"GALVANOTROPISM" OF ROOTS.

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I.

The galvanotropic orientation of animals may probably be used for analysis of certain features of central nervous activity.1 Therefore it is necessary to obtain a conception of the mode of stimulation by passage of direct current. In relation especially to the results of studies, in this laboratory2 and elsewhere, upon the conductance of plant cells, and because of the structurally simpler conditions of response, we have paid attention to the well known "galvanotropic curvature" of roots.

Every one interested in plant irritability has always considered the "galvanotropic response" of the roots as one of the most remarkable facts described. Discovered by Elfving in 1882, the "galvanotropic response" was studied by Müller-Hettlingen, 1883; Brunchorst, 1884; Rischawi, 1885; Ewart and Bayliss, 1906; Schellenberg, 1906; and in a rather long paper by Gassner, 1906. Indications are given also by Sztics, 1913, and a general review of the subject can be found in Stern's book (1924).

Based on all these observations, it is generally admitted that for high densities of current, or for long exposures, a curvature towards the + pole is obtained (so called Elfving's curvature); that, on the other hand, for lower densities of current, or for shorter exposures,
the curvature is directed toward the — pole (genuine "galvanotropic response"). This last is considered as a tropism, the first curvature being said to be purely traumatic.

The definition of the true "galvanotropism" of the root can be therefore expressed in the following manner: It is a growth curvature, directed towards the cathode, located in the region of maximum growth, irreversible by plasmolysis and requiring the presence of the tip of the root.

The origin of this curvature is naturally the real question. For the explanation of this origin several theories have been advanced. Brunchorst sees in the curvature an injury by the electrolysis products, especially the H₂O₂ that may be produced. Rischawi considers the phenomenon similar to the electrosmotic water displacement in the albumin cylinders of du Bois Reymond's experiments. Ewart and Bayliss attribute the response to chemotropic stimulation by the products of electrolysis, all idea of traumatic curvature being excluded.

On the contrary, for Gassner the facts may be explained as a traumatic response of the organism to a unilateral injury of the tip of the root.

In fact, to all these explanations the same objection may be made: the technical conditions were often too crude and, in a certain number of cases, too vague to be used adequately as bases for explanations. For instance, Ewart and Bayliss used platinum electrodes directly in contact with the plant. In other cases, it is true, so called unpolarizable electrodes were employed. Others (Brunchorst, Gassner, Schellenberg) used carbon electrodes, often dipping directly in the same liquid as the root tips but sometimes surrounded by a septum made by a porous plate. For many cases the density of current corresponding to the position of the roots in the trough is not known.

It was thought interesting for these reasons to reproduce these experiments, trying always to avoid the errors pointed out.

The actual experiments were carried out keeping in mind the following points: (1) Reduction of polarization products by use of unpolarizable electrodes, (2) prevention of diffusion of the products of electrolysis by use of agar blocks, (3) gradient of densities of current easily controllable by use of troughs with definite geometrical shapes and sizes.
II.

Technique.

1. Trough 1.—Paraffine blocks were carved out following the indications of Fig. 1. These troughs are characterized by their variable cross-section, one end being a square of 5 cm. of side, the other end being 2 cm. × 5 cm. The distance of these two sections is 25 cm. and each section is closed by a block of agar gel. The agar was purified agar which had been soaked in 2 per cent HCl for 24 hours; then in 1 per cent ammonia for 12 hours; then subjected to running water for 48 hours, all with frequent shaking. After this treatment the water was more or less pressed out and the agar washed several times with distilled water, this being also used to make the gel, of which the concentration was 10 per cent in dry weight of agar. This agar gel is poured in place, care being taken to obtain a plane surface at both ends of the trough (the real electrode surfaces) and cups being provided in each block for the electrodes. These cups as well as the trough are filled to a definite height with tap water or with a balanced salt solution (diluted Knop solution). This liquid was removed immediately after each experiment and the trough was washed for several hours by a continual flow of tap water.

2. Trough 2.—The other type of trough is similar, the differences being only in the replacement of the agar blocks by porous plates 2 mm. thick.

3. Electrodes.—The electrodes used were carbon cylinders 2.5 cm. in diameter, a good contact being assured for the leads; or unpolarizable electrodes, either calomel electrodes (employed in a few cases only,
the inner resistance being too high) or of zinc-zinc sulfate. In this last case the electrodes, which were kept in a concentrate solution of zinc sulfate, were rapidly washed before use under running tap water. Furthermore, care was taken to have the same hydrostatic level in cups and electrode.

4. Current.—The potential differences applied to the electrodes varied from 0.5 volts to 115 volts. The density of current (according to the position of the root in the trough) varied from 0.058 ma./sq. cm. to 1 ma./sq. cm. The time of exposure to the action of the current was changed between 15 minutes and 360 minutes.

5. Material.—The plants used were *Vicia faba* (broad Windsor beans) and *Phaseolus vulgaris* (Burpee’s improved bush lima beans). The seedlings were grown in sawdust at 20°C and their roots were practically straight. They were used when the length of the roots was 4 to 6 cm. In a few cases experiments were made with secondary roots with the same results as with primary ones. Normally the roots dipped for 8 to 10 mm. in the solution.

III.

Results.

1. When Trough 1 is used alone, whatever the P.D. or density of current may be, and whatever the duration of the experiment (between 15 minutes and 360 minutes) no curvature ever occurs.

When Trough 2 is used, with the same conditions, curvatures are shown if carbon electrodes are used and always towards the cathode.

