STUDIES ON THE INDUCTION IN VISUAL PROCESS TAKING ELECTRICAL PHOSPHENE AS AN INDEX (5)

EXPERIMENTS ON THE PROPAGATION OF THE INDUCTION
ACROSS THE BLIND SPOT (2)*

TAROW INDOW, TAKAAKI KOYATSU AND TOSHIRO YOSHIDA

Keio University

By means of measuring the enhancement of the electrical excitability of the eye when it is pre-illuminated by stimulating patterns, Motokawa has discovered a number of phenomena which are now well known as the retinal induction (2, 11, 12, 18, 21). The induction is divided into two types, direct and indirect, and it is the latter which especially attracts our interest because it propagates over the retina from one part to another, according to Motokawa, in the form of wave exactly in the same way as light does in space. In fact, marvellous demonstrations were made that in the propagation of induction the phenomena of absorption, reflection, refraction and even the Doppler effect do occur in the retina or somewhere else (15, 16). Besides, Motokawa in his ingenious experiments succeeded in measuring the index of re-

fraction and the velocity of propagation etc. (7, 15, 16, 19).

In the experiment concerning retinal induction, silver electrodes are in contact with the brow and cheek around the eye and the eye is electrically stimulated by a single constant current pulse of 0.1 sec. in duration. The stimulation gives rise to "phosphene" which is usually described by the subject as vaguely defined clouds of flash in the peripheral field of view. The reciprocal of the electrical threshold for the phosphene is defined to represent the excitability of the eye. The excitability of the dark-adapted eye is increased from E_0 to E if it is exposed, prior to the delivery of the electrical pulse, to a white luminous patch such as W in Fig. 1 (the temporal sequence

Fig. 1.

b). This enhancement in excitability will be given hereafter by the index

* This research was undertaken, as one in the series of investigations, by the group of the Department of Psychology in Keio University who are working in the field of the retinal induction. The group consists, at present, of the authors, also S. Ohinata, T. Kozaki and U. Nagumo, née Kuno. The authors wish to express their warmest thanks to Prof. Motokawa of Tohoku University for his continuing interest throughout the series of investigations. Thanks are also to Dr. M. Fish who kindly read through the manuscript and gave helpful criticisms and advices concerning English. This study was financed by the Ministry of Education.

$\zeta_B = (E - E_0)/E_0 \times 100$. A further enhancement is observed, however, if a luminous figure, e.g., the yellow one Y is presented and then W is given in its vicinity (Fig. 1), and the enhancement observed under this condition ζ_A (the temporal sequence a) is somewhat larger than ζ_B . For simplicity, this will be called hereafter the indirect induction of Y at W. The amount of induction is given by $(\zeta_A - \zeta_B)$ which Motokawa named the contrast effect (CE). In general, ζ is a function of the interval of time between the cessation of W and the delivery of the electrical pulse but the interval was fixed at 1.5 sec. all through this study because only the indirect induction of Y to W was at issue. It is well known that CE is maximum at 1.5 sec. interval in this case.

If the blue luminous figure B (Fig. 1) is presented in between the presentation of Y and that of W (the temporal sequence c), however, it is observed that CE vanishes unless the interval of time between B and W is too short. This phenomenon is called "neutralization" as it is believed that the indirect induction once caused by Y is wiped out by the indirect induction propagated from B. The two inductions are, of course, complementary in nature. The indirect induction of a figure *per se* can not be detected unless the W is presented in its vicinity for the induction decreases fairly rapidly as the distance between W and the figure increases (10, 13). On the other hand, to test whether neutralization takes place or not is an extremely convenient device for detecting the arrival at a point of the induction that is to start from a figure at a certain distance because a surprisingly small amount of the induction propagated is sufficient to give rise to the neutralization (17). In this sense, in Fig. 1, Y is called *Detector* and

B *Inducer* and the propagation of the induction from B to W is proved by absence of the induction of Y, i.e., $CE = 0$.

