Propagation Velocity and Total Reflection of Spreading Induction in the Light-Adapted Human Retina

By

Koiti Motokawa and Mitsuo Komatsu

(本川 弘一) (小松 三夫)

From the Department of Physiology, Tohoku University, Sendai

(Received for publication, September 5, 1957)

INTRODUCTION

A spreading process called "spreading induction" is started at the margin of an illuminated part of the retina, and, mediated by this process, a field of retinal induction is established around the illuminated area. The velocity of propagation in the dark-adapted retina has been measured by three different methods, and consistent results have been obtained by these different methods. However, measurement of the velocity at the light-adapted retina seemed to be more difficult, because it was shown that spreading induction suffered from a stronger decrement in the light-adapted retina than in the dark-adapted.

Katayama and Aizawa succeeded in measuring the velocity of spreading induction in the dark-adapted retina; they measured the difference in time necessary for arrival of spreading induction at two points differently distant from the margin of an illuminated area of the retina. The velocity was given by the ratio of the distance between the two points to the difference in time measured.

In the present investigation, the same method was used to investigate the dependence of the velocity on the intensity of adapting light. On the other hand, a new indirect method which is based on the principle of total reflection has been introduced, and the data obtained by the direct and the indirect method were compared with each other.

EXPERIMENTAL

Method

The optical systems used are illustrated in Fig. 1. The lamp, L, of a slide-projector was used as a light-source. The intensity and the wave-length of light were controlled by means of suitable filters represented by G in Fig. 1. An
inducing patch, I, and a white test patch, Wh, were presented on a vertical screen at a distance of 30 cm. in front of the subject's eye. The patch, I, was square in shape and 1 × 1 cm² in size. The test patch, Wh, was a circle of 1 mm. in diameter. The positions of I and Wh are shown in the inset. The distance, d, between I and Wh was variable. The eye was exposed to the two patches, I and Wh, successively by means of a sector pendulum, which is shown also in the inset. The exposure times of I and Wh were 2.5 msec., and the interval, τ, between I and Wh was variable.

Another set of optical system was used for light adaptation of the eye. The set consisted of a light-source, L, a diaphragm, D, smoked glass, G, and opaque glass, O, and a half-mirror, M. The latter was situated immediately before the eye so that the eye was subjected to a wide, uniform illumination. The intensity of the adapting light was controlled by D and G.

Curves showing retinal induction were obtained by these arrangements, and are illustrated in Fig. 2. In these experiments the intensity of the adapting light was 1 lux, and those of I and Wh 10,000 lux. The broken curve in this figure shows the change of electrical excitability of the eye following its exposure to the white test light alone. The continuous curves in the same figure refer to similar changes of electrical excitability following successive exposure to I and Wh, the interval between both exposures being 100 msec. The distance between I and Wh was 2.5 mm. on the vertical plane. The maximum of the continuous curve is seen at 2, 1, 2 or 3 sec. from the test flash, Wh, when the inducing flash was white, red, green or blue. The higher electrical excitability represented by
the continuous curve over the broken curve is a manifestation of retinal induction caused by the inducing light, I. The intensity of induction is measured by the maximal difference between both curves, and this difference is designated "contrast effect (C.E.)". The C.E. is generally a function of distance; it decreases exponentially as the distance increases, when the interval separating both exposures is fixed. With a fixed distance the C.E. depends on the interval between I and Wh. The dependence is shown in Fig. 3. In this figure, the C.E. is represented as a function of the interval, \( \tau \), for a given distance—say 2.5 mm. For this distance, the C.E. is zero when the interval is less than 5 msec. This means that no induction appears yet at this point when the test of induction is carried out too early with Wh. After a latency of about 5 msec. the C.E. increases almost linearly with the time interval and reaches a constant level, which is the higher the shorter the distance. It is also to be noted that the latency increases with the distance, and this fact may be so interpreted that the time necessary for propagation of spreading induction is included in the latency. If the velocity is constant, there must be a linear relation between the latency and the distance.
Fig. 3. Direct method for measuring velocity of spreading induction. Ordinates: Contrast effects. Abscissae: Time interval, τ, between red inducing light, I, and white test light, Wh. Arrangement of patches and experimental procedure are shown in inset, where d denotes distance between I and Wh. Latencies of C.E. were measured from intersections between horizontal lines A, B, C and D and C.E.-τ relations, and plotted against distances, d, in inset.

