Prof Mc Kendrick

Royal Institution of Great Britain.

WEEKLY EVENING MEETING,

Friday, March 31, 1876.

George Busk, Esq. F.R.S. Treasurer and Vice President, in the Chair.

Professor James Dewar, F.R.S.E. Part II.*

The Physiological Action of Light.

On a former occasion I communicated the results of a research on the "Physiological Action of Light" executed conjointly with Professor T. G. McKendrick. The principal facts then established may be thus summarized.

Comparative Physiology of the Action of Light.—The impact of light upon the eyes of members of the following groups of animals, viz. mammalia, birds, reptiles, amphibia, fishes, and crustaceans, produced a variation amounting to from three to ten per cent. of the normal current. At that time we found light caused a negative variation in the case of warm-blooded animals.

Transmission of Action to Brain.—The electrical variation may be traced into the brain. Instead of severing the eye from the brain and cutting the optic nerve, simply remove the head of the frog. Then suppose one of the electrodes in contact with the surface of the brain and the other in contact with the surface of the cornea, an effect is obtained from the action of light similar to that just described.

Action due to Change in Retina.—This action is really due to an alteration in the retina itself. This must be definitely proved, because it was a legitimate criticism that the change produced by the action of light may be due to contraction of the iris; the iris being a muscular structure contracting on the action of light by a well-known reflex mechanism in normal circumstances, and even after removal of the eye from the head. A contraction of the iris might produce a negative variation or diminution of the electrical current, but it is difficult to imagine that it could cause an increase or positive variation. In order, however, to get rid of this difficulty, cut off the front part of the eye altogether, and place one electrode so as to touch the surface of the vitreous humour while the other impinges on the transverse section of the optic nerve, a current is

* See R. I. Proceedings, vol. vii. p. 360.

obtained—no doubt weaker, but still a current sufficiently strong for detecting any variation which light may produce. In these circumstances, light still produces the variation I have described. To make it more definite still, pick out the retina with a fine glass point, and leave only the sclerotic and perhaps fragments of the choroid. Even then an electrical current is obtained; but this current is not affected by light. It is, therefore, proved that the variation produced by the action of light is due to some change or other occurring in the retina when light impinges upon it.

Rays of the Spectrum.—Which rays of the spectrum produce the greatest effect? We know, of course, that the rays which are the most luminous to our consciousness are the yellow rays. The colours of a very pure spectrum were obtained, the eye being brought into the various rays successively, and the result noted. To obtain comparative results, the operations were repeated as quickly as possible. It was found, in studying the results, that those rays which we regard as the most luminous produce the greatest variation. For instance, the low red rays at the end of the spectrum produce very little effect, and if you go below the red into the heat rays there is no action. But the effect increases till you reach the yellow, and if you go on to the violet it gradually becomes less and less until, beyond the violet, there is no action.

Relation of Electrical Variation to Luminous Intensity.—Experiments made have conclusively shown that a quantity of light, one hundred times in excess of another quantity, only modifies the electric variation to the extent of increasing it from three to five times its original amount. The effects observed vary in such a manner as to correspond closely with the relative variations that would result if the well-known psycho-physical law of Fechner was applicable to this class of phenomena.

The effect of Fatigue.—The retina, on the action of light, behaves in a similar manner as regards fatigue, to a muscle that has been exhausted by repeated stimulation. The muscle diminishes in its mechanical effect for the same stimulation and recovers during repose. The amount of electric variation in the case of the eye diminishes for the same amount of light stimulation, unless the organ has had sufficient time to recover its normal condition. In this case, the recovery takes place in the absence of light.

We have continued this investigation in various new directions, and have arrived at results which may be thus shortly detailed.