Among a number of important discoveries made by Motokawa taking occurrence of the neutralization as an index, we find the fact that the induction does not traverse the blind spot (17). This fact was easily confirmed in our laboratory. Under the conditions that the blind spot intervenes between the retinal images of Y, W and that of B in Fig. 1, the amount of CE was shown to remain the same with the one obtained when B was absent (the temporal sequence a). That means, the induction initiating from B does not reach W "across the blind spot" (4).

It is a remarkable fact that if a stimulus pattern is given in such a way that a part of it falls in the blind spot while the remaining part stretches well into the sensitive region of the retina, then it gives rise to perception of the complete pattern without any gap. In other words, the part falling into the blind spot is, so to speak, compensated in perception in accordance with the whole pattern. For brevity, this fact will be called hereafter the phenomenon of compensation or perception "across the blind spot". In the previous experiments we showed that once a white figure B1 presented across the blind

Fig. 2.

spot was perceived as a whole without any gap (Fig. 2), the induction initiated

from B reached W (4). It was also ascertained that this phenomenon could not be ascribed to the scattered light from B. Hence, once a kind of continuity is perceived, so to say, to "bridge the blind spot", the blind spot seems to lose its blocking effect upon the propagation of induction and it becomes a traversable medium for induction.

The purpose of the present experiments was to investigate the following possibilities. When the blind spot become functionally equivalent to any other region of the retina in the sense that the compensation takes place and the blind spot becomes traversable for the induction, then the phenomenon of reflection, refraction and also absorption would be demonstrated with the beam of induction even in the region

corresponding to the blind spot in the same way as in any other retinal region.

APPARATUS AND GENERAL PROCEDURE

The apparatus for delivering a single constant pulse of 0.1 sec. in duration to the right eye of the subject is essentially the same as that described, e.g., in (3). The subject (S) was seated in a small dark room. The distance was 56 cm. from the right eye to the transparent screen through which the rays were delivered as stimuli, i.e., Detector, Inducer and the white patch etc. In the present experiments the indirect induction caused by yellow and its neutralization by blue were exclusively dealt with since this is the pair of which the neutralization can be demonstrated even when the wave lengths are not exactly matched (22, 23). The tolerance for being comple-

Table 1

An example of protocol in determining the threshold (S:In).

R ₀		W		Induction		Neutralization			
						Large steps		Small steps	
1000	++	1000	++	1000	++	1000	+	1000	++
1500	+	2000	+	2300	+	2400	+	2300	+
1900	+	2500	$\left. \begin{smallmatrix} ? \\ s \\ s \end{smallmatrix} \right\} S$	3300	$\left. \begin{smallmatrix} ? \\ o \end{smallmatrix} \right\} S$	3300	+	3100	$o \ S$
2300	+			4000	$o \ S$	3800	$\left. \begin{smallmatrix} ? \\ s \\ f \\ o \end{smallmatrix} \right\} S$	3400	$\left. \begin{smallmatrix} s \\ o \end{smallmatrix} \right\} S$
2500	$\left. \begin{smallmatrix} ? \\ s \\ s \end{smallmatrix} \right\} S$	3000	$o \ S$	4500	$\left. \begin{smallmatrix} s \\ f \\ f \end{smallmatrix} \right\} F$	4300	$\left. \begin{smallmatrix} f \\ s \\ f \end{smallmatrix} \right\} F$	3600	$\left. \begin{smallmatrix} s \\ n \\ s \\ s \end{smallmatrix} \right\} S$
		3500	$\left. \begin{smallmatrix} s \\ s \end{smallmatrix} \right\} S$						
2700	$\left. \begin{smallmatrix} s \\ s \end{smallmatrix} \right\} S$	3800	$\left. \begin{smallmatrix} s \\ n \\ f \end{smallmatrix} \right\} F$	5000	$o \ S$	4700	$\left. \begin{smallmatrix} n \\ s \\ n \end{smallmatrix} \right\} F$	3800	$f \left\{ \begin{smallmatrix} s \\ n \end{smallmatrix} \right\} F$
2900	$\left. \begin{smallmatrix} s \\ f \\ n \end{smallmatrix} \right\} F$			5200	$\left. \begin{smallmatrix} s \\ s \end{smallmatrix} \right\} S$				
3000	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$	4000	$\left. \begin{smallmatrix} s \\ n \end{smallmatrix} \right\} F$	5400	$\left. \begin{smallmatrix} n \\ f \end{smallmatrix} \right\} F$	5000	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$	4100	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$
3050	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$	4100	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$	5500	$\left. \begin{smallmatrix} n \\ n \end{smallmatrix} \right\} F$				
R ₀ =2700		R=3500		R=5200		R=3600			
		ζ _B =28		ζ _A =86		ζ _A =31			
				CE=58		CE=3			

