast with this, the retinal induction shows a great susceptibility to a circulatory disorder in the retina, as will be reported in the following.

2. Suppression of retinal induction by mechanical pressure applied to the eyeball

As was described in the previous papers, the electrical excitability of the eye is reduced by mechanical pressure to the eyeball, and no increase in electrical excitability occurs following illumination, when the eyeball is subjected to a pressure from 200 to 250 g. The electrical excitability depressed by a pressure does not recover promptly after removal of pressure, but it takes a time of a few to several seconds for complete recovery, depending upon the intensity and duration of pressure. With the magnitude of pressure used and a duration of 2 seconds, recovery was found complete 8 seconds after removal of pressure. This can be seen also in Fig. 3, in which the continuous curve marked by squares represents the effect of the

![Figure 3](image)

Fig. 3. Experiments showing high susceptibility of retinal induction to mechanical pressure applied to eyeball. $E_r$: electrical excitability after illumination and application of mechanical pressure. $E_0$: Electrical excitability of resting eye. Abscissae: Pressure. Difference between curve marked by circles and that marked by squares represents retinal induction. Temporal sequences of stimuli are shown in inset where R and P represent red inducing light and pressure respectively.
white test light, Wh, preceded by pressure stimuli of various degrees. The ordinate of the curve is expressed in per cent of the electrical excitability without pre-illumination. The white test light brought about supernormal excitability of about 120 per cent irrespective of the magnitudes of pressure. When the inducing light, R, was given 1 second prior to the pressure, the other procedure being the same as above, the supernormality caused by the white test light was found to be the same as before; in other words, no retinal induction appeared, as is shown by the continuous curve marked by circles. The supernormality was higher than that for the test light alone when no pressure stimulus was given, that is, retinal induction could be seen without pressure. From these experiments it is obvious that the pressure stimulus following the inducing light destroyed the retinal induction set up by the inducing stimulus. It is to be noted that a pressure as small as 50 g. is effective to depress retinal induction. The results represented by broken curves in Fig. 3 refer to experiments in which the interval between the pressure stimulus and the white test light was only one second. In these cases the effect of the white light was reduced as the intensity of pressure increased. It is without saying that no retinal induction could be noticed under the influence of pressure in these cases.

In Fig. 4 the time curves of direct inductions caused by various spectral lights are shown. The inducing lights used were red (650 m\(\mu\)), green (530 m\(\mu\)) and blue lights (470 m\(\mu\)) of equal energy. The broken curves connecting dots represent control curves for the test light, Wh, alone.

![Fig. 4. Time courses of direct retinal induction caused by red (R), green (G) and blue (B) lights. Ordinates: Percentage increases in electrical excitability above resting value measured without any stimuli. P: Pressure of 50 g. R, G and B are spectral lights of equal energy.](image-url)
The curves connecting open circles represent induction curves obtained by successive stimuli, colored and white. The crest of the curve appears at 2.75 seconds and 1.5 seconds respectively when the inducing light is red and blue. The curve for the green inducing light shows two humps at 1 and 2.5 seconds. In any case the form of the curve of retinal induction conforms to that of the curve which would be obtained with the colored light complementary to the inducing one. All these characteristics of the curves are lost sight of, when a pressure stimulus of 50 g. is interposed between the inducing and the test lights; the curves obtained under this condition are parallel to the control curve for the white test light alone and even lower than this.

The data presented above refer to the direct retinal induction found within the retinal area illuminated by the inducing light. Similar data concerning the indirect induction around the illuminated area are shown in Fig. 5. The white test light was presented at a distance of 3 mm. from the margin of the pre-illuminated area in these experiments. The curve of indirect induction caused by a given inducing light is in shape complementary to that of direct induction caused by the same inducing light. A striking effect of mechanical pressure on indirect induction can be seen in this figure, too (cf. continuous curves with chain curves).

In the following experiments after-effects of mechanical pressure upon retinal induction were investigated. The interval between the pressure stimulus and the white test light was so chosen that the effect of the test light was not affected directly by the pressure stimuli; the interval was

Fig. 5. Time courses of indirect retinal induction. All explanations as in Fig. 4.
at least 6 seconds. The interval between the pressure stimulus and the inducing colored light was varied in order to see how long the depressant after-effect of the pressure upon retinal induction lasted. The result is illustrated in Fig. 6. At an intensity of pressure 50 g., the percentage increase ($\zeta$) of electrical excitability over that of the dark-adapted eye was 20 when the interval between the pressure and the inducing light was shorter than 4 seconds. This value of $\zeta$ is the same as that for the white test light alone, in other words, the inducing light could not evoke no induction at all in this period of after-effect. When the interval was lengthened to over 6 seconds, the induction developed in full scale: $\zeta$ values steeply rose from 20 to 71 between 4 and 6 seconds after removal of the pressure. The depressant after-effect lasted longer, as the intensity of pressure was increased, for example, the after-effect disappeared 7 and 11 seconds after removal of pressure for intensities of 100 and 200 g. respectively.

3. The effect of mechanical pressure upon color contrast

Although there is no doubt about the depressing effect of mechanical pressure upon retinal induction, it is a question whether or not the visual phenomenon of color contrast is likewise depressed by the mechanical pressure. Some experiments were done for this question.

