THE PHYSIOLOGICAL ACTION OF LIGHT[1]

II.

Determination of Electro-motive Force.—Soon after the first experiments were announced, certain physiologists said that although the results of the action of light which I have just described may be observed, to say there was a change in the electro-motive force, as stated in the earlier communications, was not correct. That the effect was due to an alteration in the electro-motive force had been proved, but experimental details were reserved for the second part of the investigations. At first Sir William Thomson's electrometer was used, but the amount of electric potential to be measured was too small to get good results. Another plan of determining the electro-motive force was adopted. This was the method introduced by Mr. Latimer Clarke, the eminent electrician, and described in his work on "Electrical Measurements." The instrument devised for this purpose is called by him a Potentiometer, and measures electro-motive forces by a comparison of resistances. Practically we found the Daniell's cell far too strong a battery to use as a standard of comparison. A thermo-electric junction of bismuth and copper was substituted for it. One end of the junction was constantly heated by a current of steam passing over it, the other being immersed in melting ice. The electro-motive force of this thermo-electric junction, as estimated many years ago by Regnault, is extremely constant, and is about the $\frac{1}{175}$th part of a Daniell's cell. By means of this arrangement the following results were obtained :—The electromotive force of the nerve-current dealt with in experiments on the eye and the brain of a frog varies from the $\frac{1}{300}$th to the $\frac{1}{400}$th of a Daniell's cell. Light produced an alteration in the electro-motive force. This change was, in many instances, not more than the $\frac{1}{10000}$th of a Daniell's cell. But though small it was quite distinct, and proved that light produced a variation in the amount of the electro-motive force. By the same arrangement the gastrocnemius muscle of a well-fed frog gave $\frac{1}{35}$th of a Daniell; the same muscle from a lean frog which had been long kept, gave $\frac{1}{240}$th of a Daniell; and the sciatic nerve of the well-fed frog $\frac{1}{480}$th of a Daniell. Dr. Charles Bland Radcliffe states, in his "Dynamics of Nerve and Muscle," p. 16, that he obtained by means of Sir William Thomson's quadrant electrometer, from a muscle a positive charge equal to about the tenth of a Daniell's cell, a much greater amount than ascertained by the method I have just described.

The electro-motive force existing between cornea and posterior portion of the sclerotic in a frog amounts to $\frac{1}{120}$th part of a Daniell, and between the cornea and cross section of the brain is about four-fifths of the above.

Effect of Temperature on the Eye of the Frog.—From numerous experiments on the irritability of muscle induced by the excitation of nerve, it has been satisfactorily proved that a temperature of about 40° C. destroys the action of motor nerves in cold-blooded animals. Up to the present time we are acquainted with no observations as to the temperature at which a terminal sense organ becomes incapable of performing its functions. Having satisfactorily proved that *the retina is the structure in the eye producing the electrical variation* observed, it becomes evident that as long as this phenomenon can be detected the retina is still capable of discharging its normal functions. In order to investigate thoroughly the effect of an increasing temperature on the sensibility of the retina, a method of procedure was adopted of which the following may be taken as a general account :—A frog was killed, the two eyes removed rapidly from the body; the one eye was placed on electrodes and maintained at the ordinary temperature of 16° C., while the other was placed on similar electrodes contained in the interior of a water bath having a glass front, the sides of the air chamber being lined with black cotton wool saturated with water. Into this chamber a delicate thermometer was inserted, and the currents coming from the two eyes were alternately transmitted to the galvanometer every five minutes by means of a commutator, the temperature and the electrical variation produced by the same amount of light being noted in each case. The general results are shown in the following table :—

Table showing Comparative Effect of Temperature on Sensibility of Frog's Eye.

Eye kept continuously at 16° C.		Eye at different Temperatures.		
Initial Effect.	Final Effect.	Temperature.	Initial Effect	Final Effect.
55	28	16° C.	58	21
61	28	19° C.	55	16
53	27	24° C.	65	14
53	39	29° C.	97	5
53	45	29° C.	103	—4
60	45	37° C.	65	—3
60	50	38° C.	65	—4
53	41	43° C.	12	—5
60	40	43° C.	no effect.	no effect.

