Huygens Institute - Royal Netherlands Academy of Arts and Sciences (KNAW)
Citation:
W. Einthoven & Jolly, W.A., The electric response of the eye to stimulation by light at various intensities, in: KNAW, Proceedings, 10 II, 1907-1908, Amsterdam, 1908, pp. 698-703
This PDF was made on 24 September 2010, from the 'Digital Library' of the Dutch History of Science Web Center (www.dwc.knaw.nl) > 'Digital Library > Proceedings of the Royal Netherlands Academy of Arts and Sciences (KNAW), http://www.digitallibrary.nl'

$$\frac{T_1}{1} = \frac{T_2}{502} = \frac{T_3}{14608} = \frac{T_4}{88234} = \frac{T_5}{156190} = \frac{R}{9!},$$

where R represents the rhombotope that is the sum of the nine forms T_1 , T_2 . T_3 , T_4 , T_5 , T_{-4} , T_{-3} , T_{-2} , T_{-1} , starting from

$$\frac{1}{2}M_{10}^{(20)} = T_5^{(20)} = I_1^{(100)} - 10I_1^{(80)} + 45I_1^{(60)} - 120I_1^{(40)} + 210I_1^{(20)},$$

by applying

$$I_1^{(20k)} = (10 \ k + 8)_9 \ T_1^{(2)} + (10 \ k + 7)_9 \ T_2^{(2)} + \dots + (10 \ k)_9 \ T_{-1}^{(2)}$$
 for $k = 5, 4, 3, 2, 1$ after some calculation the result

$$394713550 (T_{1}^{(2)} + T_{-1}^{(2)}) + 410820025 (T_{2}^{(2)} + T_{-2}^{(2)}) + 422709100 (T_{3}^{(2)} + T_{-3}^{(2)}) + 430000450 (T_{4}^{(2)} + T_{-4}^{(2)}) + 432457640 T_{5}^{(2)},$$

which after substitution of the relations given above leads back to the identity

$$T_5^{(20)} = 10^9 T_5^{(2)}$$
.

Physiology. — "The electric response of the eye to stimulation by light at various intensities". By W. Einthoven and W. A. Jolly. (Communication from the Physiological Laboratory of Leiden).

Although the electrical response of the eye to stimulation by light, which was discovered by Holmeren has since been studied by numerous observers, there has not so far been undertaken a systematic investigation of the electromotive changes which are caused by stimuli of very varying strength. Such an investigation, however, can as we hope to show, contribute not a little to our comprehension of the retinal processes.

We have in our work employed exclusively isolated frogs' eyes. We have been enabled on the one hand by means of the string galvanometer, which for the retinal currents may be regarded as the most sensitive instrument available, to record and measure very weak electromotive forces, such as are evoked by light of extremely low intensity; on the other hand we have tried by a suitable system of lenses to concentrate light of as great intensity as possible

upon the retina of the eye under observation. The rays proceeding from the crater of an arc lamp, which passed through a collimator slit in close proximity were dispersed by a spectroscopic arrangement and from the spectrum so obtained any desired portion could be isolated by a simple device.

If we made use of rays lying between the wave lengths $\lambda = 0.590 \,\mu$ and $\lambda = 0.497 \,\mu$, whose green central part — about $\lambda = 0.544 \,\mu$ — may be considered to have relatively a very strong effect on the eye 1), we could by the aid of suitably chosen diaphragms vary the light intensities in the proportion of 1 to 10° , and with the weakest intensity could obtain galvanometric deflections of several centimetres. The arrangement of our experiments did not permit of our easily diminishing the light further in an accurately measurable manner, but we hope later to be able to do so.

In some experiments white light has been used, which of course could be taken stronger than the spectral green. In this case all the rays of the visible spectrum lie at our disposal, and the light may be further increased by widening the slit or by replacing it with the crater itself. According to a rough calculation the intensity of the white light used by us, that is to say of the combined rays lying within the limits of the visible spectrum, is about 10 times greater than our maximum green. The intensities of the weakest green and of the white light are thus in the proportion of about 2) 1 to 10^{10} .

If the isolated eye, which has not shortly before been exposed to strong light, be illuminated by rays of intermediate strength a form of curve is obtained similar to that recorded by previous observers 3).

