"The Electrical Effects of Light upon Green Leaves." (Preliminary Communication.) By AUGUSTUS D. WALLER, M.D., F.R.S. Received June 6,—Read June 14, 1900.

In connection with an investigation of electrical effects of light upon the retina,* I have examined vegetable protoplasm (green leaves) with reference to electrical effects that might be expected to occur in connection with the chemical changes produced by light.

Under certain favourable conditions that I hope to determine further, a true electrical response to light is obtained, consisting in the establishment of a potential difference between illuminated and non-illuminated half of a leaf, amounting to 0·02 volt.

Among ordinary garden leaves, I have found to be well adapted to demonstration those of young Iris plants, about 6 inches high, and of "ten-week Stocks" in active growth. The former, tested by Sachs' method, exhibited no evidence of starch activity in consequence of insolation; the latter in favourable instances exhibited marked deposit limited to illuminated parts. Leaves of Tropæolum, of Begonia, and of Nicotiana have also proved to be suitable objects of study.

Most of the following description refers to young Iris leaves in the first half of the month of May.

The method of observation is as follows:—

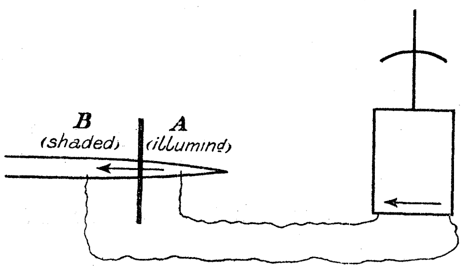

FIG. 1.—Normal Response to Light. Iris leaf. Primary "negative" effect during illumination.

A freshly cut but otherwise uninjured leaf is laid upon a glass plate and connected with a recording galvanometer by means of two unpolarisable† electrodes A and B. One half of the leaf is shaded by a piece

* 'Proc. Roy. Soc.,' March 29; and 'Phil. Trans.,' B, 1900 (in the press).

† Du Bois-Reymond's electrodes of the usual type, not D'Arsonval's, which are rendered electromotive by light. Illumination of a chloride of silver electrode by a "16-C.P." lamp at 10 cm. distance gave a reaction amounting to between 0·002 and 0·003 volt. A zinc electrode under similar conditions gave a reaction of about 0·0001 volt, in which, however, I did not attempt to distinguish separate effects of light and heat.

of black paper. Leaf and electrodes are enclosed in a box, provided with a shuttered aperture, through which light can be directed. A water trough in the path of light serves to cut out more or less heat. A glass jar inverted over the leaf and electrodes forms a moist chamber to delay drying. During illumination the galvanometer spot is deflected so as to indicate current in the leaf itself from excited part to protected part, *i.e.*, if B is shaded, light falling upon A arouses current in the leaf from A to B; if A is shaded, light falling upon B arouses current from B to A.

1. The deflection begins and ends sharply with the beginning and end of illumination.

2. It is provoked slightly by diffuse daylight, more considerably by an electrical arc light, and in greatest degree by bright sunlight.

3. It is abolished by boiling the leaf and by the action of anæsthetics.

These are the main facts proving that the living leaf responds electrically to the stimulus of light.

At this preliminary stage two points of doubt occur to mind and require to be tested, viz., possible effects of heat and of surface evaporation that necessarily accompany illumination.

These effects are small in comparison with the true response, and of opposite sign. Illumination of a dead leaf gives little or no effect, and what little effect there is, is directed in the leaf towards the illuminated half, where heating and evaporation are provoked.

The true response to light varies with varying physiological states of the leaf and of its parent plant.

Not every leaf gives response, nor is the response of equal magnitude in different leaves to luminous stimulation (arc light) of constant intensity and duration.

The external condition by which the state of leaf is most obviously governed is *temperature*.

My first experiments were made upon Iris leaves taken almost at random from young plants (old roots) about 6 inches high at the end of March (temperature not noted, but presumably below 15°). The response to light was between 0·001 and 0·002 volt.

The next set of experiments commenced on May 8th on young leaves of similar plants.