New Method of Experimenting.—One of the chief difficulties in arriving at the exact relation between the electrical variation and the different luminous and colour intensity of light, was the continually diminishing sensibility to the stimulus, owing to the abnormal conditions of the eye when removed from the head. You can easily understand how this occurs. When you begin the experiment, the eye is remarkably sensitive to light, and a large variation of current is obtained; but the amount of this current is gradually falling in consequence of the gradual change in the parts of the eye, owing to their loss of vitality and sensibility. In fact, the parts are dying—the blood is not circulating, and molecular and chemical changes are slowly occurring. In the case of the frog's eyes, however, it is a fact that the retina retains its sensibility from three to four hours, and sometimes longer. After a lapse of two hours or so, the frog's eye frequently remains in a tolerably stable condition, in which it does not lose rapidly. This condition may last for four or five hours. In order to get rid of the difficulty of gradual death of the parts, we tried various methods. In our earlier experiments, we attempted to get the eye removed as quickly as possible, and to make the observations rapidly. In the case of the warm-blooded animals, this did not lead to very good results, because the sensibility to light disappeared in a very few minutes. We also on several occasions exposed the posterior aspect of the eye in the living anæsthetized warm-blooded animal, and succeeded in bringing one electrode into contact with the severed optic nerve while the other touched the cornea. This method was troublesome and difficult.

We, however, did succeed in obtaining definite results. These experiments are now made in quite a different way. By placing a frog, rabbit, or pigeon under the influence of chinoline, the animal remains motionless. We then remove a small portion of the surface of the cranium, so as to expose a portion of the brain. One of the electrodes is brought into contact with the surface of the cornea, and the other with the surface of the brain. The blood is still circulating. A current is obtained; and all the effects I have just mentioned may be observed with ease. The animal remains in this condition, retaining its sensibility to the action of light, for as long a period, in the case of the frog, as forty-eight hours. These observations led to the discovery made recently, that there is no necessity for even exposing the surface of the brain. That is to say, the action of light can be traced, if needful, through the whole body. If, for example, we take a frog, place it in position, slightly abrade the skin on the surface of the head or back, or any part of the body, then adjust the electrodes, one in front of the cornea and the other upon the abraded skin, we obtain an electrical current which is affected by light in the usual way. But if the electrode in contact with the cornea be shifted to some other part of the body, a current may be obtained; but this current is not sensitive to light. In order to produce the specific action of light upon the eye, the retina must be included in the circuit. This discovery enabled us to perform many experiments without injuring the animal, except to the extent of abrading or removing a small portion of skin. It at once opened up the way for making observations upon warm-blooded animals (one of the chief difficulties in our earlier investigations). For example: give a rabbit or a guinea-pig a small dose of chinoline, and the animal remains prostrate and quiet. Then cut off a little of the hair from the surface of the head at the back of the neck, and abrade the skin so as to have a moist surface; bring the electrodes into position, placing one in contact with the abraded surface and the other in contact with the surface of the cornea, and you will at once obtain the effect.

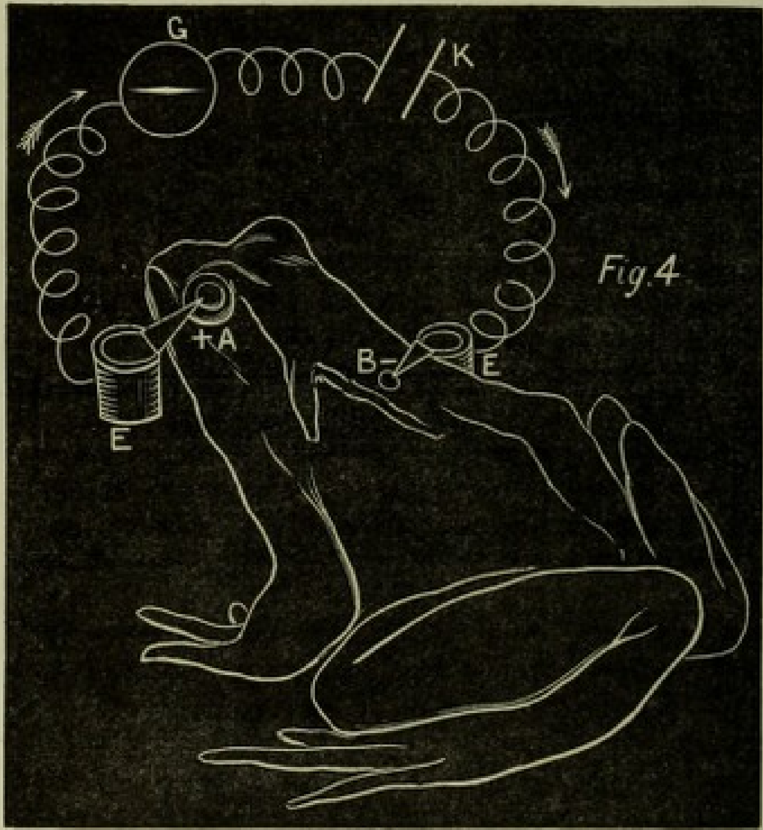

Diagram showing arrangement of apparatus in the experiment on eye of frog. A. Eye showing the electrode, E, in contact with it. B. Skin removed and subcutaneous tissue in contact with other electrode, E. K. Key. G. Galvanometer. Arrows indicate direction of current. Cornea, positive. Back, negative.

