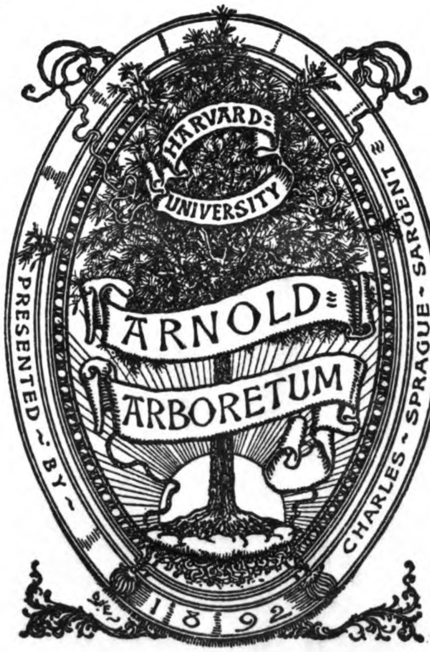
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PLANT-AUTOGRAPHS AND THEIR REVELATIONS

BY

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PLANT-AUTOGRAPHS AND THEIR REVELATIONS.[1]

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There are professors of sciences bordering on the mystical, who declare that they can discriminate the character and disposition of anyone, simply by a careful observation of his handwriting. As to the authenticity of such claims scepticism is permissible; but there is no doubt that one's handwriting may be modified profoundly by conditions, physical and mental. There still exist at Hatfield House, documents which contain the signatures of no less a person than the historical Guy Fawkes of Gunpowder Plot celebrity. And those who have seen them declare that there is a sinister variation in these signatures. The crabbed and distorted characters of the last words Guy Fawkes wrote on earth—as in the dark hours of the morning on which he was executed he set his hand to the written confession of his crime—tell their own tale of what had transpired in the solitary imprisonment of that fateful night.

Such, then, is the history that may be unfolded to the critical eye by the lines and curves of a human autograph. Under a placid exterior, there is also a hidden history in the life of the plant. Storm and sunshine, warmth of summer and frost of winter, drought and rain, all these and many more come and go about the plant. What coercion do they exercise upon it? What subtle impress do they leave behind? Is it possible to make the plants write down their own autographs, and thus reveal their hidden history? Were this possible, the fact would be fraught with far-reaching consequences.

For about the life reactions of plants, there are contending and irreconcilable hypotheses. Does the plant, like the animal, give an answering twitch to an external shock? Is there any possible relation between plant life and our own? On these points very little is definitely known. For numerous are the experimental difficulties which confront and baffle the investigator.

One school of thinkers, by far the most numerous, would have us believe that some of the most characteristic reactions in the animal are not to be found in the plant; for example, it is urged that, unlike the animal, the majority of plants are insensitive to a blow, exhibiting

[1] Reprinted by permission from pamphlet copy published by the Royal Institution of Great Britain. Lecture at the Weekly Evening Meeting, Friday, May 29, 1914.

no shuddering twitch, either mechanical or electrical; and that even in the sensitive Mimosa, an irritation does not cause an excitatory impulse, but a mere hydraulic disturbance. The pendulum then swings from these hasty assumptions to the diametrically opposite extreme. Under these circumstances the clear path is that which leads us away from theory and disputations to find the thread of fact. We must, therefore, abandon all our preconceptions, and put our questions direct, insisting that the only evidence which can be accepted is that which bears the plant's own signature.

How are we to know what unseen changes take place within the plant? If it be excited or depressed under some special circumstance, how are we, on the outside, to be made aware of it? The only conceivable way would be, if that were possible, to detect and measure the actual response of the organism to a definite testing blow. When an animal receives an external shock, it may answer in various ways; if it has voice, by a cry; if it is dumb, by the movement of its limbs. The external shock is the stimulus; the answer of the organism is the response. If we can find out in the plant the relation between the stimulus and response we shall be able to determine its state of vitality at the moment. In an excitable condition, the feeblest stimulus will evoke an extraordinarily large response; in a depressed state even a strong stimulus evokes only a feeble response; and lastly, when death has overcome life, there is an abrupt end of the power to answer at all.

We might, therefore, have detected the internal condition of the plant, if we could have made it write down its responses. In order to succeed in this, we have, first, to discover some compulsive force which will make the plant give an answering signal; secondly, we have to supply the wherewithal for an automatic conversion of these signals into an intelligent script; and, last of all, we have ourselves to learn the nature of the hieroglyphic.

RESPONSE OF PLANT AND ANIMAL.

In answering the question whether there is a fundamental unity in the response of plant and animal, we have first to find out whether sensitiveness is characteristic of only a few plants or whether all plants and every organ of every plant is sensitive. Then we have to devise apparatus by which visible or invisible reactions are detected and recorded. Having succeeded in this, we have next to survey the characteristic reactions in the animal, and find out whether phenomena corresponding to these may also be discovered in the plant.

Thus, when an animal is struck by a blow, it does not respond at once. A certain short interval elapses between the incidence of the blow and the beginning of the reply. This lost time is known as the latent period. In the plant is there any definite period which elapses between the incident blow and the responsive twitch? Does this latent period undergo any variation as in the animal, with external conditions? Is it possible to make the plant itself write down this excessively minute time interval?

Next, is the plant excited by various irritants which also excite the animal? If so, at what rate does the excitatory impulse travel in the plant? Under what favorable circumstances is this rate of transmission enhanced, and under what other circumstances is it retarded or arrested? Is it possible to make the plant itself record this rate and its variation? Is there any resemblance between the nervous impulse in the animal and the excitatory impulse in the plant?

The characteristic effects of various drugs are well known in the case of the animal. Is the plant similarly susceptible to their action? Will the effect of poison change with the dose? Is it possible to counteract the effect of one poison by means of another?

In the animal there are certain automatically pulsating tissues like the heart. Are there any such spontaneously beating tissues in the plant? If so, are the pulsations in the animal and the plant affected by external conditions in a similar manner? What is the real meaning of spontaneity?

Growth furnishes us with another example of automatism. The rate of growth in a plant is far below anything we can directly perceive. How, then, is this growth to be magnified so as to be rendered instantly measureable? What are the variations in this infinitesimal growth under external stimulus of light and shock of electric current? What changes are induced by giving or withholding food? What are the conditions which stimulate or retard growth?

And, lastly, when by the blow of death life itself is finally extinguished, will it be possible to detect the critical moment? And does the plant then exert itself to make one overwhelming reply, after which response ceases altogether?

PLANT SCRIPT.

We shall first take up the question of recording response of a plant like Mimosa. Here, at the joint of the leaf, there is a cushion-like mass of tissue known as the pulvinus. This serves as the motile apparatus. The swollen mass on the lower side is very conspicuous. Under excitation, the parenchyma in this more effective lower half undergoes contraction, in consequence of which there is a fall of the leaf. This sudden movement constitutes the mechanical response of the leaf to the impinging stimulus, just as the contractile movement of a muscle in similar circumstances forms its characteristic mechanical response. For obtaining a record, the leaf of Mimosa is attached to one arm of a lever, V; the other is loaded with a small weight, which acts as a counterpoise. A long wire, W, bent at the tip, is placed at right angles to the lever, and serves as a writer. The tip of this writer touches a smoked-glass plate, which is allowed by means of a clockwork to fall at a definite rate. (Fig. 1.) An instantaneous electric shock is applied on the leaf stalk at A. The excitation will, after a time, be propagated from A to the responding pulvinus at B, inducing the responsive fall of the leaf. After a definite period the leaf recovers from excitations and is reerected. A complete curve of response is thus obtained in which the ordinate $a \cdot b$ represents the intensity of excitation, and the abscissa $a\,c$ the period of complete recovery. (Fig. 2.) Any condition which increases excitability will also enhance the amplitude of response. Depression, on the other hand, is attended by a diminution of response. At death the response is altogether abolished. Thus, by means of testing blows, we are able to make the plant itself reveal those invisible internal changes which would otherwise have entirely escaped us.