Simultaneous color contrast was produced by the well-known method of colored shadows (Goethe, Fechner, Hering and others). The arrangement of this experiment is illustrated schematically in Fig. 7. In front
of a white screen there stand a rod (B) and two white lamps, WL₁ and WL₂. The lamp WL₂ is covered by a red filter R. F. so that the screen is illuminated simultaneously by white and red lights.

On the screen two shadows of the rod, R and G, are seen. The rod casts the shadow R by interrupting the white light, and the G by interrupting the red light.

The shadow R looks reddish, while G looks bluish-green. The coloration of G is due to simultaneous color contrast. The ratio of the intensities of the white and the red lights has to be adequate to produce conspicuous color contrast by this method. The intensity of white light was controlled by means of a neutral wedge till a conspicuous contrast appeared.

When the subject pressed his eyeball with the tip of a finger till the color shadows disappeared, he could still perceive the rod against the background. Three subjects said that the colored shadows disappeared while the other things were still clearly visible. Then, the question arose as to whether the disappearance of the colored shadows might be due to some disturbance of accommodation brought about by the pressure. Therefore the visual image of each subject was blurred artificially by means of glasses of high refractive power, and asked each subject to compare the visibility of the colored shadows and that of the other things in the visual field. They answered that all the visible things were equally blurred, but that no selective disappearance of the colored shadow could be noticed in this case.

In one of 4 subjects, mechanical pressure could, however, cause no selective disappearance of the colored shadows; he could perceive the colored shadows under pressure so long as he could perceive the other
things in the visual field.

The selective abolition of the colored shadows seemed to depend not only upon the intensity of pressure, but also upon the intensity of contrast. When the intensities of the white and the red lights were decreased in the same proportion, the contrast became less conspicuous, and under such condition the contrast was easier to be abolished by the pressure of the eyeball.

In this psychological experiment the number of subjects was not sufficiently large, and the data obtained were not so quantitative as in the other experiments. In consequence, some reservation should be made to conclude from this experiment that the psychological phenomenon of color contrast is depressed by mechanical pressure in the same degree as is the retinal induction.

DISCUSSION

As has been shown above, a very weak pressure applied to the eyeball abolishes retinal induction completely, and under certain conditions simultaneous color contrast seems to be abolished by the pressure, too.

The retinal induction is so sensitive to pressure that it does not appear even when the effect of light to increase electrical excitability above the resting level is still retained. Fig. 3 shows this situation clearly; under a pressure of 50 g., the supernormal excitability caused by the white test light alone is the same as without pressure, but no retinal induction can be seen under this pressure. According to Motokawa, Iwama and Ebe, the best physiological condition of an animal was required to make experiments on retinal induction. When the condition of the experimental animal was becoming worse owing to unfavorable conditions such as bleeding, deep narcosis, etc., the retinal induction disappeared first, and then the effect of light to increase electrical excitability, the spike-response to a photic stimulus and spontaneous spike discharges disappeared in the order.

Taking advantage of the well-known entoptic phenomenon, the movement of red blood corpuscles in the retinal capillaries can be observed when we look up into the blue sky or when the eye is illuminated by strong parallel rays of blue light.

With the same pressure apparatus used in the present experiment we made some preliminary experiment on the effect of mechanical pressure upon the movement of the red blood corpuscles in the retinal capillaries, and it was found that the rate of flow can be reduced to about 50 per cent by a pressure of 50 to 100 g. This observation justifies the interpretation that the disappearance of retinal induction caused by mechanical pressure is due to anoxia in the retinal tissue.
SUPPRESSION OF COLOR CONTRAST BY PRESSURE

SUMMARY

The electrical excitability of the dark-adapted eye is increased following an illumination. The effect of a white test light to increase the electrical excitability is remarkably modified when it is preceded by a conditioning colored light. This modification is measured by the difference between the effect of the white light preceded by colored one and that of the white test light alone. When the conditioning and the test stimuli illuminate successively one and the same retinal area, the effect is called direct induction. It is called indirect induction, when adjacent areas are illuminated by the two lights.

1. It was shown that direct induction was little affected when the eye was repeatedly excited by strong white light in the interval between the conditioning and the test lights.

2. Direct or indirect induction was shown to be very sensitive to a mechanical pressure applied to the eyeball. A pressure of 50 g. was found to be sufficient to abolish the induction when it was applied to the eye in the interval between the conditioning and the test lights. A pressure of 480 g. just stopped the pulsation at the central retinal artery.

3. The depressant effect of a mechanical pressure upon retinal induction outlasted the pressure. Complete recovery occurred in 6, 7 and 10.5 seconds after removal of pressure, 50, 100 and 200 g. respectively.

4. Simultaneous color contrast was produced by the method of colored shadows, and its susceptibility to mechanical pressure was investigated. In three of four subjects colored shadows were selectively abolished by a mechanical pressure applied to the eyeball when the intensity of inducing colored light was not too high.

5. The inhibitory effect of mechanical pressure was interpreted as due to anoxia caused by reduction of the rate of blood flow in the retinal capillaries, as was evidenced by entoptic observations of the retinal blood flow.

I am greatly indebted to Prof. K. Motokawa for his kind guidance and for many valuable discussions.

References

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