The current is led off from the cornea and the posterior surface of the bulbus. The current of rest is compensated in the usual way and the connections with the galvanometer are made in such a

¹⁾ Cf. F. Himstedt and W. A. Nagel. Die Verteilung der Reizwerte für die Froschnetzhaut im Dispersionsspectrum des Gaslichtes, mittels der Aktionsströme untersucht. Berichte der Naturforsch. Ges. zu Freiburg i. B., Xl, 1901, p. 153.

²⁾ The intensities of the light used will later be communicated in absolute measurement and at the same time the accurate proportion of the intensities of the green and white will be given.

³⁾ Cf. for instance Francis Gotch, The Journal of Physiol. 29, p. 388, 1903. Ibid. 31, p. 1, 1904. Hans Piper, Engelmann's Arch. f. Physiol. Suppl. 1905, p. 133. E. Th. von Brücke u. S. Garten, Pflüger's Arch. f. d. ges. Physiol. 120, p. 290, 1907, the latter of whom give a critical review of the literature dealing with the subject. The observers mentioned have all made use of a quickly recording measuring instrument.

manner that a current passing from the cornea through the instrument to the posterior surface of the eye deflects the image of the string in an upward direction. An action current in this direction may be termed positive, and in the reverse direction negative.

On momentary illumination of the eye there is observed a small preliminary negative deflection which is immediately followed by an upward movement of the string. After a somewhat acute peak the curve sinks, at first rapidly then more gradually, but while still distant from the zero line it mounts again. This latter ascent begins a couple of seconds after the beginning of the illumination, and the second summit, which is reached much later, often considerably exceeds the peak in height. Finally the curve gradually regains the zero line.

If the illumination be continued for some time, a new elevation occurs at the moment of darkening whose height is greater the longer the illumination has endured.

The complicated form of these curves and the striking fact that a deflection in the same direction takes place both on illumination and on darkening suggest that there are in the eye two or more different processes occurring partly simultaneously partly successively whose fusion determines the form of the electric reaction.

Further investigation confirms this suggestion, and if recourse is had to very weak or very strong light it seems even to be possible to bring about a separation of the supposed processes. The phenomena are explained in the simplest manner by the assumption that the processes are three in number, whether they are together dependent upon the same substance or each upon a separate one. For the sake of convenience we shall speak of three substances and as we do not intend in the meantime to attempt to define them anatomically in the eye, we prefer to try to describe their characteristics and to mention the conditions, under which their effects appear as pure as possible.

The first substance.

The substance which we have termed "the first" reacts more quickly than the other two. On lighting it displaces the image of the string downwards, on darkening upwards. Its effect can with difficulty be obtained pure but nevertheless it is very marked in a light adapted eye, — which for the sake of brevity we may call a light eye 1) — and the more so the stronger the illumination has been.

In the nature of the case the darkening stimulation can be taken

¹⁾ An eye which is dark adapted may be called a dark eye. Both terms are analogous to "Lichtfrosch" and "Dunkelfrosch" which are commonly used,

very strong in a light eye, and accordingly an eye which has been illuminated strongly develops on darkening a huge positive potential difference. The upward deflection so evoked can however not be of long duration, because by the darkening the light eye is beginning to be changed into a dark eye and therefore the effect of our first substance is no longer so clearly indicated.

Although in the light eye the conditions are less favourable for the lighting than for the darkening stimulus it is nevertheless possible to apply the former in either of two ways. In the first place we may suddenly increase the intensity of the light that is radiating on the eye, and secondly we may darken the light eye for a short period, so that it has not yet become a dark eye and then suddenly illuminate it.

The second method gives better results than the first and we possess numerous curves where after a short darkening of a light eye a strong light stimulus was applied. The "on effect") is a steep downward deflection and attains the considerable amount of 120 to 130 microvolts. It is true that it is followed immediately by an upstroke, the latter however is but small in comparison with the strong upstroke which under similar conditions is evoked in a dark eye.

The second substance.

The second substance reacts less quickly than the first. On lighting it moves the string with moderate velocity upwards, and on darkening slowly downwards, thus on applying stimuli of the same kind it develops potential differences which are opposed to those of the first substance. Its effect appears almost unmixed in a dark eye which is illuminated for a short time by weak light.