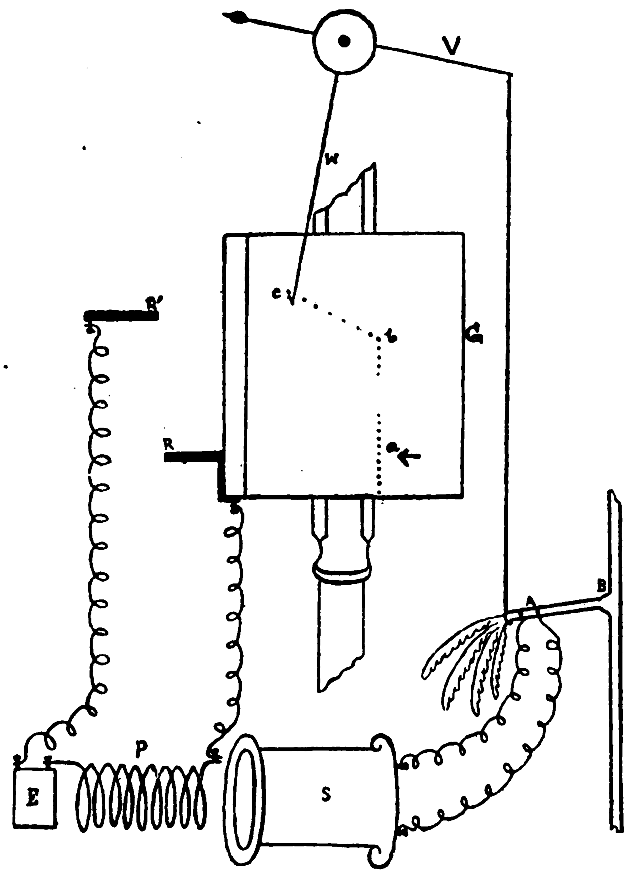

Fig. 1.—Diagrammatic representation of plant recorder. Responding leaf attached to one arm of lever V, at the fulcrum of which is attached W, the writer. G, sliding smoked glass plate for record. Recording plate is lifted and allowed to drop. At a definite position during fall, R makes momentary electric contact with R', giving rise to instantaneous electric shock at A. Moment of application of stimulus marked on recording plate by arrow *a*; arrival of excitation at B causes fall of leaf, which pulls the writer to left, describing *bc*. For determination of latent period, stimulus is applied on the pulvinus at B.

The above is a description of the theoretical method of obtaining response of the plant. In practice numerous difficulties have to be overcome. In the case of muscle-contraction, the pull exerted is considerable and the friction offered by the recording surface constitutes no essential difficulty. In the case of plants, however, the ull exerted by the motile organ is relatively feeble, and in the novement of the very small leaflets of *Desmodium gyrans* or the elegraph plant, for instance, a weight so small as four-hundredths f a gram is enough to arrest the pulsation of the leaflets. Even n the leaf of Mimosa the friction offered is enough to introduce erious errors into the amplitude and time relations of the curve. This error could not be removed as long as the writer remained in ontinuous contact with the writing surface. I was, however, able o overcome this difficulty by making an intermittent, instead of a ontinuous, contact. The possibility of this lay in rendering the

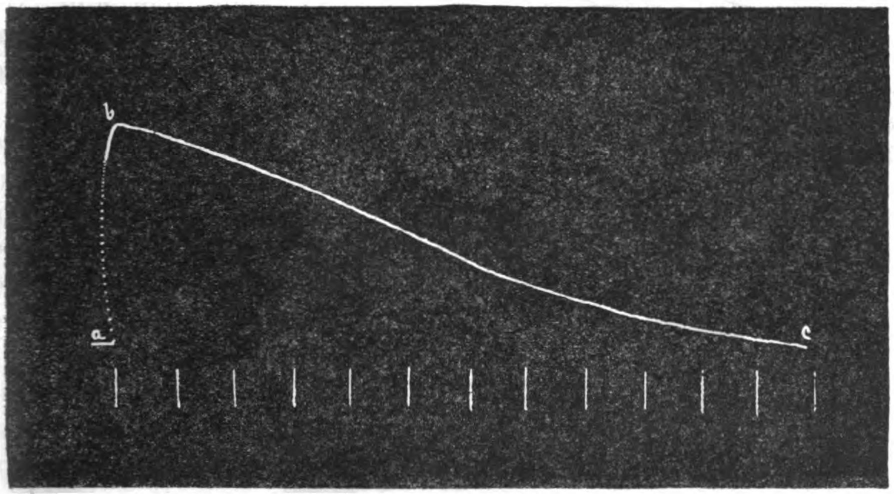

FIG. 2.—Response curve of primary leaf of Mimosa. The vertical lines below the record indicate intervals of one minute each.

writer tremulous. Fresh difficulties arose which were finally eliminated by an invention depending on the phenomenon of resonance.

THE RESONANT RECORDER.

The principle of my resonant recorder depends on a certain phenomenon, known as resonance or sympathetic vibration. In illustration of this we may construct an artificial ear tuned to a definite note. The drum of the artificial ear is made of thin soap film; a beam of light reflected from its surface forms characteristic pattern of color on the screen. To various cries this ear remains deaf, but the apathy disappears as soon as the note to which the ear is tuned is sounded at a distance. On account of sympathetic vibration the artificial ear film is thrown into wildest commotion, and the hitherto quiescent color pattern on the screen is now converted into a whirlpool of indescribably gorgeous color of peacock green and molten gold.

In the same manner, if the strings of two violins are exactly tuned, then a note sounded on one will cause the other to vibrate in sympathy. We may likewise tune the vibrating writer V with a reed C. (Fig. 3.) Suppose the reed and the writer are both tuned to vibrate a hundred times per second. When the reed is sounded the writer will also begin to vibrate in sympathy. In consequence of this the writer will no longer remain in continuous contact with the recording plate, but will deliver a succession of taps a hundred times in a second. The record will therefore consist of series of dots, the distance between one dot and the next representing one-hundredth part of a second. With other recorders it is possible to measure still shorter intervals. It will now be understood how, by the device of the resonant recorder, we not only get rid of the error due to friction, but make the record itself measure time as short as may be desired. The extraordinary delicacy of this instrument will be understood when by its means it is possible to record a time-interval as short as the thousandth part of the duration of a single beat of the heart. The complete apparatus for obtaining plant record is shown in figure 4.