The initial amount of current was, however, increased on the whole by the action of the higher temperature, thus showing that the sensibility to light does not depend on the amount of current circulating through the galvanometer. It will be observed, on inspecting this table, that the eye maintained at the temperature of 16° C. remains tolerably constant in its initial action, although it gradually gets more sluggish, whereas the final effect steadily rises. On the other hand, in the case of the eye subjected to a higher temperature, the initial effect seems to have a maximum about 29° C., then gradually diminishes, and vanishes about 43° C., the final effect continuously falling and being actually reversed. To succeed in this experiment it is necessary to heat the electrodes which are to be used in the water bath up to 40° C., in order to be certain that no changes are induced in the electrodes themselves that might be mistaken for those above mentioned. An eye that had been placed in dilute salt solution along with lumps of ice was found to have the usual sensibility to light.

Effect of Temperature on the Eye of Pigeon.—Having succeeded in experimenting with a water-bath in the manner above described, it appeared interesting to ascertain if the eye of a warm-blooded animal would be benefited by being maintained at the normal temperature of the body. The head of a pigeon was placed in the water bath at a temperature of 40° C., the eyes were found sensitive to light, the action, however, being always a negative variation; but instead of vanishing quickly, as it does at the ordinary temperature, kept up its activity for at least an hour. For example, in one experiment, the electrodes being placed on the corneas so that the currents were balanced, sensibility was active for an hour and a quarter, but half an hour later it had almost disappeared. In this experiment the sensibility of the eye is shown by the large deflection produced by a single candle at different distances, thus :—

Distance of Candle from Eye.	Divisions of Galvanometer Scale.
9 feet	100
6 feet	180
3 feet	230
1 foot	420

Sensibility of the Optic Nerve.—When the retina is entirely removed from the eye-ball, and the optic nerve is

[1] Friday evening Lecture by Prof. James Dewar, M.A., at the Royal Institution, March 31, 1876. See Nature, vol. viii. p. 204. Continued from p. 435.

still adherent to the sclerotic, no effect of light can be detected. It now appeared possible to examine this question by repeating Donders's experiment of focussing an image on the optic disc in the uninjured eye, when no electrical disturbance ought to occur. This was done in the eye of the pigeon, but an image free from irradiation on the optic disc could not be produced, and consequently there was always an electrical effect observed.

Exhaustion and Stimulation of the Retina.—When the same light from a fixed position is allowed to act on the eye for successive intervals of time, say two minutes of light and two minutes of darkness, it gradually falls off in electrical sensibility. Thus, a candle at nine inches gives the following results when successively used as a stimulus :—

	Initial Effect.	Final Effect.
1st experiment	259	254
2nd ,,	171	276
3rd ,,	140	282
4th ,,	122	274

These figures show a rapid fall of the initial effect. In these circumstances, it is evident that the image being

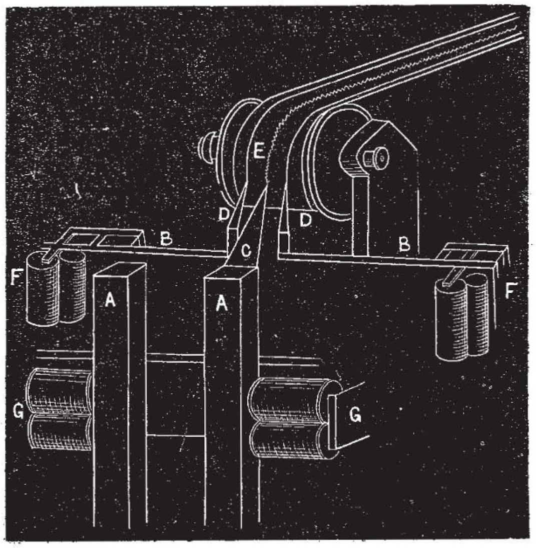

Diagram showing the recording portion of Regnault's Chronograph. A A, limbs of recording fork, worked by electro-magnets, G G. C, stilette on limb of recording tuning-fork. B B, levers in connection with armatures of electro-magnets, F F, and bearing markers, DD, which, along with C, record on E, a strip of blackened paper passing over pulley.