The responses then observed were

Warm	May 8	0·005
	,, 10	0·008, 0·025
Cold, 10°	,, 11	0·005
	,, 12	nil
	,, 13	nil

I thereafter took note of the external temperature, and tested the leaves in a warm box with satisfactory results.

A few days later (May 21st), Iris leaves even in the warm box were notably inert. Two leaves were tested with negative results, a third leaf gave a response of 0·008 volt, but its resistance was obstinately high (nearly 3 megohms), a fourth leaf gave a response of 0·004 volt (plates 1770 and 1771). On May 23rd I was unable to find a satisfactory leaf; most of the plants were fully grown and in flower. I therefore abandoned Iris and sought for other satisfactory leaves, in which it might be possible to obtain evident differences of reaction in correlation with evident differences of state.

To sum up the effect of temperature upon the response of Iris—the normal response at 15° to 20° is diminished or abolished at low temperature (10°), augmented at high temperature (30°), diminished at higher temperature (50°), and abolished by boiling.

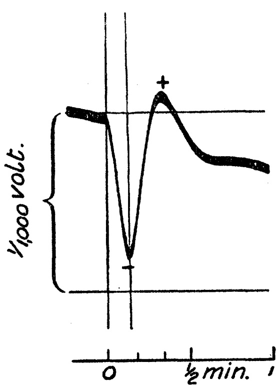

Fig. 2*a*.—Normal Response of Nerve to Excitation.

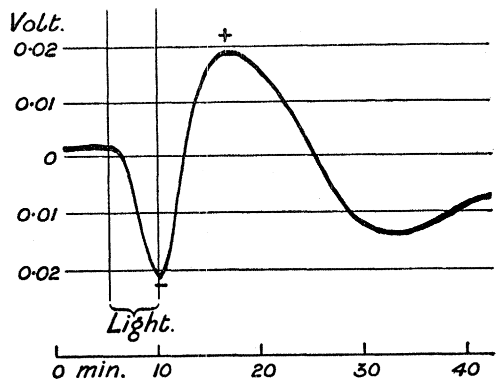

Fig. 2*b*.—Normal Response of Iris Leaf to Illumination. (1752.)

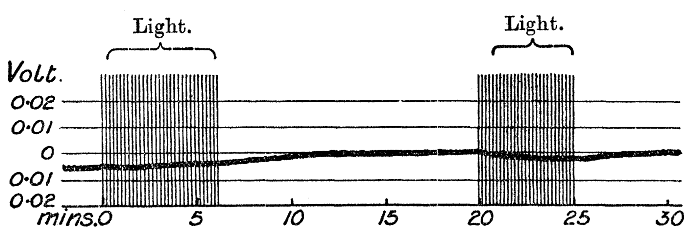

Fig. 3.—Failure of response in an inert leaf of Iris.

Time of day.—Leaves of Iris appear to give more marked response at or about mid-day, than at or about 6 P.M.

Young leaves of young plants act well. Old leaves of old plants do not act at all. The older leaves of young plants act better than the younger leaves of old plants.

Other plants.—Leaves of Tropæolum and of Mathiola, as far as I have yet seen, give a response to light, that is in the main the contrary of the ordinary Iris response, viz., "positive" during illumination, and subsequently "negative."*

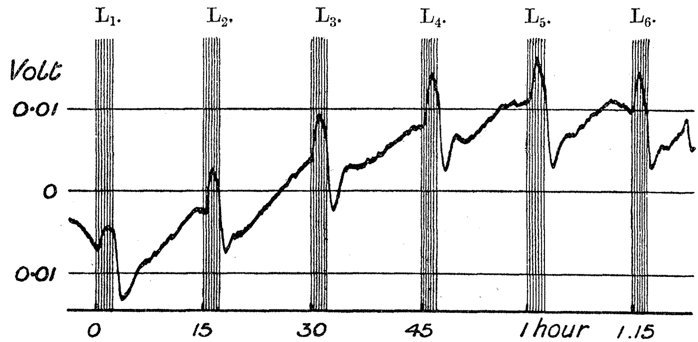

FIG. 4.—Series of Normal Responses of Mathiola annua ("positive" during illumination, subsequently "negative.") (1793.)