A test was to put Troughs 1 and 2 in series, as the objection could be made that the density or time was deficient: under these conditions curvature appears in No. 2; no curvature in No. 1, so the current and time of exposure were large enough to produce “galvanotropic” responses.

The immediate conclusion to be drawn from these experiments is that “galvanotropic” curvature is produced by the products of electrolysis.

2. Was therefore the galvanic current necessary? Sets of seedlings were put with the root dipping for 1 cm. in the water of Trough 2, for 24 hours, after the current had been passed through the water for
2 and 4 hours. Care was taken not to move or disturb the water during or after the electrolysis.

The immediate result of this test was to show a slight but definite curvature—in fact less than when the current was acting directly on the seedlings and practically not directed toward one pole or the other. The angle of deflection of the tip of the root was about 15° to 20°.

If the same experiment was made, with the same conditions (carbon electrodes, 2 or 4 hours previous passage of current) with Trough 1, no curvature is shown.

This fact proves that the blocks of agar, 10 cm. in length, are sufficient to prevent the diffusion of products of electrolysis or to slow it up so that they do not reach the middle part of the trough in time to affect the seeds.

There is therefore a difference in the curvatures when current is present or absent but the difference is merely quantitative.

We must for this reason recognize in the "galvanotropic" curvature a double effect: the first being produced by the electrolysis products; the second being the further increase of the first under the persistence of the electrical current.

The second test, showing the influence of the electrolysis products is, in fact, sufficient to show that the primary effect on the root is a traumatic one.

3. Another way to show this was to injure the root before the experiment and to place it then in Trough 1. If really injury is the first step, curvature must occur under these conditions, with non-polarizable electrodes. And it does.

Roots were placed for 2 to 3 minutes in a solution of copper nitrate \( \times 100 \); then in Trough 1 filled with tap water. The current was passed for 60 minutes. The plants were left in place in the same liquid for 24 hours (as in all the other experiments) after the passage of the current. At the end of this time a definite cathodic curvature was shown.

Experiments made after immersion of the roots for 10 minutes in the same copper solution did not give curvature.

Microchemically it is easy to show that during the short exposure the two external layers of cells are permeated by the copper ion, and
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that in the second case a much larger number of layers are injured. The latter injury corresponds practically to the killing of the root.

So, to produce the "galvanotropic" curvature in the absence of electrolysis products, the injury must be definite but not too large. A certain amount of tissue must remain in the root to react. The curvature is in fact a response from injured but not dead tissues.

IV. Interpretation.

How may we try to explain these facts? As was pointed out previously the response must surely be developed in two steps (or more).

Let us consider a root dipping in the water between the two electrodes. This body in the electrical field naturally repels the lines of flow around itself, as we know that the living cells are practically non-conducting for direct current. But under these conditions there may be accumulation on the opposite sides of ions of opposite signs. And this may be sufficient to injure the epidermic layer of the root. What are the ions which are so toxic? It may be said that perhaps any ion present in the solution used will act in this way.

In a root of circular cross-section we may thus consider two opposite halves in the epidermic layer, both injured and probably with a number of the cells killed, and acting for the remaining part as two electrodes directly applied on the internal tissues. These electrodes determine, inside of the root, an electrical field, the conducting paths being made by the cellulosic membranes imbibed with aqueous solutions. The resulting electrolysis acts now on more deeply situated cells.

The produced ions are formed in such loci that they may act directly on the plasmatic surfaces, inducing in these such changes that the relative dielectrical resistance diminishes and that free ions may migrate in or out of each cell. The result is necessarily that under the directing action of the electrical field, in all cells through the root, chains of + and − charges are formed, each cell having a + charge on the cathodic side and a − charge on the anodic side. The perduration of the current continues the same action in the same way and causes finally a relative increase of anions on the anodic side and of
cations on the cathodic side. The two halves of the root are brought, by this process, to be ionically different. The early effect of the anions on the anodic side seems not to prevent growth. The relative accumulation of cations, on the contrary, slows the growth on the cathodic side, and by further increase stops it completely. The effect of this differential state is a bending towards the cathode.

V.

In the earlier papers on galvanotropism another type of curvature has been described, the so-called Elfving's or anodic curvature. With the device described in the present paper it has always been impossible to obtain this effect, even when the root was deeply dipping in the water. We may draw from this fact the deduction that in the cases described, with very high densities of current, other factors were interfering.

The same can be said as to the S-shaped curvature described by Gassner when more than the tip of the root dips into the liquid: in the present conditions of experimentation no case of this bending was found. Is it therefore to be deducted that this type of curvature does not exist? No, probably; but that under the conditions of experimentation, insufficiently described in the papers to which reference is made, other effects are occurring. Other experiments are necessary to ascertain the conditions of production of these curvatures, as well as the change in conductance of the tissues showing or not showing these reported curvatures.

SUMMARY.

1. New experiments, made in such a way to eliminate as completely as possible products of polarization and the migration of such products when formed, have shown that the exhibition of galvanotropic curvature in roots is mainly dependent upon such products, since no curvature appears when they are excluded.

2. The polarization products injure the external layer of cells of the root; this allows these cells to act as electrodes directly applied on the internal tissues. The inner electrolysis produces such changes in the interior cells that they may be considered as becoming ionically different. This differential state is responsible for curvature.
3. "Galvanotropism" of roots, therefore, cannot be regarded as exactly comparable to the galvanotropic orientations of certain animals, but is essentially dependent upon injury.

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