The intensity of the electrical pulse is given in terms of the resistance (Ω) employed.

$$\zeta = \left(\frac{R_0 + 200}{R + 200} - 1 \right) \times 100$$

mentary was so wide in this pair that the transparent light through a sheet of yellow cellophane and that through a sheet of blue cellophane could be used without any trouble.

Since the method for obtaining the electrical threshold for the phosphene is now in dispute (8, 25), it might be well to describe the procedure we employed in detail. Some examples are given in Table 1. It was a descending series in the method of limits in a modified form. The series was begun with presentation of an electrical pulse which produced a phosphene clearly recognizable. Then the intensity of the pulse was decreased step by step and S was required to make absolute judgment concerning the phosphene on each presentation. The sign $\#$ denotes the case when the phosphene is quite distinct, $+$ the case when S is positive on occurrence of the phosphene and $?$ the case when recognition of the phosphene becomes slightly doubtful. Once the response $?$ appeared, S was required to make distinction between delivery and non-delivery of the pulse in successive presentations. As a matter of course, the order of the presentation in a pair was rigorously randomized. In these paired comparisons, the response of the subject were divided into the following categories; $\circ$ (correct response with confidence), $\times$ (false response though S is confident in his judgment), s (correct response though S is not confident), f (S is not confident and response is false) and n (S perceives no phosphene in either presentation and cannot make any distinction at all). The intensity level of the pulse being fixed, the case was designated S when $\circ$ occurred in the first comparison or s 's occurred in the first two successive comparisons or s 's and $/$ or $\circ$'s appeared in three out of four comparisons. When none of these criteria was met, the sign F was given to the case. The descending series was terminated when one of the following patterns occurred; $S-F-F$, F , $S-F-S-F-F$, $S-F-S-S-F-F$ and $S-F-F-S-F-F$,

etc., and the average of the intensities corresponding to the levels underlined was defined to be the threshold.

At the beginning of the series the intensity of the pulse was decreased by relatively large steps but the steps were gradually decreased in size as the series proceeded. We have made no rigid rule in the way of grading the intensity of the pulse and it was varied somewhat from occasion to occasion. This procedure was rather advantageous as it was thus impossible for S to anticipate the intensity of the pulse to be delivered by counting the number of steps from the first presentation of the series. If the induction is present, the series necessarily has to be terminated at an intensity of considerably lower than when it is absent. As to the way of grading the intensity, therefore, making some adjustment from one case to another seems to be indispensable. It is absolutely necessary, however, to take great caution against the possibility that the subject loses sight of the faint phosphene before the true threshold is reached since waxing and waning occur instead of a steady decrease as the intensity of the pulse is decreased (1, 11, 14, 20). Hence, the series should not be terminated unless it becomes entirely clear that no more phosphene can be aroused by a pulse of lower intensity and this is especially true where occurrence or non-occurrence of the neutralization is the point at issue. Suppose that the tide of vividness in the phosphene fails to rise half way of the series when induction is present. This might be misinterpreted as occurrence of neutralization. We have made, therefore, the following rule. On any occasion, no matter whether induction or neutralization was expected, the intensity of the pulse was decreased by the steps appropriate for determining the threshold under induction. Induction being present, the threshold would thus be determined with accuracy of desired degree. The accuracy depends in part upon the size of the steps at the end of the series. When