Leaves of Nicotiana reacted like Iris.

Leaves of Begonia have given a variety of responses strongly suggestive of the simultaneous action of two opposed forces effecting a resultant deflection in a + or − direction.

As regards Mathiola and Tropæolum, leaves empty of starch have acted better than leaves laden with starch.

Leaves of Ulva gave no distinct response (only one series of trials).

Leaves of ordinary garden shrubs and trees, &c. (*e.g.*, Lilac, Pear, Almond, Mulberry, Vine, Ivy), and petals of flowers, gave no distinct response.

Anæsthetics.—I was able to make only three satisfactory experiments with Iris leaves, before the supply of available material had come to an end.†

The first was made upon a vigorous young leaf on May 15th, the test (five minutes' illumination) being made at intervals of rather more than half an hour, with the following result:—

* "Negative" as the term is employed in physiological literature, *i.e.*, negative pole of positive element ("zincative").

† *Note added July 16th.*—I have made further trial of anæsthetics during the past month upon leaves of Begonia. The effect was perfectly clear, but slow—viz., temporary abolition of response by ether vapour, permanent abolition by chloroform vapour, augmentation by "little" CO_2, temporary suppression by "much" CO_2. I think it possible that the refractory behaviour of the Iris leaf mentioned in the text may have been due to a primary effect of the anæsthetic upon stomatal guard-cells. (*Vide* 'Proc. Physiol. Soc.,' June 30.)

Response before CO_2	=	0·008 volt.
during and after CO_2......	=	nil.
subsequently	=	0·013 ,,
during and after CO_2......	=	nil.
subsequently	=	0·010 ,,

The second experiment was made upon a rather "old" leaf on May 21st, the test being applied at intervals of 40 minutes, and the leaf chamber being at 25°.

1. Normal response.........	=	0·004 to 0·005
2. After chloroform	=	0·003, 0·002, 0·005
3. After more chloroform	=	0·005, 0·008
4. After carbon dioxide ...	=	0·002, nil, 0·001, 0 012, 0·005

Upon other leaves (Mathiola, Tropæolum) I have witnessed—

1. Augmentation of response in consequence of an air-supply containing 1 to 3 per 100 of CO_2.

2. Prompt abolition of response when a full stream of CO_2 is run through the leaf-chamber.

3. Gradual abolition of response when the air-supply to the leaf-chamber has been kept clear of CO_2; followed by gradual recovery on the readmission of a small amount of CO_2.

The action of ether upon a leaf of *Nicotiana Tabacum* was as follows:—

Time 0	Normal	= −0·0016
—	Etherisation	—
15 mins.	Etherisation	−0·0016
30 ,,	Etherisation	−0·0004
45 ,,	....	−0·0008
60 ,,	....	−0·0008
90 ,,	....	−0·0016
150 ,,	....	−0·0020

each period of illumination lasting for 2 minutes.

Nature of the Normal Response (*Iris Leaves*).

Direction.—The accidental or "normal" leaf currents observed when the electrodes are first applied to a leaf are of no significance, as regards the response to light. Such "normal" current may be due to accidental injury or to physiological inequality or to unequal imbibition of contacts, and necessarily includes the small amount of current that may arise from the unpolarisable electrodes. It may be positive negative, or non-existent.

The regular and normal response to light is independent of such

accidental currents, provided they be not due to excessive physiological differences.

The immediate effect of light is to arouse current in the half-shaded leaf, directed from the illuminated to the shaded half (*i.e.*, in the galvanometer from shaded to illuminated; *i.e.*, from resting to active tissue, as in muscle and nerve).

With illumination of moderate duration, *i.e.*, not exceeding a few minutes, this first effect lasts as long as its cause, rising towards a maximum. With longer illumination, a maximum is reached from which the effect begins to decline. The current drops to or beyond zero, giving place to the reversed current, which is the regular after-effect of illumination.