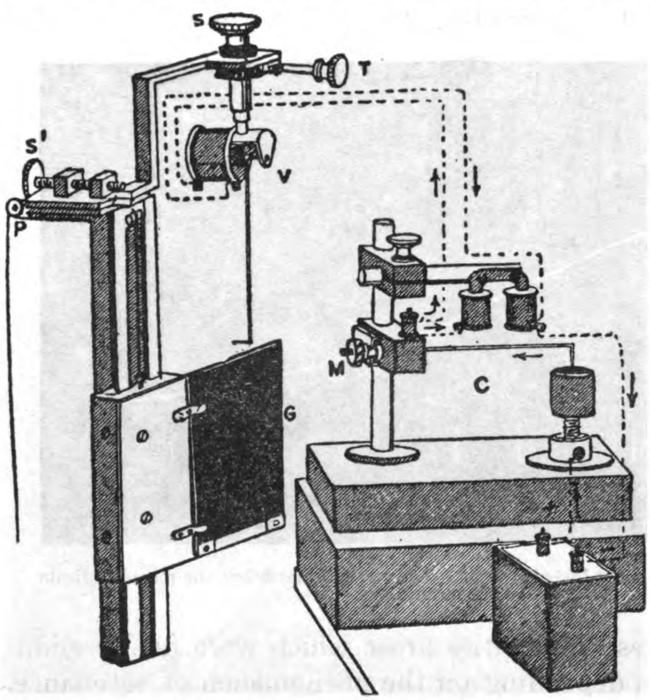

FIG. 3.—Upper part of resonant recorder (from a photograph). Thread from clock (not shown) passes over pulley P, letting down recording plate. S', screw for adjustment of distance of writing-point from recording plate. S, screw for vertical adjustment. T, tangent screw for exact adjustment of plane of movement of recorder, parallel to writing surface. V, axis of writer supported perpendicularly at center of circular end of magnet. C, reed. M, micrometer screw for adjustment of length of reed.

COMPARISON BETWEEN SENSITIVENESS OF MAN AND PLANT.

We have next to find some method of stimulation which will not cause any mechanical disturbance to the plant. In connection with this I made an important discovery which demonstrates the identical characteristics of excitation in plant and animal. In the animal tissue a constant electric current causes very characteristic xcitations at the moment of "make" or "break" of the current. n most cases there is no excitation during the continuation of the urrent. At the "make" excitation takes place only at the cathode; t the "break" of the current, however, excitation is induced once nore, but this time at the anode. These characteristic effects I find epeated also in the plant. At this point it is interesting to institute comparison between the sensitiveness of a plant and a human eing. The most sensitive organ by which an electric current can be

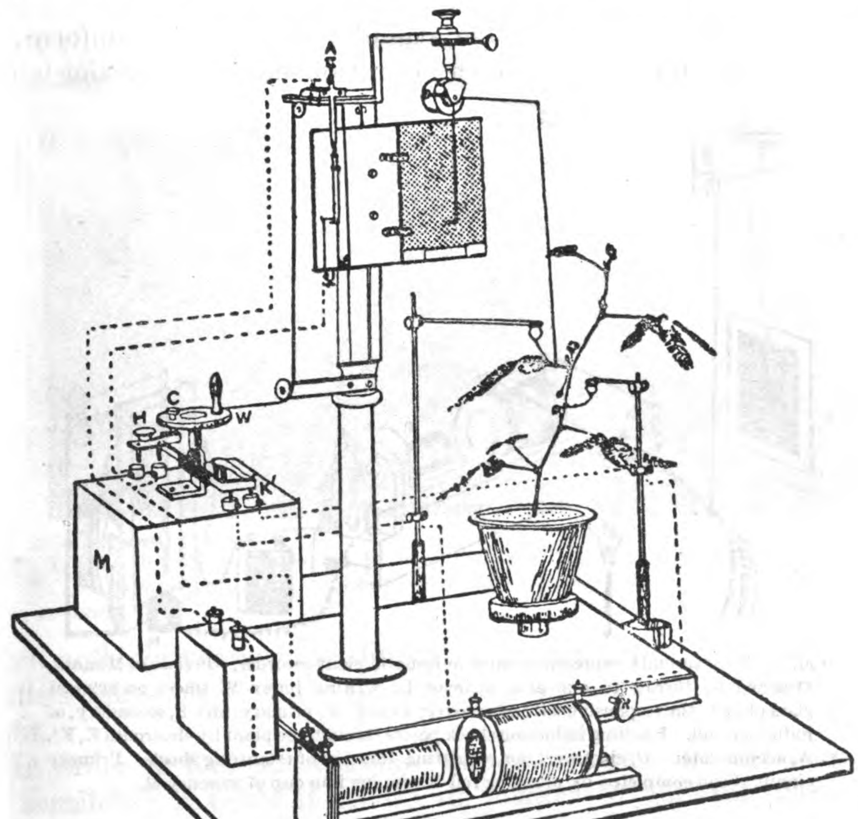

FIG. 4.—Apparatus for determination of latent period of Mimosa. M, spring motor. W, winding disk. C, projecting catch. H, release handle, pressure on which also completes primary circuit of induction coil. K', short circuit key. The automatic break consists of contact rod adjusted by micrometer screw A.

detected is our tongue. An average European, according to Laserstein, can perceive by his tongue a current as feeble as 6.4 microamperes—a microampere being one-millionth part of the unit of current. This value might be subject to certain variation, depending on racial characteristics. One might expect that the tongue of the Celt would be far more excitable than that of the stolid Anglo-Saxon. In any case the superiority of man has to be established on foundations more secure than sensibility; for the plant Biophytum, I find, is eight times more sensitive to an electrical current than a human being. With regard to the stimulus of induction shock, Mimosa is ten times as sensitive. As with the animal so also with the plant, the effect of stimulus is additive; that is to say, effective stimulation is determined not only by the intensity, but also by the duration of application. In fact, I have been able to establish in plants a strictly quantitative relation as regards the additive effect of subminimal stimulus, which is, that the effective excitation is equal to individual intensity of stimulus multiplied by the number of repetitions. In order that successive stimulations may be uniform, we have to assure ourselves that the duration of the tetanizing shock

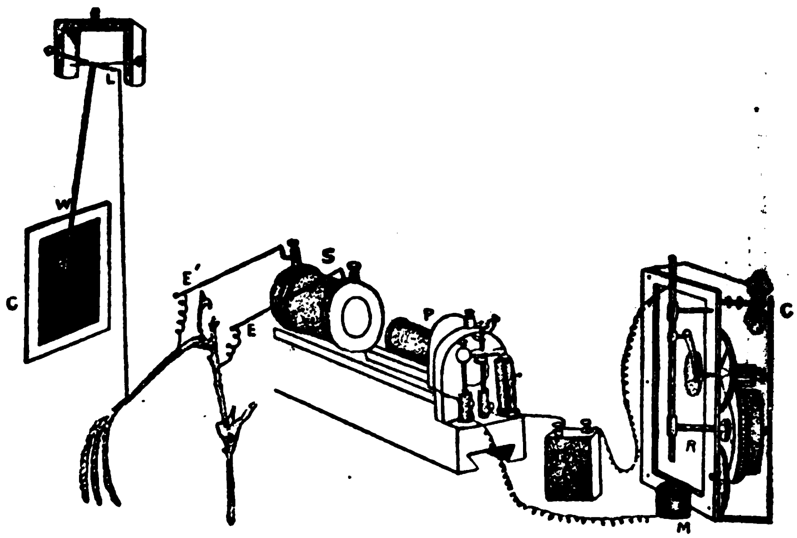

FIG. 5.—Diagrammatic representation of automatic plant-recorder. Petiole of Mimosa, attached by thread to one arm of lever L; writing index W traces on smoked glass plate G the responsive fall and recovery of leaf. P, primary, and S, secondary, of induction coil. Exciting induction shock passes through the plant by electrodes E, E'. A, accumulator. C, clockwork for regulating duration of tetanizing shock. Primary circuit of coil completed by plunging rod R dipping into cup of mercury M.

is maintained absolutely constant. This I am able to secure by means of the special device of automatic stimulator. The results of experiments to be presently described appeared so astonishing that for many reasons it became highly desirable to remove completely all elements of personal equation. In fulfilment of this, I spent several years in perfecting various instruments by which the plant attached to the recording apparatus is automatically excited by successive stimuli which are absolutely constant. In answer to this it makes its own responsive records, goes through its period of recovery, and embarks on the same cycle over again, without assistance at any point from the observer. (Fig. 5.) In this way the effect of changed external condition is seen recorded in the script made by the plant itself.