neutralization was taking place, on the other hand, the case labelled *S* would cease to appear at an earlier stage of the series. Should this occur, the steps of that stage would be too coarse to determine the threshold accurately, but we would be assured that there would be no recurrence of the phosphene at lower intensities. Then, in order to determine the threshold with accuracy, the series was started again with appropriate steps for the threshold under neutralization. In this way, when neutralization was to be tested, two kinds of series were always in use in pairs for one measurement, one only for probing possible recurrence of the phosphene at lower intensities of the pulse and another for determining the threshold with accuracy. The threshold was determined by the latter only. If possible, the order of these two series was randomized and it should be emphasized again that there was no way of knowing for *S* at what level of intensity the pulse to be delivered might stand. Ordinarily measurements were repeated twice for each *S* and four times at the critical points. Values obtained are given in the table below the figure in which the average is plotted.

Four *Ss*, *In*, *Y*, *Kz* and *Ko*, participated in the present experiments. These were the subjects with whom the phenomena of induction and neutralization could be demonstrated definitely from the beginning. They had also served as *Ss* in the other experiments of this kind (3, 4, 5, 6). One of the authors, *Ko*, took part of experimenter all through the experiments*.

In each session, *S* was dark adapted for a period of at least 20 min. before the electrical excitability of the eye (E_0) was determined as the first step of the experimentation of the session. E_0 was measured again at the end of the session. These two

values coincided very closely and the average was taken as the denominator of ζ_B and ζ_A , the index of the enhancement in the excitability caused by pre-illumination of *W* alone and the index of the enhancement by *W* preceded by *Y* and *B* etc.

RESULTS

It might be well to enumerate here, from the discoveries made by Motokawa concerning induction, some of the laws which were made use of in carrying out the present experiments.

1. The interval of time between cessation of Detector and presentation of *W* can be prolonged up to 20 sec. without appreciable change in the amount of CE (12).

2. A surprisingly small amount of the induction propagated from Inducer is sufficient to wipe out the induction caused by Detector and the phenomenon of neutralization follows practically the all-or-none law (17).

3. Provided that the induction caused by Inducer is not too weak, the neutralization takes place irrespective of the interval of time between Detector and Inducer (17).

4. The threshold of saturation for causing induction is so low that any colored figure discriminable from white can cause the induction. The occurrence or non-occurrence of neutralization again follows the all-or-none law (17, 24).

5. In general, the presentation of a white figure does not cause its own induction and also it has no effect upon the induction caused by Detector and by Inducer (9, 12).

6. The retinal region once illuminated by a white light reflects induction of any kind. Hence, pre-illuminating the retina, prior to presentation of Inducer by an appropriate pattern consisting of white contour serves as the collimator and a beam of induction is

* When *Ko* participated as *S*, U. Nagumo took trouble to be experimenter. The authors are grateful to her collaboration.

image of B1 appeared occasionally. The after-image of P was dark blue so that its contour was not distinct at all. However, it is to be noted that no gap existed in the portion of the after-image that corresponds to the blind spot. A part of B1 (the chamber of white walls) and the whole of B were seen in the periphery. Nevertheless, B was still identifiable as blue though it was considerably desaturated. It appeared in the midst of the after-image of the chamber but the intervening black space between B and the walls was not distinct.

Two subjects, In and Y, participated in this experiment. As shown in Fig. 4, occurrence of the refraction was convincing when P was present (o in Fig. 4) while the induction proceeded straight to the point 1 when P was absent (x in Fig. 4). It became also clear that passing through the pipe-shaped path on the right side of the blind spot ($B1_1$), the beam of induction was made narrow enough not to affect the neighboring points.