If when illuminating with light of very low intensity, the darkening follows rapidly upon the lighting, in a similar way as in a momentary illumination, there is recorded a curve of simple form, with a steeper anacrotic part which is evoked by the lighting and a less steep katacrotic part evoked by the darkening. The top of the curve lies, within certain limits higher the more the energy of the illumination is increased either by using greater intensity or longer duration of the light. These limits are determined by the functioning of the other two substances, which when their effects become perceptible influence the form of the curve and considerably complicate it. If a strong momentary illumination be applied there appears a short negative preliminary deflection by the function of the first substance

¹⁾ A convenient expression introduced by Gotch.

and the very slow second elevation which follows must be attributed to the functioning of the third substance.

The third substance.

The third substance reacts in the same direction as the second substance but more slowly. On lighting it displaces the image of the string slowly upwards and on darkening still more slowly downwards. So much slower is the third substance than the other two that its effect in a recorded curve appears as a rule almost entirely isolated, and thus can be easily followed.

The effect of the third substance falls out under two conditions (1) In a fully light adapted eye and (2) in a dark eye submitted to very faint light for a short time.

Specially remarkable are the curves obtained if the duration of the lighting of a dark eye is systematically changed, and we wish to direct attention more particularly to the "off effect" in such cases. If the duration of the light is very short and the light is weak, then as already mentioned the effects of the second substance appear unmixed. The off effect here consists in the descent of the curve to the zero line.

If the duration of the light is taken a little longer, and the effect of the other two substances begin to become perceptible, the off effect is determined by the resultant of three forces: The first substance tends to displace the image of the string upwards. It is at first acting weakly but its strength increases regularly during illumination so that it soon surmounts the effect of the other substances. In the case of longer lighting the off effect therefore is always an upward movement which increases with the duration of the lighting.

The second substance tends to depress the image of the string, acts first with moderate strength but decreases gradually during lighting. As the second substance in particular is acting in a dark eye the conditions for its functioning grow during the illumination more unfavourable. A strong darkening effect can not be expected in a dark eye.

The third substance is so slow, that the darkening effects of the first and second take place usually at a moment when the third substance is still tending to displace the string upwards. The darkening effect of the third substance itself, consisting in a slow descent of the string, appears much later and fairly isolated.

The general result is that we can observe in a series of curves, — obtained from a dark eye where the light has been gradually lengthened in duration, -— that the darkening effect, in the first

curves a negative deflection, becomes in the later ones a positive deflection. The latter, on further lengthening of the duration of light, gradually increases in size. In the conflict between negative and positive deflections, there is sometimes seen an upward movement, which is immediately preceded by a small downward one.

Of the various particularities which occur in the course of the experiments we shall only briefly mention the latent period. The duration of this period is dependent to so high a degree upon the intensity of the illumination, that it is possible to some extent to judge of the intensities of light used by previous observers from the latent periods recorded by them. With very weak lighting there appear latent periods of the second substance which may exceed two seconds.

In opposition to Gotch and Garten Waller¹) also mentions latent periods as large in amount as we have observed and others much larger, but as Waller in his experiments made use of a slow Thomson galvanometer, there remained the possibility that there were two opposite forces which at first neutralised one another and then after an interval one obtained the mastery. The forces assumed by Waller agree with our first and second substances.

A more detailed description of our experiments accompanied by a reproduction of some of our curves will appear elsewhere.

Geophysics. — "The height of the mean sea-level in the Y before Amsterdam from 1700—1860". By Prof. H. G. VAN DE SANDE BARRUYZEN.

Our section has been engaged in former years with an investigation of the subsidence of the land in the Netherlands, and it is especially to Dr. F. J. Stankart, member of the committee for that investigation, that we owe several important communications on this subject.

Twenty years ago, when calculating the results of the precise levelling, I made some computations in order to determine the subsidence of the land but have not published them. The interesting paper on this subject of Mr. Ramaer, head-engineer, director of the hydrographic survey, has now induced me to re-examine my former notes and as they perhaps may contribute towards the solution of the problem, whether the land under Amsterdam has subsided since

¹⁾ Augustus D. Waller, Philosoph. Transact. of the Royal Soc. of London, Ser. B, vol. 193, p. 123, 1900.