THE SLEEP OF PLANTS.

In studying the effect of a given change in the external condition an assumption has to be made that during the time of experiment there has been no spontaneous variation of excitability. Is the plant equally excitable throughout day and night? If not, is there any particular period at which the excitability remains uniform? Is there again a different time during which the plant loses its sensibility—going, as it were, to sleep? On these points no definite information has been available. The fanciful name of sleep is often given to the closure of leaflets of certain plants during darkness. These movements are brought about by variation of turgor, and

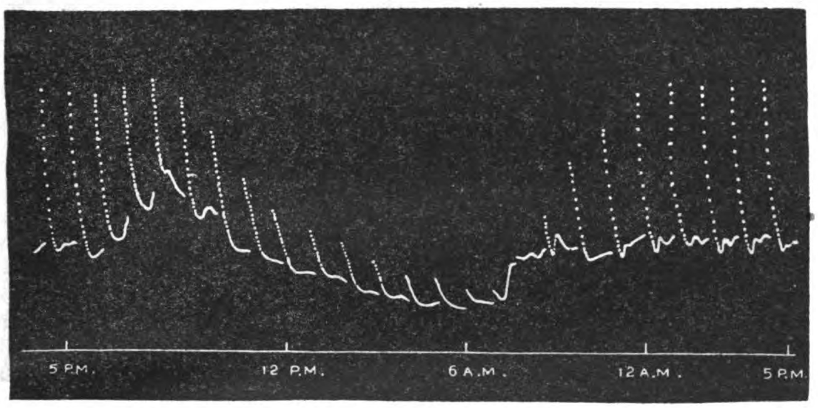

FIG. 6.—Record for twenty-four hours, exhibiting diurnal variation of excitability (spring specimen). The displacements of base line are due to nyctitropic movements.

have nothing whatever to do with true sleep; for similar closure of leaflets takes place under the precisely opposite condition of strong light.

In order to find out whether Mimosa exhibits diurnal variations of sensibility I made it record its answer to uniform questioning shocks, repeated every hour of the day and night. The amplitude of the answering twitch gave a measure of the "wakefulness" of the plant during 24 hours. The results obtained were quite unexpected. The plant is found to keep up very late, and fall asleep only at the early hours of the morning. It makes up for its late hours by gradually waking up by noon. (Fig. 6.) It then remains in a condition of uniform sensibility all the afternoon. This period of uniformity is chosen for investigations on the effect of changed external conditions on excitability.

EFFECT OF LIGHT AND TEMPERATURE.

Does the plant feel the depressing effect of darkness? The following record shows the effect of a passing cloud. (Fig. 7.) It is the sudden change which exerts a marked depressing effect. Th plant partially regains its sensibility when accustomed to darkness When brought suddenly from darkness to light there is also a transien depression followed by enhanced excitability.

Temperature has also a marked effect on excitability. Up to critical point warmth increases excitability, the recovery being als

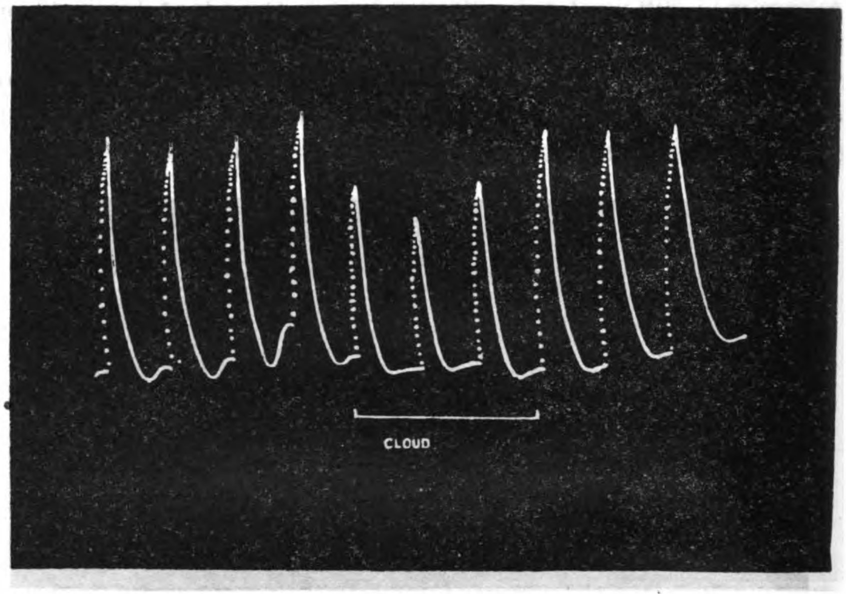

FIG. 7.—Effect of cloud. Dotted up-curve indicates responsive fall, and continuous down-line exhibits slow recovery. First four responses normal; next three show depression due to diminution of light brought on by cloud, the duration of which is indicated by horizontal line below. Last three records show restoration of excitability brought on by clearing of sky. All records read from left to right.

hastened. Cooling conversely depresses excitability. The motile excitability is abolished at about 20° C.

EFFECT OF AIR, FOOD, AND DRUGS.

The plant is intensely susceptible to the impurities present in the air. The vitiated air of the town has a very depressing effect. According to popular science, what is death to the animal is supposed to be life for the plant; for does it not flourish in the deadly atmosphere of carbonic acid gas? The record (fig. 8) shows that, instead of flourishing, the plant gets suffocated just like a human being. Note the gasp of relief when fresh air is introduced. Only in the presence of sunlight is the effect modified by photosynthesis. In contrast to the effect of carbonic acid, ozone renders the plant highly excitable. Sulphuretted hydrogen, even in small quantities, is fatal to the plant. Chloroform acts as a strong narcotic, inducing a rapid abolition of excitability. The ludicrously unsteady gait of the response of plant under alcohol (fig. 9) could be effectively exploited in a temperance lecture. The next record is in the nature of an anticlimax, where the plant has drunk (pure water) not wisely but too well. The gorged plant is seen to have lost all power of

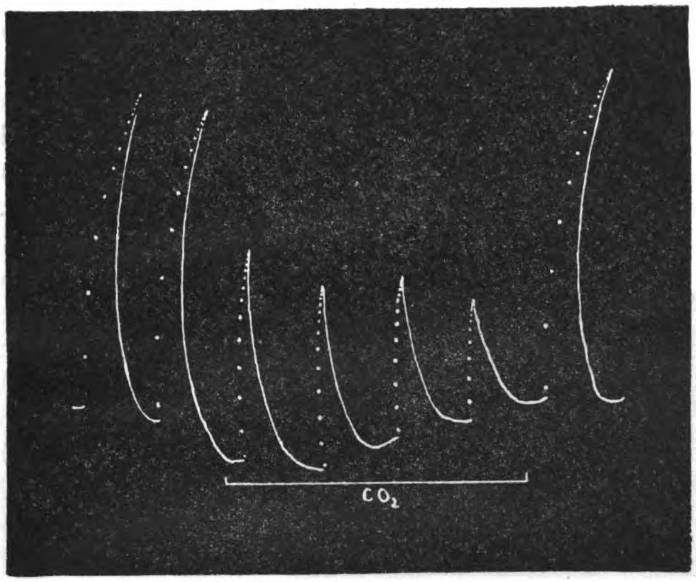

FIG. 8.—Effect of carbonic acid gas.