Encouraged by this finding, the ex-

periment was repeated with the stimulating pattern in which the white line at the left side of the blind spot ($B1_2$) was completely concealed. Namely, in this case, B1 did not "bridge the blind spot" and it served only as a gun for sending a sufficiently narrow beam of induction. In order to change the blind spot to a traversable medium for induction, so far, including the experiments in the previous papers, such a pattern has been always in use that a continuous line is perceived across the blind spot along which the induction is to propagate. Hence, the purpose of this experiment was to test the following hypothesis. To bridge the blind spot in the direction of its propagation might not be a necessary condition for the induction to traverse the blind spot. In other words, the occurrence of the compensation of any kind, e.g., perception of the complete prism-shaped figure P in this case, might be sufficient to make the blind spot functionally equivalent to other regions of the retina.

Three Ss, In, Y and Kz, participated in this experiment and the results are

Fig. 5.

shown in Fig. 5 by circles. This was Kz's first experience as S in experiments involving the phenomena of refraction and of propagation across the blind spot. The results clearly showed that the induction not only traversed the blind spot but also refracted in it even when there was no bridge across the blind spot in the course of the propagation. It was also demonstrated that concealing the center of P did not alter the results if the gap was not perceived as the result of the compensation.

By replacing P by a thin yellow bar standing vertically (0.2×13 cm.), it was ascertained that the neutralization could be demonstrated at point 1 (• in Fig. 5). The induction proceeds straight under this condition. When no figure, neither the prism nor the bar, was presented and hence there was no compensation, the induction was blocked by the blind spot and the neutralization was not obtained at point 1 (× in Fig. 5).

Experiment II

The experiment was undertaken with the pre-illuminating pattern shown in Fig. 6 to test the hypothesis that the

Fig. 6.

reflection of induction would also be observed in the region corresponding to the blind spot. In Fig. 6, R denotes a white bar which was seen without any gap across the blind spot. It can be expected from the results of Experiment I that, if the compensation is present with R, the blind spot is traversable for induction. Should the region corresponding to R reflect the beam of induction from B, the neutralization would be obtained at point 2. On the contrary, if the beam passes through the region it will reach point 4.*

Two Ss, In and Ko, participated in the experiment and the results are shown in Fig. 7. There seems to be no doubt that the reflection takes place in

Fig. 7.

the region corresponding to the blind spot in the same way as it does in any other region of the retina. Although the part of the contour at which the beam hits the bar was occasionally seen slightly blurred in comparison with the other part of the contour falling in the sensitive region of the retina, the reflection was thus clearly demonstrated.

* In this argument, it is assumed that, passing through the region corresponding to R, the beam does not change its course by refraction. The refractory index of the beam in a retinal region once illuminated by a white light is not known since it is reflection or even total reflection that occurs in this case (15, 16).

Experiment III

When we discovered in Experiment I that the induction was refracted by the region once illuminated by the prism-shaped figure P, we were, in truth, astonished not only by the phenomenon of refraction itself but also by the fact that the beam of induction could pass through a region of such width. In order to discriminate clearly the refracted beam from that not refracted, P has to be of the size indicated in Fig. 3 and the width of the part which is to transmit the beam has to be 0.6 cm. The induction which reached the point W was, however, strong enough to cause the neutralization. This fact made us wonder whether the phenomena of absorption might fail to take place in the region corresponding to the blind spot or whether the index of absorption might at least be smaller than that in the sensitive region of the retina. Experiment III was designed to test this hypothesis. The stimulus pattern shown in Fig. 8 was used in the

Fig. 8.

temporal sequence indicated in Fig. 9. When the fixation mark 1 was in use, the part of the yellow absorbing figure A that intercepts the beam fell in the blind spot, but when the mark 2 was fixated, the blind spot did not lie on

Fig. 9.

the path of the propagation of induction. The width of A was varied by concealing its left side (the side toward Y and W) in an appropriate way. Because A was dominant in size, the white bar B1 was introduced to prevent the indirect induction, if any, of A towards W. Two Ss, In and Y, participated in this experiment and the results are shown in Fig. 9, where o indicates CEs when the blind spot was involved and x CEs when the blind spot was not involved. The threshold of width for the traversal of a region once illuminated by A was thus determined with accuracy and it became clear that the absorption occurred in the blind spot exactly in the same way as in any other region of the retina. All conditions except the shape of the transmitting figure (e.g., luminosity of the yellow, that of B, and the distance from B to W, etc.) were exactly the same as those in Fig. 3. Hence it was no wonder that the beam could pass through the region corresponding to P in Experiment I.

