

A NOTE ON THE RETINAL ACTION POTENTIAL
OF THE HUMAN EYE.

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THE first to record retinal action currents from human subjects were Dewar and M'Kendrick [Dewar, 1877], who observed a deflection of their slow Thomson galvanometer in the same direction as with animals. Kahn and Löwenstein [1924] emphasized the difficulties of the method. They reproduce their best curve, obtained with the string galvanometer, but are not prepared to state that it represents the true form of the retinal response. Hartline [1925] developed the technique and showed that the method might be put to some use in comparing retinal and sensory data. The best records have been obtained by Sachs [1929]. Some of his tracings have been published by Kohlrausch [1931] and are in general agreement with our own. His success is in part attributable to long practise in the avoidance of winking and other movements of the ocular muscles.

Our original intention was to investigate the technique with a view to its possible utilization as a method of comparison with sensory events. An attempt in this direction was, however, carried out only with respect to flicker and fusion. Winks at on and off were found to cause changes of potential very similar to well-known types of retinal action current. A great deal of the time at our disposal was spent in training ourselves as subjects and in establishing the true form of the response under standard conditions. As the records gradually became consistent and repeatable within reasonable limits we decided to take up a simple problem, viz. to compare responses from the central retinal field with responses from peripheral retinal fields under optimal conditions. For such work the human eye is interesting because it is possible in the same retina to compare the action potential from an organ in which cones predominate with that from one in which rods are far more numerous than cones.

METHOD.

Records from the human subject were obtained with the directly coupled valve amplifier and string galvanometer which have lately been used for registering action potentials in the cat's eye [Granit, 1933; Creed and Granit, 1933]. The subject was seated opposite the stimulating apparatus with his head supported in a padded frame attached to the back of the chair. Leads were taken from the anæsthetized conjunctival sac and from the mouth by means of cotton wicks communicating with Ag-AgCl-Ringer-Locke electrodes. In the course of 20 experiments, each lasting about 30 min., some 330 records were taken.

The standard conditions ultimately adopted were as follows. The subject was in a state of considerable dark-adaptation, the lighting of the room being only such as to enable the experimenter to handle the apparatus. The stimulus was a circular sheet of ground glass illuminated from behind and of about 10 ml. brightness. It subtended about 7° at the subject's eye and carried a cross of luminous paint for central fixation. For peripheral stimulation a piece of faintly illuminated paper 30° to one side was used as a fixation mark. These conditions are optimal in that further increase of area has little effect on the amount of potential developed, increased brightness makes the suppression of winking at the beginning of the stimulus almost impossible, and light-adaptation is accompanied by smaller responses.

RESULTS.

The normal response in central and peripheral vision.

Fig. 1 shows a response which, we are satisfied, represents a very close approximation to the true curve of retinal action potential in the human eye. The silent features of such curves are: absence of *a*-wave, small *b*-wave of about 0.2 millivolt or slightly less, small secondary rise (*c*-wave), and absence of definite off-effect. The only certain difference between central and peripheral responses is the lesser amount of potential developed in the latter. With one observer this difference averaged about 5 p.c.; with the others it was consistently about 15–20 p.c. and thus outside the limits of possible error. The latent period preceding the deflection was never less than 40σ and commonly exceeded 60σ .

It is interesting to note that the curve of potential is of the same type in the central and peripheral retina. The *b*-wave may have a more definite peak in peripheral vision, but this result was not constant and we

hesitate to accept it as significant. The use of a smaller area, restricting the number of rods participating in the central response, was found to be of little service in our attempt to compare central and peripheral effects. The responses then became too small.

Comparison with the cat's retinal action potential.

It is interesting to compare Fig. 1 with the response of the cat's eye when leads are taken from the eyeball and from the decerebration wound [see Granit, 1933] under otherwise similar conditions. The latter shows

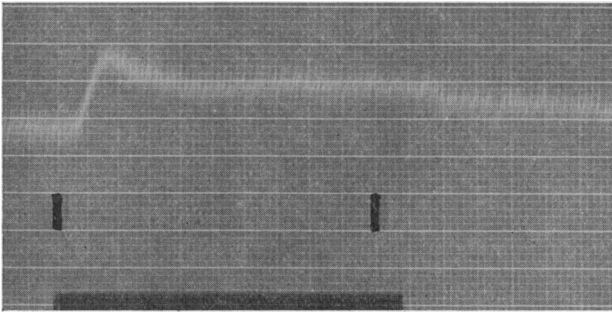


Fig. 1. Curve of retinal action potential for observer R. G. with central vision. Diameter of stimulating disc about $5^{\circ} 30'$ of visual angle. The *b*-wave deflection is 0.15 millivolt. For general conditions see text. Time marker gives 100σ and 20σ . An interval of 1 sec. is marked in ink. Stimulus directly photographed. Observer unshielded and picking up quick oscillations which broaden the contour of the string.

a small *a*-wave, a *b*-wave with a sharp peak rising to about 0.5 millivolt, a much larger *c*-wave, and a more definite off-effect. It is difficult to believe that the human eye is so much more efficiently shunted as to account completely for these differences. A more satisfactory explanation is provided by the fact that the cat's curve of retinal action potential evoked by a stimulus one hundred times less bright resembles, both in shape and size, the human response of Fig. 1. It is therefore probable that the human eye is pitched to a higher level of stimulation and that more light is required to produce a given response. The nocturnal habits of the cat lend support to this suggestion. The human response is not significantly altered by using nose, temporal bone, or forehead instead of mouth for the indifferent electrode.