In the inset of Fig. 3, distances are plotted as ordinates against latencies as abscissae. The latencies were determined from the intersections between the C.E.-τ relations and a horizontal line A, B, C or D. As can be seen in the inset, there is a linear relationship between the latencies and distances, regardless of the indicator used for determination of latencies. As the relations A, B, C and D are all parallel to one another, values of velocities determined by the slopes of these lines will be identical. The values so determined refer to the vertical plane 30 cm. in front of the eye. In order to obtain velocities in the retina, one has only to multiply these values by a factor 17/300, where the posterior nodal distance of the eye is assumed to be 17 mm.

Results

1) Dependence of the velocity on the intensity of white adapting light

By the method described above the dependence of the velocity on the adaptation level of the eye was investigated in two subjects. The results obtained are summarized in Table I. The intensity of the red inducing light used was 64,000 lux throughout this experiment. As can be seen in this table, the velocity increases with the intensity of the adapting light, and reaches a constant level at about 1 lux. It is to be noted that the velocity at the highest level is
TABLE I

Dependence of the Velocity of Spreading Induction on the Intensity of White Adapting Light

The Intensity of Red Inducing Light was 64,000 lux.

<table>
<thead>
<tr>
<th>Intensity of adapting light in lux</th>
<th>Velocity in retina (mm.per sec.)</th>
<th>Subjects</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.000</td>
<td>1.7</td>
<td>K. M., T. K.</td>
</tr>
<tr>
<td>0.006</td>
<td>2.6</td>
<td>T. K.</td>
</tr>
<tr>
<td>0.010</td>
<td>4.2</td>
<td>K. M.</td>
</tr>
<tr>
<td>0.014</td>
<td>5.8</td>
<td>T. K.</td>
</tr>
<tr>
<td>0.040</td>
<td>16.7</td>
<td>K. M.</td>
</tr>
<tr>
<td>0.100</td>
<td>33.4</td>
<td>K. M.</td>
</tr>
<tr>
<td>0.400</td>
<td>39.0</td>
<td>K. M.</td>
</tr>
<tr>
<td>1.000</td>
<td>41.3</td>
<td>T. K.</td>
</tr>
<tr>
<td>4.000</td>
<td>42.8</td>
<td>K. M.</td>
</tr>
</tbody>
</table>

about 25 times as high as the velocity in the dark-adapted retina. In contrast to the remarkable effect of the intensity of adapting light, the intensity of inducing light has almost no effect upon the velocity, as will be shown in the following: The experiments were carried out at two different adaptation levels, and the intensity of the red inducing light was varied from 100,000 to 100 lux. As can be seen in Table II, the velocity is almost independent of the intensity of inducing light. In other words, the all-or-none law applies to the velocity of spreading induction.

TABLE II

The Intensity of Inducing Light (Red) and the Propagation Velocity of Spreading Induction in the Human Retina Adapted to White Light of Constant Intensity

<table>
<thead>
<tr>
<th>Intensity of inducing light in lux</th>
<th>Velocity in retina (mm. per sec.)</th>
<th>Subject: K.M. Adapted to 4 lux</th>
<th>Subject: T.K. Adapted to 1 lux</th>
</tr>
</thead>
<tbody>
<tr>
<td>100,000</td>
<td>37</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td>10,000</td>
<td>36</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>1,000</td>
<td>41</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>38</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

Motokawa et al. showed in a preceding paper that the velocity is independent of the wave-length of inducing light in the dark-adapted human retina. The same is true of the light-adapted retina; in the retina adapted to white light of 1 lux, values of velocity 38, 42, 39 and 41 mm./sec. were obtained in the
present experiment for red, green, blue and white inducing lights respectively. All these values may be regarded as identical with one another within the scope of experimental error.