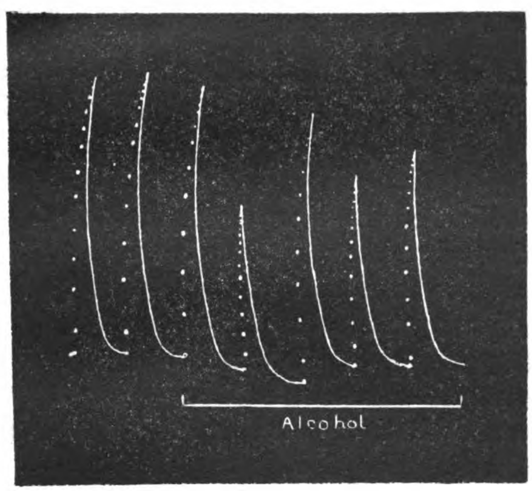

FIG. 9.—Effect of vapor of alcohol.

movement. I was, however, able to restore the plant to normal condition by extracting the excess of liquid by application of glycerin. (Fig. 10.)

UNIVERSAL SENSITIVENESS OF PLANTS.

It may be urged that the various reactions of irritability may hold good only in the case of the particular plant Mimosa, and that the majority of plants are quite insensitive. I shall presently show that this view is quite erroneous. In Mimosa diffuse stimulation causes relatively greater contraction of the more excitable lower half of the pulvinus, and this differential action is magnified by the long petiolar index. Had the upper half of the pulvinus been equally excitable as the lower, then the antagonistic reactions would have balanced each other. In radial organs we do not observe any lateral movement as in Mimosa. This is not owing to insensitiveness, but to equal contractions on all sides balancing each other. The shortening of length of various radial organs like soft stem, tendril, pistil, and stamen, can easily be shown by means of magnifying levers. Again, if we take a hollow tubular organ of some ordinary plant, say the peduncle of daffodil, it is clear that the protected inner side of the tube must be the more excitable. When this is cut in the form of a spiral strip and excited by means of an electric shock, we observe a responsive movement by curling, brought about by greater contraction of the inside of the strip. If again we take a tendril which has curled round a support, the outside is fresh and free from irritation and therefore more excitable. In this case the response is by uncurling, due to greater contraction of the more excitable outer side of the spiral.

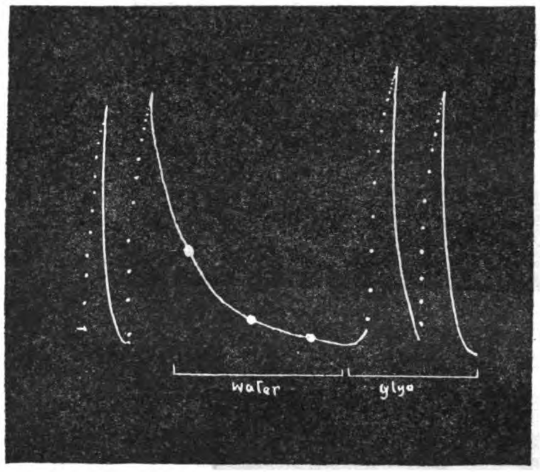

FIG. 10.—Abolition of motile excitability by excessive absorption of water, and subsequent restoration by withdrawal of excess.

In the case of woody plants, responsive movement is prevented by the rigid support. Even in such a case I have been able to demonstrate its excitation by means of electric response, first exhibited at this very hall 13 years ago.[1] No plant could appear more stolid and irresponsive than the common radish; appearances are, however, deceptive, and we find it giving a series of vigorous responses in answer to successive stimuli. The electric response comes to an end with the death of the plant.

LATENT PERIOD OF PLANT.

I next take up the very difficult problem of finding out how long it takes for the plant to perceive and respond to a blow. In attempt-

[1] Bose—Friday evening discourse, May 10, 1901.

ing to make such measurements the results are vitiated by our personal limitations. The conditions of the experiment demand accurate measurements of time-intervals shorter than a hundredth part of a second; but sluggishness of our perception makes such an attempt an impossibility. It is therefore absolutely necessary to invent a special device by which the plant itself should be compelled to write down its own latent period. In the case of the leg muscle of a frog the latent period, according to Helmholtz, is about a hundredth part of a second. This result is not without some error, on account of the inertia of the recording lever, and the inferring of time relations from a neighboring chronographic record. In my resonant recorder these errors have been reduced to a minimum. In the first place, the curve of response or phytogram is at the same time a chronogram. Secondly, the weight of my plant recorder is only a hundredth part of the usual muscle recorder. The latent period of the animal tissue undergoes appropriate variation with

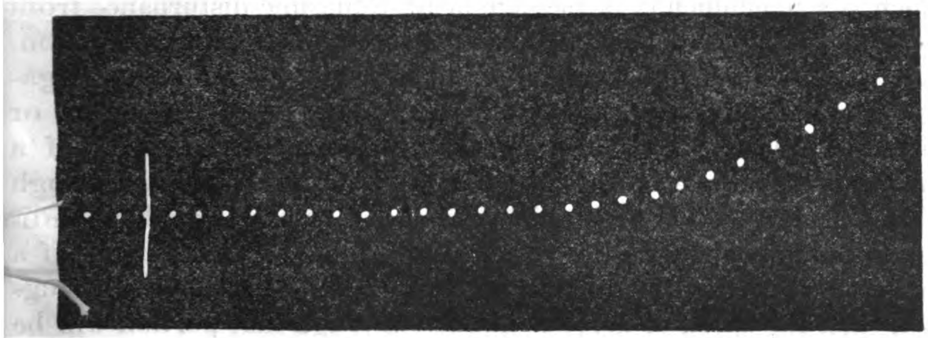

FIG. 11.—Record showing the latent period of Mimosa. This recorder vibrates 200 times per second. The time-interval between successive dots is here 0.005 sec.

changing external conditions. With feeble stimulus it has a definite value; this becomes shortened under a stronger blow. Again, when we are tired our perception time becomes prolonged. Every one of these results is equally applicable in the case of the plant. The delicacy of the resonant recorder will be understood from the response curve exhibiting the latent period of Mimosa (fig. 11). Here determination is carried to a thousandth part of a second, the value being 0.076 seconds, or eight times its value in an energetic frog. The reliability of this method can be gauged from successive records under uniform conditions, when the results are found to be identical. Another curious thing is that a stoutish plant will give its response in a slow and lordly fashion, whereas a thin one attains the acme of its excitement in an incredibly short time. Perhaps some of us can tell from our own experience whether similar differences obtain among human kind. The perception time of the plant becomes very sluggish under fatigue; when excessively tired it temporarily loses its power of perception. In this condition the plant requires at least half an hour's absolute rest to regain its equanimity.

EXCITATORY IMPULSE IN MIMOSA.