At the end of an illumination of moderate duration, the current rapidly subsides and gives place to a reversed current directed in the leaf towards the previously illuminated half.

This effect and after-effect of illumination are similar in appearance to the effect and after-effect in nerve produced by tetanisation, extending, however, over longer periods of time (figs. 2*a* and 2*b*).

Magnitude.—The electromotive force of the response has a value that usually ranges from 0·005 to 0·020 volt.

The leaf resistance (interpolar distance = 5 cm., and breadth = about 1 cm.) is generally between 500,000 and 1,000,000 ohms.

The current deflection with these values is between 5 and 40 cm. of scale, with a possible accidental effect of ± 1 cm.*

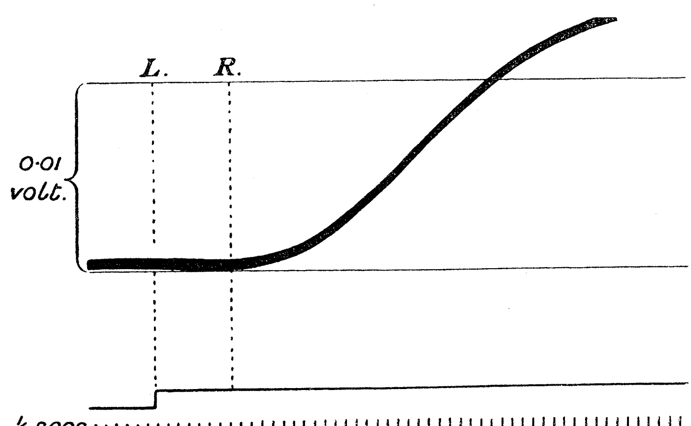

Fig. 5.—Interval of Time between Illumination L and Response R, of a vigorous Leaf of Iris. (1733.)

* The sensitiveness at which this galvanometer was used was such that 10^{-9} A = 1-cm. scale. With the recording galvanometer, 1 cm. of ordinate = $3 \cdot 10^{-8}$ A.

Summary of Observations on Iris.

Date.	No.	Group		Temperature.	Response to light. (Volt.) Effect.	Response to light. (Volt.) After-effect.	Resistance. (Ohms.)
March	1732	1	Sunlight	"Cool"	−0·0015	+ off scale	—
May 10	1735	2	Arc light........	"Warm"	−0·025	+0·020	710,000
	1736	2	,, ,, ...	,,	−0·021	+0·017	740,000
	1737	2	,, ,, ...	,,	−0·010	+0·010	740,000
	1738	2	,, ,, ...	,,	−0·013	—	710,000
,, 11	1739	3	Sun	,,	−0·008	—	1,000,000
	1740	3	,, ...	,,	−0·005	+0·005	590,000
	—	3	Arc (evening)	"Cool"	Nil.	Nil	—
,, 12	—		Sun and arc	10° to 12°	Nil.	Nil	—
,, 13	1743	4	Arc	10° to 17°	−0·001 to −0·003	—	425,000
	1744	4	,, ...	17°	−0·005	—	565,000
	1745	4	,, (all subsequent experiments with arc light through water tank)	50°	−0·007	—	450,000
,, 14	1746	5	Showing that the response is increased with rise of temperature	13°	−0·004	—	300,000
	,,	5		25°	−0·020	—	170,000
	,,	5	....	13°	−0·008	+0·006	770,000
,, 15	1747	5	....	11°	−0·004	+0·005	810,000 / 630,000
	1748	5	....	25°	−0·008	+0·008	450,000
	,,	5	....	25°	−0·008	+0·010	450,000
	1749	6	....	25°	−0·018	—	390,000
	,,	6	....	25°	−0·017	—	390,000
	1751	6	....	25°	−0·013	—	—
,, 16	1752	7	Leaf giving a very well marked and regular response. On the second day the resistance is much increased; the response is sluggish, with a long latent period, and no positive after-effect at first	25°	−0·023	+0·017	950,000
	1753	7		25°	−0·023	+0·028	950,000
	1754	7		25°	−0·023	+0·025	950,000
,, 17	1756	7		12°	−0·020	Nil	3,250,000
	1757	7		25°	−0·035	+0·015	2,450,000
	1760	7		17°	−0·020	+0·020	3,400,000
	1761	7		16°	−0·030	+0·020	4,250,000