always localised on the same minute portion of the retina, only a few of the rods and cones of that structure are really exhausted. If the eye be allowed repose in the dark for a period of from half an hour to an hour, it will regain as much as triple the exhausted sensibility. But another mode of proving that only a minute portion of the retina was affected was to show that an alteration of position of the image by a slight movement of the luminous body was followed by a new electric variation. In order to vary and extend the action of a retinal image it is necessary to suspend a steady lamp by means of an indiarubber cord or spiral spring, so as to be able, by inducing vibrations in any direction, to stimulate in rapid succession different retinal areas. On oscillating a pendulum of this kind, an electrical variation is observed whenever the amplitude of the vibrations is increased, and by inducing a combination of vibrations, the electrical variation observed corresponds to what would be found if the luminous intensity were sixteen times as great as that of the stationary light. Similar experiments may be made by throwing an image from a small silver mirror connected with a metronome. The rapid exhaustion of the eye may be most readily demonstrated by cutting off the anterior half of the eye, leaving the vitreous humour in contact with the retina, observing the effect of a candle, and then subjecting it to the action of a magnesium lamp. The sensibility will now be enormously diminished. The electrical variations resulting from the respective actions of a candle and a magnesium lamp placed at the same distance from the eye were as follows :—

	Initial Effect.	Final Effect.
Candle	38	78
Magnesium lamp	120	135

This experiment proves that an increase of 200 per cent. in the illuminating power of a source of light only triples the electrical effect. Thus the eye becomes less sensitive as the illumination increases.

Chronometrical Observations.—A series of experiments have been begun with the object of measuring the time required from the initial impact of light before electrical variation is produced. As the electrical variation has been shown to agree with our consciousness of luminous effects, it became an interesting point to ascertain whether the time occupied by the action of light upon the eye of the frog is similar to the time occupied in its action upon the eye of man. A good many years ago, Prof. Donders and his pupil, Schelske, performed a number of experiments by which they determined that the time required by the human being to observe light and to signal back the impression occupied about $\frac{1}{10}$th of a second. That is to say, $\frac{1}{10}$th of a second is occupied by the action of light on the eye, the transmission of nerve-current to the brain, the change induced in the brain during perception and volition, the time for the transmission of the nerve-current to the muscles, on signalling the result, and the time occupied by muscular contraction. The true period of latent stimulation in the case of man must therefore be a very small fraction of a second. In order to attempt a solution of this problem a chronograph made by Dr. König, of Paris, was employed. A diagram of the recording portion of the instrument is given above. The experimental arrangements were as follows : the galvanometer, the eye apparatus, and the chronograph being in separate rooms, one observer was stationed at the galvanometer for the purpose of signalling the moment the needle worked, which was recorded by one of the markers D in the diagram, the other marker being used to register the time of initial action.

The *first experiment* was to transmit at a known moment, through the eye circuit in the dark room, a quantity of current equal in amount to the electrical variation produced, when the eye was stimulated by a flash of light from a vacuum tube, and to record the difference of time between the origin of the current and the observer's signal from the galvanometer.

The *second experiment* was to flash a vacuum tube at a known moment in a room where the eye was placed, and to record as before the instant the galvanometer was effected. From the first observation we ascertain the minimum amount of time necessary to overcome the inertia of the instrument, the observer's personal equation, and the signalling under the conditions of the experiment. If this result is subtracted from the record of the second observation, the difference will represent the latent period of light stimulation. From a large number of experiments made on the eye of the frog we have found the latent period amounts to less than $\frac{1}{10}$th of a second, but its absolute value must be ascertained by some method not liable to the variations that are inevitable to the process described. Altogether the problem is one of great difficulty, but further investigations are in progress. J. D.