We next take up the question of the function of transmission of excitation. It has hitherto been supposed that in Mimosa the impulse caused by irritation is merely hydromechanical and quite different from the nervous impulse in the animal. According to this hydromechanical theory, the turgid plant tissue is imagined to be like india-rubber tube filled with water. The application of mechanical stimulus is supposed to squeeze the tissue, in consequence of which the water forced out delivers a mechanical blow to the contractile organ of the plant. The propagation of mechanical disturbance is thus occasioned by the bodily transfer of fluid material in a pipe. In strong contrast to this is the transmission of nervous impulse, which is a phenomenon of passage of protoplasmic disturbance from point to point. The molecular disturbance, constituting excitation, passes along the conducting nerve, and this point-to-point propagation of molecular upset is known as the transmission of excitatory or nervous impulse. If by any means the physiological activity of a portion of the nerve be enhanced, then excitation will pass through the particular portion with quickened speed. Such favorable condition is brought about by the application of moderate warmth. If a portion of nerve, on the other hand, be rendered physiologically sluggish, then the speed of nervous impulse through that portion will be slowed down. There are certain agents which paralyze the nerve for the time being, causing a temporary arrest of the nervous impulse. Such agents are known as anesthetics. There may, again, be poisonous drugs which destroy the conducting power. Under the action of such poisonous agents the nervous conduction is permanently abolished.

We are now in a position to distinguish between mechanical and nervous transmission. The mechanical conduction of water through a pipe will in no way be affected by warmth or cold; the pipe will not lose consciousness and stop the flow of water, if it be made to inhale chloroform, nor will its conducting power be abolished by applying round it a bandage soaked in poison. These agents will, on the other hand, profoundly affect the transmission of excitation. The nature of an impulse may thus be discriminated by several crucial tests.

If physiological changes affect the rate of conduction, then the impulse must be of a nervous character; absence of such effect, on the other hand, proves the mechanical character of the impulse.

Of the various physiological tests, Pfeffer employed that of the narcotic drug. Chloroform applied on the surface of the stem of Mimosa failed to arrest the impulse. This result, at first sight, appears most convincing and has been universally accepted as a disproof of the existence of nervous impulse in Mimosa. A little reflection will, however, show that under the particular conditions of the experiment the conducting tissue in the interior could not have been affected by the external application of the narcotic, the task being, in fact, as difficult as narcotizing a nerve trunk lying between muscles by the application of chloroform on the skin outside.

The question of nervous impulse in plants has thus to be attacked anew, and I have employed for this purpose twelve different methods. They all prove conclusively that the impulse in the plant is identical in character with that in the animal. Of these I shall give a short account of three different modes of investigation. It is obvious that the transmitted impulse in Mimosa must be of an excitatory, or nervous, character:

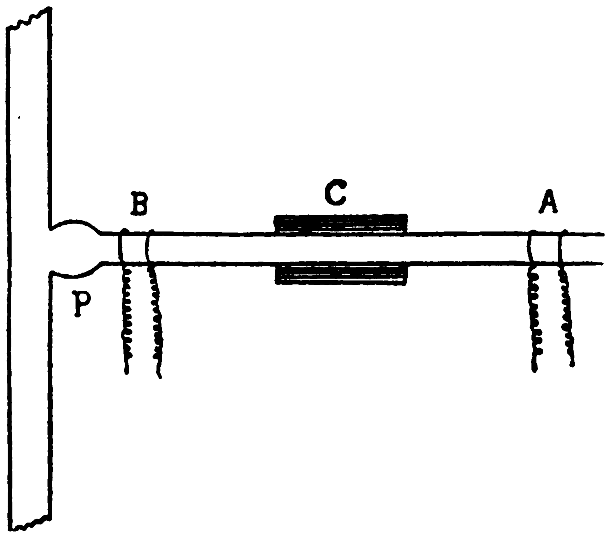

FIG. 12.—Experimental arrangement for determination of velocity of transmission and its variation. Record is first taken when stimulus is applied near the pulvinus at B (latent period) and then at a distant point on the leaf-stalk at A. Difference of two gives time for transmission from A to B. The band of cloth C is for local application of warmth, cold, anesthetics, and poison.

(1) If excitation can be initiated and propagated without any physical disturbance. The central fact in the mechanical theory is the squeezing out of water for starting the hydraulic impulse. The hydromechanical theory must necessarily fall to the ground if excitation can be effected without any mechanical disturbance whatsoever. I have shown that excitatory impulse is initiated under the polar action of current in the complete absence of any mechanical disturbance, the intensity of the current being so feeble as not to be perceived even by the very sensitive human tongue.

(2) If it can be shown that physiological changes induce appropriate variation in the velocity of transmission of the impulse.

(3) If the impulse in the plant can be arrested by different physiological blocks by which nervous impulse in the animal is arrested.

For the last two investigations the research resolves itself into the accurate measurement of the speed with which an impulse in the plant is transmitted, and the variation of that speed under changed condition. A portion of the tissue at C may, for example, be subjected to the action of cold or of a poison (fig. 12). In order to find the speed of normal transmission, we apply an instantaneous stimulus, say, of an electric shock, at B, near the pulvinus. A short interval, the latent period, will elapse between the application of stimulus and the beginning of responsive movement. After the determination of the latent period we apply stimulus once more at A and observe the time which elapses between the application of stimulus and the response. The difference between the two periods gives us the time required for the excitation to travel from the point of application of stimulus at A to the responding organ at B. Hence we obtain the speed of impulse in the plant. The experiment is repeated once more after the application of a given agent at C. If the speed undergoes any variation, it must be due to the action of the given agent.

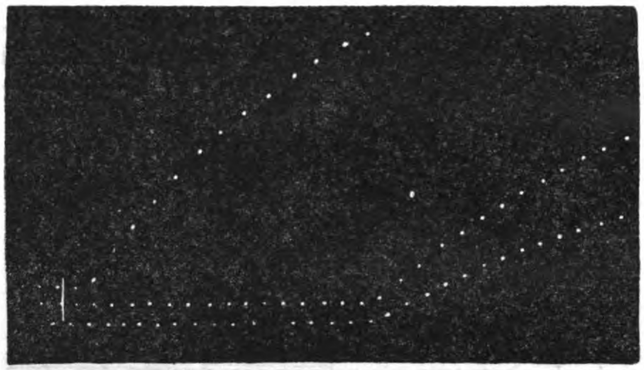

FIG. 13.—Determination of velocity of transmission in Mimosa. The two lower records are in response to stimulus applied at a distance of 30 mm.; the upper record exhibits latent period in response to direct stimulus applied on the pulvinus. Successive dots in this and following records are of intervals of one-tenth part of a second.

DETERMINATION OF SPEED OF EXCITATORY IMPULSE IN PLANTS.[1]

As relatively long intervals have to be measured in the determination of velocity, the recorder has its frequency adjusted to 10 vibrations per second, hence the space between successive dots represents an interval of one-tenth of a second. In figure 13 is given a record for determining the velocity of transmission. The two lower figures give practically identical results of successive experiments when stimulus was applied at a distance of 30 millimeters. The uppermost is the record for direct stimulation. From these it is seen that the interval between stimulus and response is 1.6 seconds, and that the latent period is 0.1 second. Hence the true time for the excitation to travel through a distance of 30 millimeters is 1.5 seconds, the velocity being 20 millimeters per second.

[1] For a more detailed account confer:
Bose, An automatic method for the investigation of velocity of transmission of excitation in Mimosa Phil. Trans. of Royal Society, Series B, Vol. 204.
Bose, Researches on irritability of plants (Longmans Green, 1913).