Summary of Observations on Iris—*continued.*

Date.	No.			Tempera-ture.	Response to light. (Volt.) Effect.	Response to light. (Volt.) After-effect.	Resistance. (Ohms.)
May 19	1764	8	No response	27°	—	—	5,650,000
	1765	9	,, ,,	27°	—	—	550,000
	1766		,, ,,	30°	—	—	1,400,000
	1768	10		15°	−0·003	+0·006	560,000
	1769		After immersion in boiling water	15°	+0·0003	—	94,000
,, 21	1770	11	Unusually high resistance. Two previous leaves gave no evident response	17°	−0·008	—	2,850,000
	1771	12		25°	−0·004	+0·005	500,000
	1772			25°	−0·005	+0·010	—
	1773		Chloroform (no effect)	25°	−0·003	—	500,000
	1774			25°	−0·002	—	250,000
	1775			25°	−0·005	+0·005	340,000
	1776		Chloroform (no effect)	25°	−0·005	+0·005	370,000
	1777			25°	−0·008	—	370,000
	1778		Carbon dioxide (abolition)	25°	−0·002	—	250,000
	1779			25°	Nil.	—	250,000
	1781		Recovery after CO_2	25°	−0·001 to −0·012	—	250,000
	1782			25°	−0·005	—	300,000
	,,		After immersion in boiling water	25°	Nil	—	150,000
,, 23	—	13	Sun and arc (no response)	22°	Nil	—	—

Latency.—The effects and after-effects occur very sharply at beginning and end of strong illumination of moderate duration. The latent period is between 3 and 10 sec.

Fatigue and Recovery.—The effects of successive illuminations (of 5 minutes' duration) progressively diminish if repeated at "short" intervals (10 minutes). At intervals of about 1 hour, successive illuminations of 5 minutes produce approximately equal effects.

With the leaf of Mathiola, I have used periods of illumination of 2 minutes at intervals of 15 minutes without provoking any obvious sign of fatigue.

Conclusions.—The leaves of certain plants under favourable conditions of life exhibit electromotive effects and after-effects, amounting to $\pm$ 0·02 volt in response to illumination.

As in the case of animal tissue, it is possible that the negative (zincative) effect may be significant of dissimilation, and the opposite effect or after-effect significant of assimilation.

The absence of distinct response in petals indicates that chloroplasts are essential to the reaction.

The absence of distinct response in the green leaves of trees and shrubs is possibly due to a lower average metabolism in such leaves, as compared with the activity of leaves of small young plants, in which leaf-functions are presumably concentrated within a smaller area.

"On the Viscosity of Gases as affected by Temperature." By LORD RAYLEIGH, F.R.S. Received June 20,—Read June 21, 1900.

A former paper* describes the apparatus by which I examined the influence of temperature upon the viscosity of argon and other gases. I have recently had the opportunity of testing, in the same way, an interesting sample of gas prepared by Professor Dewar, being the residue, uncondensed by *liquid hydrogen*, from a large quantity collected at the Bath springs. As was to be expected,† it consists mainly of helium, as is evidenced by its spectrum when rendered luminous in a vacuum tube. A line, not visible from another helium tube, approximately in the position of D_5 (Neon) is also apparent.‡

The result of the comparison of viscosities at about 100° C. and at

* 'Roy. Soc. Proc.,' vol. 66 (1900), p. 68.

† 'Roy. Soc. Proc.,' vol. 59 (1896), p. 207; vol. 60 (1896), p. 56.

‡ I speak doubtfully, because to my eye the interval from D_1 to D_3 (helium) appeared about equal to that between D_3 and the line in question, whereas, according to the measurements of Ramsay and Travers ('Roy. Soc. Proc.,' vol. 63 (1898), p. 438), the wave-lengths are—