2) Total reflection of spreading induction

The law of refraction may be represented in terms of velocities of light in two media as follows:

$$\frac{\sin i}{\sin r} = \frac{V_1}{V_2}$$  \hspace{1cm} (1)

where $i$, $r$, $V_1$ and $V_2$ denote the angle of incidence, the angle of refraction, the velocity in the first medium and that in the second medium respectively.

When $V_2$ is greater than $V_1$, a beam of light coming from the first medium is totally reflected at the boundary of the two media for angles of incidence greater than a certain critical value, $i_c$. In the special case in which the angle of incidence is equal to $i_c$, the refracted light runs parallel with the boundary surface. Then the following relation holds:

$$\frac{\sin i}{\sin r} = \frac{\sin i_c}{\sin 90^\circ} = \sin i_c = \frac{V_1}{V_2}$$  \hspace{1cm} (2)

If the critical angle, $i_c$, can be determined experimentally, the velocity in the second medium, $V_2$, may be determined from the known velocity, $V_1$, according to the formula (2).

As the velocity of spreading induction is greater in the light-adapted part of the retina than in the dark-adapted, the spreading induction coming from a dark-adapted part can totally be reflected at the margin of a retinal image of a white figure or of its after-image, because the retinal image or the after-image represents a light-adapted part of the retina. The phenomenon of total reflection can be demonstrated by the arrangement of patches shown in the inset of Fig. 4. In this arrangement I represents a blue inducing patch of 20 lux, P a white parabolic reflector to reflect the spreading induction caused by I, and Sc a white screen to prevent the spreading induction from reaching directly a linear white reflector, R, whose intensity was 0.04 lux. The reflector, R, was usually perpendicular to the axis of the parabolic reflector, and this position was regarded as standard. The parallel beams of spreading induction produced by the set of I and P will reach the linear reflector and be reflected there, if the angle of incidence is greater than the critical angle. The angle of incidence could be controlled by tilting the linear reflector from its initial position. D was a blue detector whose direct induction blue in character was to be neutralized by the yellow spreading induction initiated by the blue inducer, I. Wh was a white test light to test the state of induction at the detector, D. The patch, Wh, was always presented at the tip of the linear reflector. If the incident angle is critical, the refracted yellow induction will proceed along the upper margin of the linear reflector and reach the very part of the detector at which the neutralization is tested by Wh. Thus, neutralization will or will not be seen at this point according to whether the incident angle is critical or not.

The temporal sequence of experimental procedure is shown also in the inset
Fig. 4. Experiment to measure critical angle of incidence for total reflection of spreading induction. Arrangement of patches and experimental procedure are shown in insets. D: Blue detector of 20 lux. I: Blue inducer of 20 lux. P: White parabolic reflector. R: Linear reflector consisting of white line of 0.04 lux. R was tilted by angle from standard horizontal position. θ: Angle of incidence. Sc: White screen to prevent spreading induction from reaching directly linear reflector, R. Ordinates: Contrast effect at point Wh of detector. Abscissae: Angle of incidence. Neutralization of induction at point Wh occurs only when the refracted spreading induction proceeds along R.

From formula (2) the velocity, \( V \), in the retinal part, R, which was adapted to an illumination of 0.04 lux, will be given as follows:
In the same way, velocities for various degrees of light adaptation were determined, the illumination of \( R \) being varied from 0.04 to 1 lux. The results are summarized in Fig. 5 I, in which A, B, and C refer to intensities of adapting light 0.04, 0.1 and 1 lux respectively. As can be seen in this figure, the range of incident angles over which the neutralization occurred was displaced from right to left as the intensity of the adapting light was increased. This means decreases in critical angle or increases in velocity with increasing intensities of adapting light.