The velocity of excitatory impulse in the plant is slower than those of higher, but quicker than those of lower animals. The speed of the impulse is, however, subject to variation under different conditions. One significant result that came out was that while a plant carefully protected under glass from outside blows looked sleek and flourishing, yet as a complete and perfect organism it proved to be a failure. Its conducting power was found atrophied or paralyzed. But when a succession of blows rained on this effete and bloated specimen, the stimulus canalized its own path of conduction and it became more alert and responsive, and its nervous impulses became very much quickened.

INFLUENCE OF TEMPERATURE ON VELOCITY.

A decisive experiment to discriminate between the theories of mechanical and nervous transmissions consists in the determination of the effect of temperature on the speed of transmission. Temperature has no effect on mechanical propagation, whereas a moderate variation of it profoundly affects nervous transmission. The

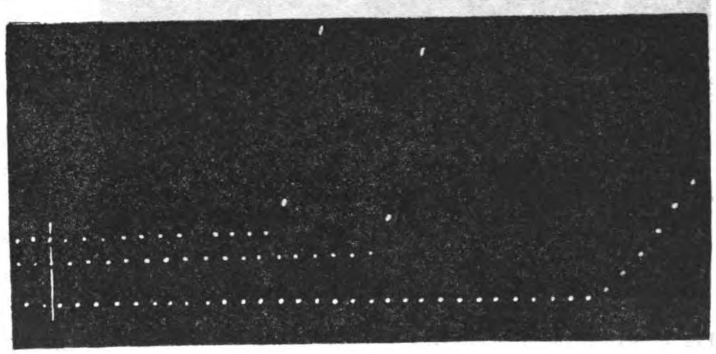

FIG. 14.—Effect of rising temperature in enhancing velocity of transmission. The three records from below upwards are for temperatures 22° C., 28° C., and 31° C., respectively.

result given in figure 14 is quite conclusive as regards the excitatory character of the impulse in plants. It is seen that with rising temperature the time required for transmission through the same distance is continuously reduced. In the present case the velocity is seen to be more than doubled by a rise of temperature through 9°.

The converse experiment is to subject a portion of conducting petiole to the action of cold. This retards the speed of conduction. Excessive cold temporarily abolishes the conducting power.

INDUCED PARALYSIS AND ITS CURE BY ELECTRIC TREATMENT.

As an aftereffect of the application of intense cold, the conducting power remains paralyzed for a considerable length of time. It is a very interesting and suggestive fact that I have been able to restore the conducting power quickly by subjecting the paralyzed portion of the plant to a measured and moderate dose of electric shock. The application of too strong an intensity is, however, very detrimental.

BLOCK OF CONDUCTION BY THE ACTION OF POISON.

I have also succeeded in arresting conduction of excitation in plants by local application of poisonous drugs. The defect of Pfeffer's experiment lay in his attempt to arrest the impulse by the application of a volatile anesthetic like chloroform on a surface of a thick stem. The chloroform escapes in the form of vapor; the access of the solution under these conditions to the interior of the tissue by absorption can only be slight and therefore ineffective in arresting the excitatory impulse. It occurred to me that the physiological block induced by a drug could be rendered more effective in two different ways: First, by the selection of a thin leaf stalk instead of a thick stem for the purpose of the experiment, so that the access of the solution to the interior became less difficult; in the second place by the employment of strong non-volatile toxic agents, like solutions of copper sulphate or of potassium cyanide. The choice of a strong poison was deemed advisable, because the absorption of even a small quantity might in such a case prove effective in abolishing the conducting power. My anticipations were fully justified. By the application of copper sulphate the conducting power was found arrested in the course of 20 minutes; but the more deadly cyanide solution abolished the conducting power in a period as short as five minutes. (Fig. 15.)

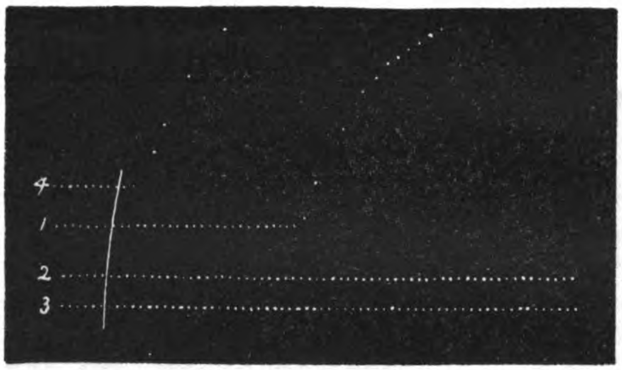

FIG. 15.—Abolition of conduction by local application of potassium cyanide. (1) Normal record; (2) arrest of conduction after application for five minutes; (3) persistent abolition of conduction, even when stimulus was increased fifteen-fold; (4) record of direct stimulation.

Accounts have thus been given of some typical experiments by which the nervous impulse is discriminated from the mechanical impulse. It has been shown that excitation may be initiated and transmitted in the plant in the complete absence of any mechanical disturbance. It has been shown that the various conditions which accelerate, retard, or arrest the nervous impulse in the animal also enhance, retard, or block the impulse in the plant in a manner which is identical. I have, moreover, from my investigations on the plant nerve, led to the discovery of certain hitherto unknown characteristics of the animal nerve. The investigation on the simplest type of plant nerve is expected to cast a flood of light on the obscure phenomenon of nervous impulse in general and the causes operative in bringing about the degeneration of the normal function of the nerve.

SPONTANEOUS PULSATION.

In certain animal tissues a very curious phenomenon is observed. In man and other animals, there are tissues which beat, as we say, spontaneously. As long as life lasts, so long does the heart continue to pulsate. There is no effect without a cause. How, then, was it that these pulsations became spontaneous? To this query no fully satisfactory answer has been forthcoming. We find, however, that similar spontaneous movements are also observable in plant tissues, and by their investigation the secret of automatism in the animal may perhaps be unraveled.

Physiologists, in order to know the heart of man, play with those of the frog and tortoise. "To know the heart," be it understood, is here meant in a purely physical and not in a poetic sense. For this it is not always convenient to employ the whole of the frog. The heart is therefore isolated and made the subject of experiments as to what conditions accelerate and what retard the rate and amplitude of its beat. When thus isolated, the heart tends of itself to come to a standstill, but if by means of a fine tubing it be subjected to internal hydrostatic pressure its beating will be resumed and will continue uninterrupted for a long time. By the influence of warmth the frequency of the pulsation may be increased, but its amplitude diminished. Exactly the reverse is the effect of cold. The natural rhythm and the amplitude of the pulse undergo again appropriate changes under the action of different drugs. Under ether the heart may come to a standstill, but on blowing this off the beat is renewed. The action of chloroform is more dangerous, any excess in the dose inducing permanent arrest. Besides these there are poisons also which arrest the heartbeat, and a very noticeable fact in this connection is that some stop it in a contracted and others in a relaxed condition. Knowing these opposed effects, it is sometimes possible to counteract the effect of one poison by administering another.

RHYTHMIC PULSATIONS IN DESMODIUM.

The existence of such spontaneous movements is seen in the well-known Indian plant *Desmodium gyrans*, or the telegraph plant, whose leaflets dance up and down more or less continuously. The characteristics of the automatic pulsations in the plant could not be determined on account of the apparent impossibility of obtaining a record. The leaflets are too minute and the pull exerted too feeble to overcome friction of the recording surface. This difficulty I have been able to remove by the device of my oscillating recorder. From the records thus obtained I am enabled to say that the automatic movements of both plants and animals are guided by laws which are identical.

