

Cone Electroretinography by Flicker

It is generally assumed that the *b*-wave of the human retinal action potential is due to the stimulation of the rods. With an intensity of 2,000 lux, the *b*-waves fuse at a frequency of about 20 flashes per second. At lower intensities the fusion frequency in our experiments decreased. A linear relation was found between fusion frequency and the logarithm of stimulus intensity. However, the subjective fusion frequency, determined by cone activity, is known to reach values around 50–60 flashes per second. These high values are never obtained with the *b*-waves of the electroretinogram as index. This is but one of several reasons for assuming the *b*-waves to express rod activity.

According to Karpe and Tansley¹, the threshold of the scotopic *b*-wave of the electroretinogram is higher than the sensory threshold. In agreement with expectations from the general theory of the electroretinogram², Adrian³ found the photopic electroretinogram to be characterized by larger initial negative *a*-waves. It was therefore held that flicker at very high light-intensity might give evidence for cone activity by changing into (negative) *a*-wave flicker from the low-frequency (positive) *b*-wave flicker. This proved to be the case. When we increased the light-intensity until the *b*-waves were preceded by well-developed *a*-waves, the *b*-waves decreased (Figs. A–C) and the *a*-waves increased (B–C) as flicker frequency rose (see legend of diagram). The *b*-waves disappeared at a flash frequency of about 20 per sec. The negative *a*-waves appeared to have maximum amplitude at about 25–35 flashes per sec. It seems very likely that their quick return after each flash is due to a true off-effect. This off-effect becomes more pronounced if the PII component of Granit's analysis has been removed. Onset of fusion of fast flicker was accompanied by decrease of amplitude. It depended upon stimulus intensity in the same way as the *b*-flicker at lower intensities. Fusion coincided with sensory fusion. The highest fusion frequency observed was at about 55 flashes per second. A reduction of light-intensity to one-tenth reduced the fusion frequency to 35.

From the results obtained by Granit², it appears likely that the decrease of the subnormal *b*-waves with increasing frequency of stimulation by inter-

mittent light is caused by an accumulation or increase of post-excitatory inhibition. The amplitude of the rapid potential changes, *a*-wave and off-effect, goes on increasing even after the fusion frequency of the rods has been exceeded. Actually the human retina, which to the ordinary range of stimulus intensities behaves like an *E*-retina, turns into an *I*-retina at higher intensities. Similar transitions are known for other eyes (for example, frog²), and the suppression of the *I*-properties at lower intensities has been ascribed to a general inhibition exerted by the rods on the cones.

Enroth⁴ has recently shown that the limiting conditions for fusion in individual retinal elements of the cat's eye can be strictly determined. Fusion in, for example, an off-response results if the difference between the latencies of the off-response and the pre-excitatory inhibition is equal to the length of half a flicker period. We assume that the fusion of the rapid potentials in the human retina follows a similar pattern.

These observations are of some general interest because they seem to offer means of studying objectively the photopic function of the human retina.

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¹ Karpe, G., and Tansley, K., *J. Physiol.*, **107**, 272 (1947).

² Granit, R., "Sensory Mechanisms of the Retina" (Oxford Univ. Press, 1947).

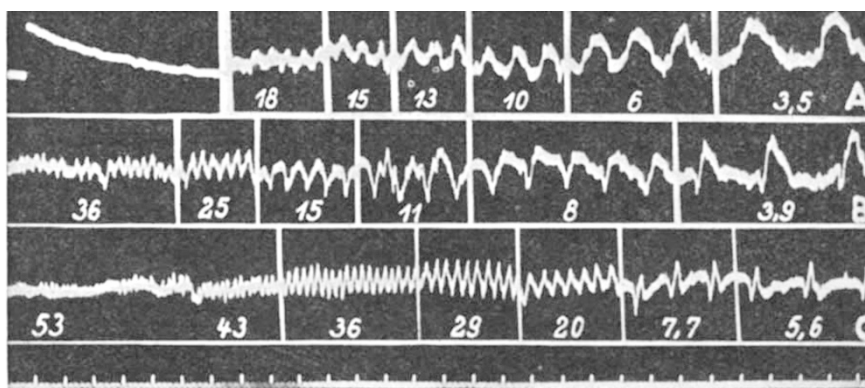
³ Adrian, E. D., *J. Physiol.*, **104**, 84 (1945).

⁴ Enroth, Ch., Proc. VII Scand. Physiol. Soc., *Acta Physiol. Scand.* (in course of publication).

Paper Chromatography of the Pyrogallol Tannins

By one-dimensional paper partition chromatography, some of the phenolic substances allied to the pyrogallol tannins have been separated. When using the well-known solvent phases such as butanol/acetic acid and phenol, previous workers¹ have found that the simpler phenols tend to give long diffuse trails. The preparation of the more complex phenols, such as are found among the pyrogallol tannins, is complicated by their ready oxidation in the presence of

bases. Tailing of the spots in neutral and acidic solvents is influenced by the acidity of the mobile phase (cf. organic acids²). Addition of strong organic acid to the eluting solvent causes separation into well-defined spots. Unfortunately, formic acid greatly increases the rate of run of the tannin, the spots coming too close to the solvent front for clear definition. Two new solvents have now been found which separate many mixtures of complex phenols into well-defined spots: (1) phenol/acetic acid/water, prepared by adding 30 ml. glacial acetic acid to approximately 500 ml. liquid phenol and just saturating



Flicker electroretinogram at different intensities and frequencies of stimulation. The numbers in each row give the frequencies. Upper row, (A): intensity approximately 2,000 lux. Fusion of the sub-normal *b*-waves occurs at 18 stimuli per second. Middle row, (B): intensity approximately 2,600 lux; the *b*-waves are preceded by negative *a*-waves, the amplitude of which *I* increases with increasing frequency. Simultaneously the *b*-waves decrease in amplitude. Fusion frequency is 36 stimuli per second. Lower row, (C): intensity approximately 24,000 lux. After passing the fusion frequency of the *b*-waves, the *a*-potentials display a further increase in amplitude the maximum of which is reached at about 25–35 stimuli per second. Fusion at 53 stimuli per second. Calibration, upper left-hand corner, 0.1 mV.; time marker, 1/10 sec.