Action of Light in Warm-blooded same as in Cold-blooded Animals.—By the use of chinoline we were able to make experiments of the kind just described for a considerable time, without the necessity of maintaining artificial respiration. The result of those investigations upon warm-blooded animals has been to show that in these, as in the cold-blooded, light produces first an *increase* in the electric current on impact; continued light usually causes the electrical current to diminish; and on the removal of light, there is a second rise, as described in the case of the frog. In our earlier investigations, we always observed in the case of warm-blooded animals (when the eye had either been quite removed from the body or was receiving an inadequate supply of blood), that the action of light caused a negative variation, that is, a *diminution* in the electrical current. By improved methods, however, which have the effect of placing the eye in conditions more normal, we find that light causes a *positive* variation, that is, an increase; thus agreeing with what had hitherto been observed in the eye of the frog. This is a point worthy of notice. Du Bois-Reymond showed, even in the case of sensory nerves, that physiological action caused a *negative* variation. But it appears that in the case of the retina the action of the normal stimulus is to cause a positive not a negative variation.

Experiment with the Living Lobster.—The action of light can be readily shown in this animal. Fix it loosely in a cloth, and lay it on the table in a slightly oblique position. With a small trephine remove a circular portion of the carapace, about three millimètres in diameter, and expose the moist tegumentary surface. Bring one electrode into contact with this surface, while the other touches the cornea. The usual effects of light may then be noted; but in the case of the lobster, the variation caused by the impact is greater than what

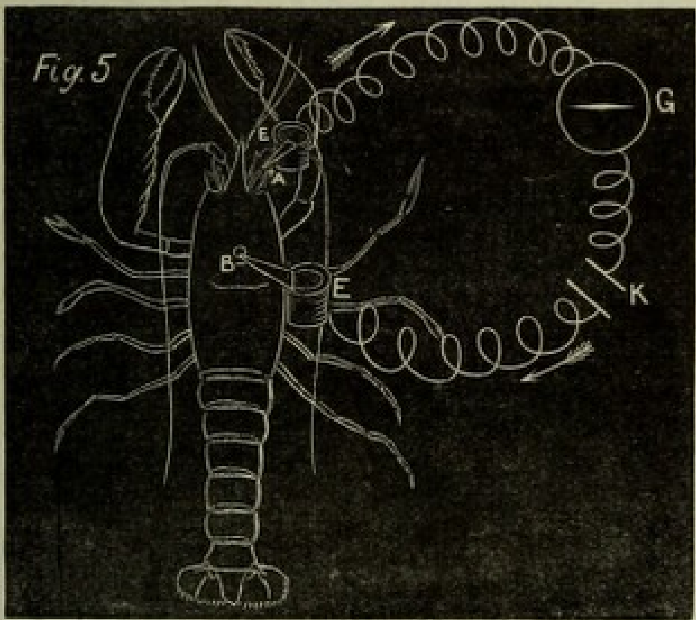

Diagram showing arrangement ot apparatus in experiment on living lobster. A. Corneal surface, having electrode, E, in contact with it. B. Portion of carapace removed so as to expose moist surface for electrode, E. K. Key. G. Galvanometer. Arrows indicate direction of current.

we have noticed in any other animal, often amounting to one-tenth of the total amount of current. Another interesting experiment, comparable with that of the two eyes just described, may be made on the lobster by placing an electrode in contact with each cornea. The result frequently is apparently no current, but in reality the currents neutralize each other. Light falling on the one eye causes the needle to move, say to the left, while if it fall on the other eye, the needle swerves to the right. When the eye of the lobster, removed from the body, was divided longitudinally into segments, each segment was found sensitive to light. The effect of light was then to increase the primary current, but no inductive action was observed on withdrawal.