It is to be kept in mind that in observing A it is impossible for S to tell

whether it is above or below the threshold in its width and he has no way of intensionally adjusting his responses so as to yield the regularities obtained in Fig. 9. As a matter of course, different widths were repeated in randomized order.

DISCUSSION

The propagation of induction cannot traverse the blind spot under the ordinary conditions in the dark room, i.e., when the blind spot is not involved in any way with perception of luminous figures. However, if a continuous figure is perceived across the blind spot, irrespective of the direction of the figure, not only does the blind spot lose its blocking effect upon the propagation of induction but it also becomes functionally equivalent to other regions of the retina in the sense that the phenomena of refraction, reflection and absorption are demonstrated in the blind spot as well as in other retinal regions. Besides it became clear that the refractory index and the index of absorption are respectively the same in both. Coincidence in both cases of the threshold for traversal of induction was determined with accuracy of up to 1 mm. (Experiment III). However, as it was not of primary concern in Experiment I to make precise determination of the refractory index, we are not in a position to state the accuracy with which the index in the blind spot is compared with that in other regions of the retina. It is still true, however, that in the blind spot the beam of induction followed the course expected from the refractory index as determined by Motokawa in the sensitive region of the retina.

The fact that a continuous figure can be perceived across the blind spot is quite conspicuous though nobody knows exactly what physiological pro-

cess underlies the phenomenon and at what level of the nervous system the process takes place. In the same way, the facts discovered by Motokawa that the induction propagates, reflects, refracts and is absorbed are undeniable though Motokawa provides no hypothesis about physiological processes underlying these phenomena. As a matter of course, we are not in a position to speculate concerning the physiological processes in either case. It may be said, however, from the results of the present experiments that whatever the physiological processes may be, they occur at the same level and interact with each other.

It is the retinal region once illuminated by a light, and not the excitation in the retina under the illumination, that reflects, refracts and absorbs the beam of induction. For this reason, presentation of the white bar or of the prism-shaped figure or of the absorbing figure always precedes that of Inducer in the experiment concerning induction. It is to be kept in mind, therefore, that what was discovered in the present experiment is as follows if stated with exactness. Once the blind spot is involved in perception of a figure in the sense that the compensation takes place, it is in the state of being functionally equivalent to any other region of the retina at the moment when the induction arrives, though the stimulation responsible for the compensation has already ceased to exist. In the report of Experiment I we include a description of the after-image of the figure perceived across the blind spot. It is our impression, however, that presence or absence of the after-image is rather irrelevant to the matter under discussion.

SUMMARY

1. The procedure for determining

the electrical excitability was discussed and it was mentioned that great caution was being taken in our procedure against the possibility of terminating the descending series before the true threshold is reached.

2. Concerning the enhancement of the excitability when the eye is pre-illuminated by stimulation patterns, the phenomena discovered by Motokawa, i.e., the reflection, the refraction and the absorption of the beam of induction were shown to occur also in the region corresponding to the blind spot under the condition that the reflecting bar or the prism-shaped figure or the absorbing figure is perceived across the blind spot as a result of the compensation.

3. In order to make the blind spot which blocks propagation of the induction under ordinary conditions into a traversable medium for induction, it was discovered sufficient that perception of a continuous figure of any direction, not necessarily in the direction of the propagation, takes place across the blind spot.

4. It was quantitatively ascertained that the refractory index and the index of absorption remain respectively the same when these are determined in the region corresponding to the blind spot as in other regions of the retina.

5. It was argued that whatever physiological processes may underlie the fact that the beam of the induction shows the phenomena of refraction, reflection and absorption, these would be processes occurring at the same level of the nervous system and interacting with each other.

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