PERIODIC EXCITABILITY OF THE HUMAN RETINA

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Motokawa and Iwama (7) showed that there appear three distinct minima in the strength-frequency curve of the human retina obtained in their stimulation experiments with sinusoidal alternating currents, and considered these minima as due to a phenomenon of resonance. This consideration is based on the assumption that the human retina has natural frequencies which correspond to the optimum frequencies found in the strength-frequency curve. If this assumption is correct the same natural frequencies should be demonstrated by means of some other methods.

In general, a natural frequency of a vibrating system can be found by the following two methods: The one is the method of resonance, and the other consists in measuring the period of free vibration. In the latter case the system must be set in motion by an external force acting for a brief period, and then the free vibration of the system is observed. In the present investigation this principle was applied to the human eye to find its natural frequencies.

METHOD

A single electric shock was applied to the eye through a pair of silver electrodes, of which the one was placed at the forehead and the other at the occiput, the electrical contact between the skin and the electrodes being secured with electrode-paste. The time course of the change in electrical excitability of the retina due to such a sensitizing stimulus was investigated by measuring the threshold voltage for a second test-stimulus which was delivered at varying intervals after breaking off the sensitizing stimulus. The index of excitation was an electric phosphene. As the sensitizing stimulus (S.S.) a constant current pulse of 5 msec. in duration was used, and the test-stimulus (T.S.) consisted of a constant current pulse of 100 msec. in duration and of varying intensities. The intensity of the S.S. was fixed at about 80% of the threshold voltage as measured by an electric shock of the same duration as the S.S. so that an electric phosphene was evoked only when the S.S. was followed by a T.S. of sufficient intensity. The use of a superthreshold S.S. was avoided because it was found difficult to discriminate the phosphene caused by the S.S. from that evoked by the T.S. at a very short interval between them. The direction of stimulating currents showed no essential effect upon the general course of the excitability change caused by the S.S.

The interval between the two stimuli was controlled by means of a spring

1 Motokawa, K. (1950). Received for publication February 22, 1950.
rheotome whose scale had previously been calibrated. Measurements were carried out under such conditions of illumination as the eye showed the highest sensitivity to an electric stimulus. Such conditions were fulfilled in the following way: A 60 watt lamp was placed behind the subject so as to cast the shadow of the subject's head on a white wall standing in front of the subject. Determination of electric thresholds was performed while the subject was gazing at the shadow on the wall.

To express quantitatively the electrical excitability of the eye at varying moments after the end of the S.S., a quantity \( \zeta \) was introduced, which is defined as follows: \( \zeta = \left( \frac{(E - E_0)}{E_0} \right) \times 100 \), where \( E_0 \) represents the excitability tested by the T.S. alone, and \( E \) that tested by the successive stimuli S.S. and T.S.

**RESULTS**

If \( \zeta \)-values are plotted as ordinates against time intervals between the S.S. and T.S. an excitability curve with a time course of a damped oscillation is obtained. An example is shown in Fig. 1. The period of oscillation is about 54 msec. in the earlier part of oscillation and seems to become a little shorter towards the end of oscillation. The same relation can be seen in Fig. 2, which represents the data from another subject. Similar measurements were carried out with sensitizing and test-stimuli of varying duration and it was found that the general form of the excitability-time curve depends little upon the duration of the stimuli.

Next, the effects of light- and dark adaptation of the eye were investigated. In a series of experiments the eye was exposed to a white wall illuminated by

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**Fig. 1.** Time course of electrical excitability of human retina after a subthreshold electric shock. Ordinate: increase in electrical excitability in percentage of resting level. Time sequence of sensitizing- (S.S.) and test-stimuli (T.S.) is shown in the inset. Downward deflection indicates direction of stimulating currents flowing from forehead to occiput through the head.
white light of 10,000 lux, and under these experimental conditions the excitability-time curves were determined by the same procedure as stated above. An example of the data obtained in this series of experiments is shown in \((a)\) of Fig. 3. The electrical threshold of the eye is generally higher under these conditions of illumination than under moderate light adaptation. The amplitudes of oscillation are much smaller, and the period of oscillation seems to be a little shorter under strong light adaptation than under moderate adaptation.

Fig. 3 (b) represents an excitability-time curve obtained from one and the same subject under complete dark adaptation. As can be seen in the figure, the general character of the curve resembles that of the curve \((a)\). In the curves

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**Fig. 2.** Excitability-time curve after a subthreshold electric shock. Explanation as in Fig. 1.

**Fig. 3.** (a): under light adaptation. (b): under complete dark adaptation.
illustrated in Fig. 1 and 2, the points determined immediately after the end of the S.S. lie on the ascending branch of the first oscillation of each curve, while the corresponding points of the curves shown in Fig. 3 are situated at the first minimum of each curve. In other words, the initial phase of the oscillation is different in the two cases. This difference seems to depend upon various factors, among which the direction of the stimulating currents is the most important one. When constant current pulses are used as conditioning and test-stimuli, the initial phase of the curve is positive or negative according to whether the two stimuli are of opposite or the same direction, irrespective of the absolute direction of the currents. When the S.S. is of such a long duration that the T.S. is superimposed upon the S.S. the curve begins, contrary to the experiments stated above, with a positive or negative phase depending upon whether the two stimuli are in direction the same or opposite to each other.