This observation is interesting as a confirmation of the views of physiologists regarding the mode of action of a compound eye.

Mode of Experiment on Eye of Fish.—Recently we were enabled to perform an experiment upon the eye of a fish in a very simple way, by a method adopted in Professor Stricker's laboratory in Vienna some months ago for another purpose. Take a fish and give it a very small dose of woorara. It soon becomes almost motionless, and sinks in some cases to the bottom of the vessel. The animal would soon die in consequence of paralysis of the movement of the gills necessary for respiration. But, if we take the animal out of the water, put it upon a glass plate, introduce a little bit of cork under each gill, and then by means of an indiarubber tube placed in the mouth allow a little water to flow over the gills, the fish will live out of water in that condition for many hours. By this method we were able to perform the experiment upon the eye of a fish with the same results.

Observation on Human Eye.—Having succeeded in detecting the action of light on the retina of the living warm-blooded animal without any operative procedures, it appeared possible to apply a similar method to the eye of man. For this purpose, a small trough of clay or paraffin was constructed round the margin of the orbit, so as to contain a quantity of dilute salt solution, when the body was placed horizontally and the head properly secured. Into this solution the terminal of a non-polarizable electrode was introduced, and in order to complete the circuit the other electrode was connected with a large guttapercha trough containing salt solution, into which one of the hands was inserted. By a laborious process of education, it is possible to diminish largely the electrical variation due to the involuntary movements of the eye-ball, and by fixing the eye on one point with concentrated attention, another observer, watching the galvanometer, and altering the intensity of the light, can detect an electrical variation similar to what is seen in other animals. This method, however, is too exhausting and uncertain to permit of quantitative observations being made.

Explanation of Variation in Direction of Current.—One phenomenon particularly attracted the attention of physiologists, and especially of those who first saw the experiments: viz. that sometimes, in the case of the eye of the frog, light produced an increase in the electrical current, and in other cases a diminution. This we could not at first account for. But we have been able to make out that the positive and negative variation, or the increase or diminution of the natural current on the action of light, depends upon the direction of the primary current, when the cornea and brain are in circuit. If the cornea be positive and the brain be negative, then light produces an *increase* of the electrical current. If, on the other hand, the cornea be negative and the brain positive, light then produces a *diminution* in the electrical current. It is thus conclusively shown that the current superadded, or if we may use the language, induced by the action of light, is always in the same direction; only in the one case it is added to, and in the other subtracted from, the primary current.

The Use of equal and opposite Currents.—We have performed many experiments in which equal and opposite currents were transmitted through the galvanometer at the same time, and observed the effect of light in these circumstances. By the use of resistance coils, it was not difficult to balance the current from the eye; but, owing to the inconstancy of even a Daniell's cell in such experiments as these, it was impossible to avoid fluctuations which might possibly have been mistaken for those due to the action of light. This difficulty was got over by what we formerly called *the double eye experiment*, in which two similar eyes are placed in reversed positions on the electrodes, so that the current from the one neutralizes that of the other. When this is accomplished, it is easy by means of a blackened box, having a shutter at each side, to allow light to fall on either the one eye or the other, and it is then shown that the galvanometer needle moves either to the right or left, according to the eye affected. Instead of removing the eyes from the head and balancing them as just described, it is a much better method to apply the two electrodes directly to the corneas in their natural position. By a little manipulation, it is possible to obtain two positions, that seemingly give no electrical current. In these circumstances, light, allowed to fall on the one eye or the other, produces the effects above detailed.

Action of Polarized Light and Colours of Spectrum.—The next point recently investigated is the action of polarized light and the various complementary colours. We arrived at the results of our earlier experiments with the colour-spectrum in various ways, such as by passing light through solutions having various absorptive powers, by the direct coloured rays of the spectrum, &c., but always with the same conclusion—namely, that the most luminous rays produce the greatest effect. For studying the action of polarized light, we have recently used the simple contrivance of a black box, having a hole on one side of it, placed over the eye. Opposite the hole we placed two cylindrical tubes of brass, each carrying a Nicol's prism, and between the two prisms a thin plate of quartz is introduced, producing the various colours of polarized light on rotating one of the prisms. The general results were exactly the same as when we used the colours of the spectrum. In all cases, the impact of the yellow rays produced the greatest effect. It has also been ascertained by this method that the effect of the *impact* of light is much more regular than the effect of its removal. The results of one series of observations are given in the two following tables:

Action on Frog's Eye of Colours of Polarized Light.