The velocity for each adaptation state was calculated in the same manner as stated above, and is represented in comparison with the corresponding velocity determined by the direct method in Table III. As can be seen in this table, the values for 0.04 lux by the direct and by the indirect method coincide with each
Propagation Velocity and Total Reflection of Spreading Induction

TABLE III
Dependence of the Velocity of Spreading Induction on the Adaptation State of the Eye

<table>
<thead>
<tr>
<th>Intensity of adapting light in lux</th>
<th>Velocity in mm. per sec. (direct method)</th>
<th>Velocity in mm. per sec. (indirect method)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.04</td>
<td>16.7</td>
<td>16.7</td>
</tr>
<tr>
<td>0.1</td>
<td>33.4</td>
<td>28.7</td>
</tr>
<tr>
<td>1.0</td>
<td>41.3</td>
<td>35.4</td>
</tr>
</tbody>
</table>

other, but some discrepancy is seen between the data obtained by both methods for higher intensities; the values by the indirect method are somewhat lower than the corresponding ones by the direct method. What is responsible for this discrepancy? It seems that the difference of adapting procedure in the two methods is responsible for the discrepancy, because the latter was reduced by reducing the difference in experimental condition as far as possible in the further experiment to be mentioned. In the direct method the eye was exposed continuously to the adapting light of constant intensity, but in the indirect the linear reflector was presented only for a period of 2 seconds each time, and such procedure was repeated every 15 seconds. In another word, the light adaptation in the indirect method was intermittent, instead of continuous. Therefore, the initial part of the spreading induction reflected by the parabolic reflector must have passed through the linear reflector during illumination, but the later one which was traveling through the dark area between I and R just before the end of illumination must have passed through the after-image of R. It is obvious that the area of the after-image is less light-adapted than the area of the retinal image itself. This must be the reason why the values of velocity determined by the indirect method were lower than the corresponding ones by the direct method. We became aware of this situation after the experiment, and were compelled to carry out another series of experiments with a continuous illumination of the linear reflector, inspite of great difficulty in assuring sufficiently long fixation of the eye. The data obtained by this method are represented in Fig. 5 II. The curves A, B and C correspond to those marked by the same alphabets obtained by intermittent light adaptation in Fig. 5 I. It is to be noted that the range of neutralization is narrower in experiment II than in experiment I, probably because of more uniform light adaptation in II. The velocities computed from the data of experiment II are represented in the last column of Table III. As can be seen in this table, the agreement with the values obtained by the direct method has been improved by the continuous adaptation in the second series of experiment.

DISCUSSION

The values of velocity computed from the law of refraction have been
shown to agree satisfactorily with those determined by the direct method. The refracting medium used in our experiments was a retinal image of a white line. When the intensity of illumination of the line is over 1 lux, the critical angle for total reflection is only about 2.5°. Therefore spreading induction incident upon the retinal image of a white line with angle of incidence from 2.5° to 90° must be reflected by the retinal image. This means that a retinal image of a white line represents a very good reflector for spreading induction. For this reason a retinal image or an after-image of a white line has been used as a screen. When an inducer is enclosed by a white line figure, only a small fraction of the spreading induction produced by the inducer can reach the outside of the white line figure. Such a protecting action of a white line figure was discovered by Motokawa in 1951, and has been utilized extensively in various experiments of retinal induction, but the mechanism of the protecting action has remained obscure.

**Summary**

A process called "spreading induction" is started at the margin of a retinal image and propagated into the surrounding retinal areas. Thus a field of retinal induction is established around a retinal image.

1. The velocity of propagation was determined by measuring the latencies of the propagating process at various distances from the margin of a retinal image, and it was shown that the velocity depends greatly on the adaptation state of the retina, but only little on the intensity and hue of the light stimulus.

2. The value of velocity was 1.7 mm. per sec. in the dark-adapted retina and 42 mm. per sec. in the retina adapted to an illumination stronger than 1 lux.

3. When spreading induction comes across a white retinal image, it can totally be reflected at the margin of the retinal image. The critical angle of incidence for total reflection was determined, and on the basis of the law of refraction the velocity of spreading induction in the light-adapted part, the retinal image, was computed from the critical angle determined experimentally and the known velocity in the dark-adapted retina.

The so computed values were found to agree satisfactorily with those determined by the direct method.

**References**