An alternative possibility, which would explain both the smallness of the *b*-wave and the long latent period in the human eye, is that the

negative component P III [Granit, 1933] of the action potential may be larger than in the cat and may hinder the deflection caused by P II. The absence of *a*-wave and of marked off-effect make this suggestion unattractive.

Flicker and retinal potentials.

Observations with intermittent light were made by Sachs [1929] on his own eye. The records from his work published by Kohlrausch [1931] are, however, all responses to continuous stimulation. The disappearance of the sensation of flicker is stated to be accompanied by the disappearance of ripples in the electrical record. We have tried to determine how closely retinal and sensory data could be correlated in this way. It was com-

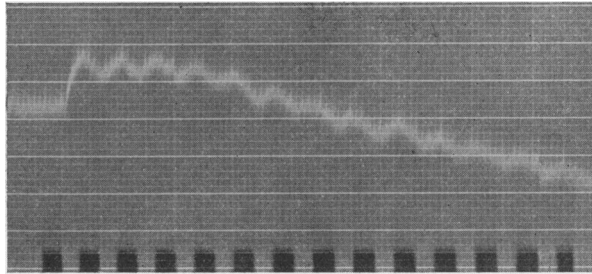


Fig. 2. Retinal action potential of observer R. S. C. Intermittent light at about eight flashes a second. Standard conditions. Considerable base-line drift.

paratively easy (Fig. 2) to confirm the fact that very coarsely flickering stimuli give wavy responses. But it was found impossible, owing to the smallness of the oscillations and the unsteadiness of the base line, to determine accurately the "fusion point" in the records. An obviously flickering stimulus would give a tracing indistinguishable from one obtained with steady illumination. This does not imply that retinal and sensory "fusion" occur at different rates of alternation. Indeed it seems certain on other grounds that the retinal frequency cannot be lower than the sensory, and there is some reason for believing them to be closely related [Creed and Granit, 1933]. Our experiences described above only indicate that the question whether this relation is one of identity cannot be solved by this technique. Even with elaborate shielding of the observer and increased amplification, it is unlikely that a sufficiently steady base line could be obtained.

DISCUSSION.

The fact that the peripheral response is similar in type to the central one, but develops less potential, is worth commenting upon. In the periphery of the retina rods are nearly twenty times as numerous as cones [Chievitz, 1889; Fincham, 1925]. It is therefore safe to assume that a much greater number of rods have been stimulated there than in the centre, even though the latter area was certainly not rod-free.

The amount of potential developed may depend upon four factors: (i) the sensitivity of the receptor (thus it increases with dark-adaptation), (ii) the number of receptors participating in the reaction (studied by Graham [1932] in an eye lacking internuncial neurones), (iii) synaptic interaction [Granit, 1933], (iv) size of negative wave. If the potential were developed in the rods and cones themselves, only the first two of these factors would come into play. The high sensitivity of rods as compared with cones in the dark-adapted eye would then presumably result in larger action potentials from the periphery than from the centre of the retina. The reverse, however, is found to be the fact. The available evidence, summarized by Granit [1933], indicates that the potential is developed in the retinal synapses or neurones, proximal to the rods and cones. Thus we are led to consider factor (iii), which at present is difficult to evaluate. According to Chievitz [1889] there are about 80 receptors for each ganglion cell 21° from the fovea, whereas in the fovea itself the ratio is 1 : 1. Far fewer bipolar and ganglion cells are therefore involved in our peripheral than in our central responses, and this may account for the difference observed. We cannot say to what extent sensitization of the rods and synaptic interaction may compensate in the periphery for a decreased number of nerve cells, but the explanation of our findings which has just been outlined is in keeping with other evidence as to the site at which retinal action potentials are developed. In view of the similarity of form between central and peripheral responses, there is unlikely to be any significant difference in the relative sizes of P II and P III.

SUMMARY.

1. The retinal action potential of the human eye has been recorded with a string galvanometer and a directly coupled amplifier under standard conditions.

2. Responses from the periphery of the retina (30° from the fixation point) resemble those from the centre in general features, but less potential is developed. The significance of this is discussed.

3. Responses to intermittent illumination at slow rates of alternation show corresponding ripples in the electrical record. It is not possible to correlate the findings directly with sensory data on fusion frequency.

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REFERENCES.

- Chievitz, J. H. (1889). *Arch. Anat. Physiol.*, Lpz. (Physiol. Abt.), Suppl. Bd. 139.
Creed, R. S. and Granit, R. (1933). *J. Physiol.* **78**, 419.
Dewar, J. (1877). *Nature*, **15**, 433-5.
Fincham, E. F. (1925). *Trans. Opt. Soc. Lond.* **26**, 198.
Graham, C. H. (1932). *J. cell. comp. Physiol.* **2**, 295.
Granit, R. (1933). *J. Physiol.* **77**, 207.
Hartline, H. K. (1925). *Amer. J. Physiol.* **73**, 600.
Kahn, R. H. and Löwenstein, A. (1924). *Graefes Arch. Ophthalm.* **114**, 327.
Kohlrausch, A. (1931). *Handb. norm. path. Physiol.*, Berlin, **12/2**, 1460.
Sachs, E. (1929). *Klin. Wschr.* **8**, 136.