	Initial Effect.	Final Effect.
Purple	rise of 3	rise of 14
Light Blue	" 5	" 12
Red Violet	" 5	" 15
Blue	" 7	" 20
Red	" 8·5	" 15
Orange Red	" 10	" 22
Green Blue	" 10	" 24
Green	" 13	" 24
Yellow	" 16	" 24
Rose	" 8	" 19

Action on Frog's Eye of Spectrum of Oxyhydrogen Flame.

	Initial Effect.	Final Effect.
Yellow, near Orange	rise of 70	rise of 10
Green Yellow	" 25	" 5
Green—low	" 15	" 0
Green—high	" 15	" 0
Green—higher	" 18	" 8
Yellow Green	" 85	" 35
Yellow	" 80	" 40

Determination of Electro-motive Force.—Very soon after the first experiments were announced, certain physiologists said, that although we had obtained the results of the action of light which I have just described as indicated by the galvanometer, we had no right to say that there was a change in the electro-motive force as stated in the earlier communications. We had, however, satisfied ourselves that the effect was due to an alteration in the electro-motive force, but reserved details to the second part of our investigations. At first, in attempting this 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 electro-motive force of the nerve-current dealt with in our 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 enabled us to say positively 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 $\frac{1}{130}$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 we have 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 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 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 two 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.—We have formerly shown that when the retina is entirely removed from the eye-ball, and the optic nerve is still adherent to the sclerotic, no effect of light can be detected; and it now appeared possible to examine this question by repeating Donders' 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 9 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 always localized 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, we have observed an electrical variation 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.

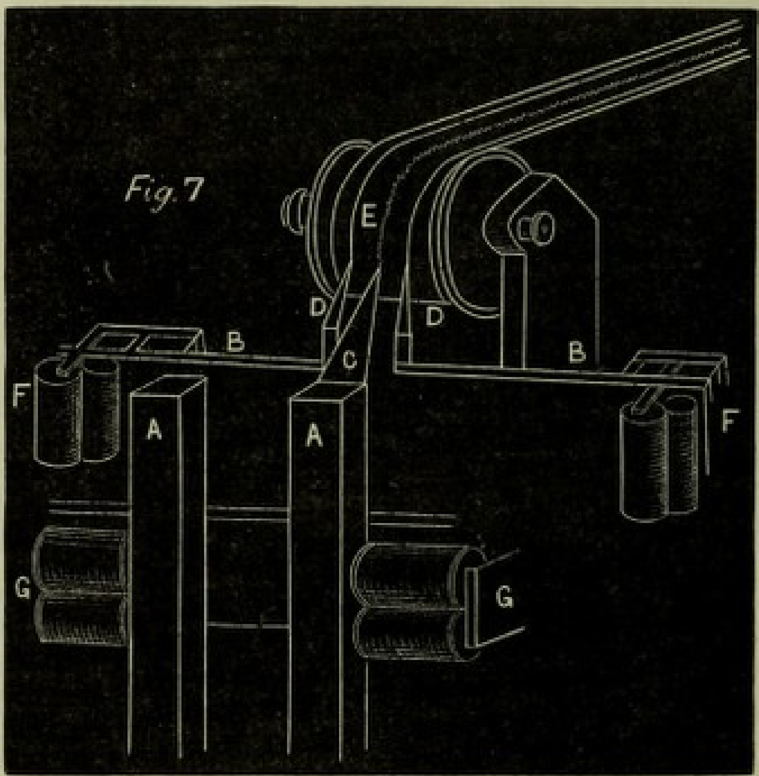

Diagram showing the recording portion of Regnault's Chronograph. A A. Limbs of recording fork, worked by electro-magnets, G G. C. Stilette on limb of recording tuning fork. B B. Levers in connection with armatures of electro-magnets, F F, and bearing markers D D, which, along with C, record on E, a strip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

Chronometrical Observations.—The last point I wish to bring under your notice, is what we have recently been doing in the way of measuring the time required from the initial impact of light before the 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, Professor 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 we have used a chronograph made by Dr. König, of Paris. 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 affected. 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 we hope to continue the investigations.

[J. D.]

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