This group of phenomena may be explained as follows: In case the two stimuli are separated by an interval from each other an interaction would take place between the off-effect of the S.S. and the on-effect of the T.S. in such a manner that a positive phase ensues when both sorts of effects are of the same direction, and that a negative phase results when they are of opposite direction. In the second experiment in which no off-effect of the S.S. to interact with the on-effect of the T.S. is present, an interaction would occur between the on-effect of the S.S. and that of the T.S. Since the direction of the on-effect is the same as the direction of the current, the initial phase of the curve must, in this case, be positive or negative according to whether the two stimuli are of the same or opposite direction.

As shown by Motokawa and Iwama (7), the natural frequencies of the human eye as revealed by stimulation with alternating currents are about 18, 36 and 54 cycles per sec. The period of oscillation obtained from the data of the present experiments are summarized in Table I. It can be seen in this table that the period is on an average 54.85 msec. That is, the natural frequency determined by the present method is 18.2 c.p.s., and this value coincides closely with the lowest optimum frequency as determined by the method of resonance.

It must be due to the insufficient number of points taken in the above experiments that the excitability-time curves show no oscillation which would

<table>
<thead>
<tr>
<th>Exp.</th>
<th>Interval between 1. and 2. maxima in msec.</th>
<th>Interval between 2. and 3. maxima in msec.</th>
<th>Average</th>
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<td></td>
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<td>54.85</td>
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correspond to the higher optimum frequencies of the strength-frequency curve studied by Motokawa and Iwama. The following experiment was undertaken in order to demonstrate that harmonic oscillations are superimposed upon the fundamental oscillation which has been shown above to correspond to the lowest optimum frequency of the strength-frequency curve. In this experiment an induction shock was used as the T.S. The data are shown in Fig. 4, which shows that the curve, in reality, is composed of a few component oscillations having different frequencies, although the periods of these superimposed oscillations cannot accurately be determined. At any rate, this finding lends direct support to the interpretation by Motokawa and Iwama that the minima observed in the strength-frequency curve of the human retina are based upon resonance.

**DISCUSSION**

The fact that the excitability-time curve takes a periodic course provides evidence of the periodic excitability of the human retina. In nerve and muscle such a curve takes, however, an aperiodic time course under physiological conditions, but it can take a periodic course under some experimental conditions such as at a low calcium concentration of the medium, and it is under such conditions that nerve and muscle show repetitive responses to a single stimulus, as shown by a number of investigators (Fessard 2, Monnier and Coppée 5, Katz 4). The periodic excitability of the retina must be a property of nervous elements in the retina which represents a part of the central nervous system. The higher parts of the central nervous system show automatic excitability, as evidenced by brain potentials. Such automatic excitability is seen also at lower parts of the central nervous system, in particular, of lower animals; Adrian (1) showed that spontaneous potential changes can be observed at the optic ganglion of some
lower animals. There is, however, scarcely any true spontaneous discharge of the nervous elements of the human retina; the periodic excitability manifests itself when the retina is stimulated. The present investigation serves to demonstrate the periodic excitability of the human retina, but cannot answer the question as to whether this property plays an important role in the physiological function of the retina, because the property has been revealed by non-adequate stimuli. In order to make the physiological significance of the property clearer, I performed some experiments with an adequate stimulus in combination with an electric one, using subthreshold light as a sensitizing stimulus which was followed by a constant current pulse, but I could not succeed in this attempt, probably because the sites of attack of the two stimuli are different in such a manner that the one attacks photoreceptors while the other stimulates nervous elements (6,3). The question raised above should, therefore, be answered by further investigations.

SUMMARY

The human retina was stimulated by a subthreshold electric shock, and the change in electrical excitability caused by this stimulus was investigated by another electrical stimulus delivered at varying intervals after cessation of the sensitizing stimulus. Stimulating electrodes were placed at the forehead and the occiput, the index of excitation being an electric phosphene.

1. The excitability-time curve shows a periodic course, the amplitude of oscillation decreasing exponentially.

2. The frequency of oscillation is 18 cycles per sec., and this agrees closely with the lowest optimum frequency of the retina as determined by stimulation with alternating currents.

3. More detailed study of this phenomenon revealed that some oscillations with higher frequencies are superimposed upon the fundamental oscillation observed above. This finding corresponds to the fact that there appear three or more minima in the strength-frequency curve obtained in stimulation experiments with alternating currents.

4. Thus, the periodic excitability of the human retina can be demonstrated in the two ways, i.e. by the present method and by the method of resonance.

REFERENCES

1. ADRIAN, E. D. J. Physiol. 75: 26, 1932.