Firstly, when for convenience of experiment we cut off the leaflet, its spontaneous movements, like those of the heart, come to a stop. But if we now subject the isolated leaflet by means of a fine tube to an added internal hydrostatic pressure, its pulsations are renewed and continue uninterrupted for a very long time (fig. 16). It is found again that the pulsation frequency is increased under the action of

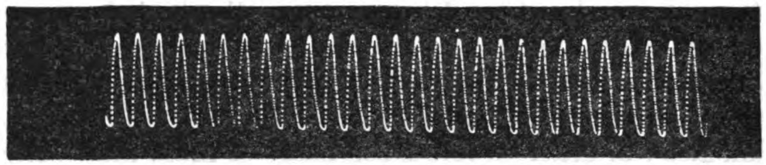

FIG. 16.—Record of automatic pulsations in *Desmodium gyrans*.

warmth and lessened under cold, increased frequency being attended by diminution of amplitude and vice versa. Under ether there is a temporary arrest, revival being possible when the vapor is blown off (fig. 17). More fatal is the effect of chloroform. The most extraordinary parallelism, however, lies in the fact that those poisons which arrest the beat of the heart in a particular way arrest the plant pulsation also in a corresponding manner, the arrest produced being either at systole or diastole, depending on the characteristic reaction of the poison. Taking advantage of the antagonistic reactions of specific poisons, I have been able to revive a poisoned leaflet by the application of another counteracting poison.

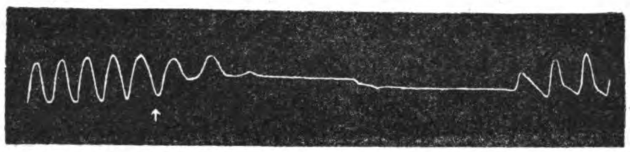

FIG. 17.—Arrest of pulsation of Desmodium under ether; restoration of pulsation on blowing off ether. The arrow indicates the time of application.

Let us now inquire into the causes of these automatic movements, so called. In experimenting with certain types of plant tissues I find that an external stimulus gives rise to the same amplitude of response, whether the stimulus be feeble or strong. What happens, then, to the excess of the incident energy? It is not really lost, for these particular plant tissues have the power of storage. In this way energy derived in various ways from without—such as light, warmth, food, and so on—is constantly being accumulated. When a certain point is reached, there is a bubbling overflow, and we call this overflow spontaneous movement. Thus what we call automatic is really an overflow of what has previously been stored up. When this accumulated energy is exhausted, then there is also an end of spontaneous movements (fig. 18). But a fresh accession of stimulus from outside renews these pulsations.

In the matter of these so-called spontaneous activities of the plant I find that there are two distinct types. In one the overflow is initiated with very little storage, but here the unusual display of activity soon comes to a stop. To maintain such specimens in the rhythmic condition, constant stimulation from outside is necessary. Plants of this type are extremely dependent on outside influences, and when such sources of stimulus are removed they speedily come to an inglorious stop. Averrhoa is an example of this kind. In the second type of automatic plant activity I find that long-continued storage is required before an overflow can begin. But in this case the spontaneous outburst is persistent and of long duration, even when the plant is deprived of any immediately exciting cause. These, therefore, are not so obviously dependent as the others on the sunshine of the world. Our telegraph plant, Desmodium, is an example of this.

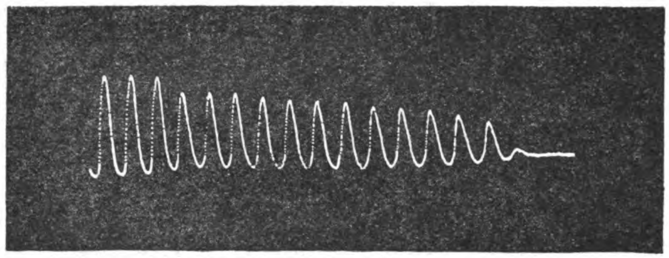

FIG. 18.—Gradual stoppage of pulsation in an isolated Desmodium leaflet due to rundown of stored energy.

INSTANTANEOUS RECORD OF GROWTH.

As a further example of automatic activity we may take the phenomenon of growth. The rate of growth is so extremely slow that even the proverbial pace of the snail is two thousand times quicker. It would take an average plant 200 years to cover the short distance of a mile. This extreme slowness is a serious drawback in the investigation on growth. For even with the existing magnifying growth recorders it would take many hours for the variation of growth to be recorded under the given changed conditions in the environment. The results thus obtained are subject to errors brought about by the variation of growth which takes place spontaneously in the course of a few hours. Growth can be assumed to remain constant only for a short time; on this account it is necessary to conclude an experiment in the course of a few minutes.

By means of microscopic projection it is possible to magnify growth; but such an arrangement will not be self-recording. There is again a serious error introduced by the action of strong light, which profoundly modifies the rate of normal growth.

These difficulties have been overcome in my high magnification crescograph, which records the absolute rate of growth in a time so short as the single beat of the pendulum. The various magnifications available are a thousand or ten thousand times. For demonstration purposes I have been able to secure a magnification of a million times. The infinitesimal growth thus becomes magnified so as to appear rushing forward as if in a race. The actual rate of growth and its variations under the action of drugs, of food materials, of various electrical and other forms of stimuli, are thus recorded in the course of a few minutes. The great importance of this method of investigation in agriculture is sufficiently obvious.

The plant has thus been made to exhibit many of the activities which we have been accustomed to associate only with animal life. In the one case, as in the other, stimulus of any kind will induce a responsive thrill. There are rhythmic tissues in the plant which, like those in the animal, go on throbbing ceaselessly. These spontaneous pulsations in the one case, as in the other, are affected by various drugs in an identical manner. And in the one case, as in the other, the tremor of excitation is transmitted with a definite and measured speed from point to point along conducting channels. The establishment of this similarity of responsive actions in the plant and animal will be found of the highest significance; for we now realize that it is by the study of the simpler phenomena of irritability in the vegetal organisms that we may expect to elucidate the more complex physiological reactions of the animal.

THE PLANT'S RESPONSE TO THE SHOCK OF DEATH.

A time comes when, after an answer to a supreme shock, there is a sudden end of the plant's power to give any further response. This supreme shock is the shock of death. Even in this crisis there is no immediate change in the placid appearance of the plant. Drooping and withering are events that occur long after death itself. How does the plant, then, give this last answer? In man, at the critical moment, a spasm passes through the whole body, and similarly in the plant I find that a great contractile spasm takes place. This is accompanied by an electrical spasm also. In the script of the death recorder the line, that up to this point was being drawn, becomes suddenly reversed and then ends. This is the last answer of the plant.

These, our mute companions, silently growing beside our door, have now told us the tale of their life tremulousness and their death spasm in script that is as inarticulate as they. May it not be said that this, their story, has a pathos of its own beyond any that we have conceived?

We have now before our mind's eye the whole organism of the perceiving, throbbing, and responding plant, a complex unity and not a congeries of unrelated parts. The barriers which separated kindred henomena in the plant and animal are now thrown down. Thus ommunity throughout the great ocean of life is seen to outweigh pparent dissimilarity. Diversity is swallowed up in unity.

In realizing this, is our sense of final mystery of things deepened r lessened? Is our sense of wonder diminished when we realize in he infinite expanse of life that is silent and voiceless the foreshadowngs of more wonderful complexities? Is it not rather that science vokes in us a deeper sense of awe? Does not each of her new dvances gain for us a step in that stairway of rock which all must limb who desire to look from the mountain tops of the spirit upon he promised land of truth?