Letters to the Editor.

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Nervous Impulse in Mimosa pudica.

Is the conduction of the excitatory impulse in the plant essentially similar to that of the nervous impulse in the animal? This problem is of great theo-retical interest. In his "Nervous Mechanism of Plants" (1926), Bose states that the intercommunication and interaction between more or less distant organs in the plant are brought about, as in the animal, "in two different ways-by translocation of matter and by transmission of motion. The first is effected by the slow movement of fluid carrying chemical substances in solution, such as occurs in the circulation of sap; the second by the *rapid* propagation of protoplasmic excitation such as the nervous impulse in the animal." In his presidential address at the Indian Science Congress, Lahore (1927), Bose makes his position perfeetly clear by the statement that in physiological investigations the inquirer is primarily concerned with the function of the organ and not with its outward form. In support of this he adduces the case of insectivorous plants (Drosera, Dioncea, and Nepenthes) which are universally acknowledged to possess digestive organs, in spite of the fact that the organs are very different in appearance from those of the more complex animal. The employment of the same term for these plant and animal reactions is justified by the fact that the function of digestion is performed by similar processes in both: the solution of organic food-material by a glandular secretion, and the subsequent absorption of the dissolved product.

The plant-world offers a unique opportunity for the study of the gradual evolution of a simple and primitive organ into one of greater complexity. In regard to the nervous function, it is to be remembered that the conducting tissue in the animal kingdom itself exhibits wide variation : from the simpler type as in the Medusæ to the more complex in the higher animals. The conducting tissue of the plant would naturally be expected to be much simpler in structure, and as a matter of fact it is very different in appearance from the nerve of the higher animals. The question to be decided is whether or not the process of conduction of excitation is similar in the two cases (being usually detectable by the contractile movement of the terminal motor organ).

There are several physiological tests of a crucial character by which the nature of the transmission of the impulse in *Mimosa* can be ascertained; whether it is dependent upon a movement of sap, or is a conduction of protoplasmic excitation. Sir J. C. Bose has been kind enough to offer me every facility for working in his Research Institute at Calcutta, and an account of the following experiments on transmission of excitation in *Mimosa* will doubtless be of interest to readers of NATURE. It may be stated that the series of experiments which I repeated were accomplished without a single failure. Limitation of space allows me to describe only one typical example of each series.

The experiments were carried out in winter (January 1929). Though the physiological condition of *Mimosa* was not so favourable as in summer, yet I encountered no difficulty in obtaining the following

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results in a green-house (temp. 30° C.) in which the sunlight was uniformly diffused by glass thinly coated with white paint.

EXPERIMENTAL SERIES 1. Discriminative Polar Action of Electric Current in Excitation.—In an animal nerve, a feeble electric current initiates excitation at the cathodic point at 'make' (there being no excitation at the anode); the transmitted excitation is detected by the twitch of the terminal muscle.

In the parallel experiment with *Mimosa*, I made suitable electric connexions with two opposite petioles at a distance of 20 mm. from the motile pulvinus. When the point on the right petiole was made the cathode, an excitatory impulse was generated which, travelling against the direction of the normal transpiration current, reached the pulvinus and caused the fall of the leaf after an interval of 1.5 sec. Making allowance for the latent period of the pulvinus, the velocity of transmission of excitation in this winter specimen was found to be 14.3 mm. per second. Reversal of the direction of the current by a Pohl commutator caused cathodic stimulation of the left petiole, resulting in the fall of that leaf.

Similar results were obtained with the secondary petiole of a leaf, in which the propagation of the excitatory impulse is exhibited by the upward closure of the sensitive leaflets (Fig. 1). Bose found that the

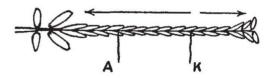


FIG. 1.—Effect of feeble current. K, cathode: excitation transmitted across feeble anode A. Arrows indicate directions of propagation of impulse which ultimately causes closure of all leaflets to right and left.

velocity of transmission in *thin* petioles is very much higher, being 100-350 mm. per second. My results fully confirm this.

It will be noted (1) that the impulse was transmitted in the complete absence of any hydromechanical disturbance; (2) that excitation was originated and conducted without any wound which might have induced the secretion of some hypothetical stimulant which could be translocated by the movement of sap; (3) that the direction of transmission of impulse was inwards, against the direction of the normal transpiration current; (4) that the speed of transmission was incomparably higher than that of the slow movement of sap; and (5) that the characteristic polar action of the current which initiates nervous impulse in the animal also caused an excitatory impulse in the plant.

EXPERIMENTAL SERIES 2. Arrest of Conduction by Anodic Block.—With feeble current, the impulse in the animal nerve is transmitted across the anode; but with a stronger current, the depression of conductivity at or near the anode is so great that the impulse is arrested by an anodic block.

In Mimosa, parallel effects can easily be demonstrated in the secondary petiole, conduction taking place in both directions as in the nerve. On starting a feeble current (1.4 microamperes), the cathodic excitation at K was transmitted (Fig. 1) to the right and to the left (across the feeble anode). The experiment was repeated with a stronger current (3.5 microamperes); the impulse initiated at the cathode K' was now transmitted to the extreme right end of the secondary petiole; whilst the impulse to the left was completely arrested at A' by the depression of conductivity caused by the stronger anode (Fig. 2).

EXPERIMENTAL SERIES 3. The Reflex Arc.--The phenomenon of the reflex arc is well known in the animal, where the afferent or ingoing impulse due to peripheral stimulation is reflected at a centre and is transmitted along a new path as an efferent or outgoing impulse.

It is very surprising that exactly parallel effects are observable in *Mimosa*. Peripheral stimulation of the

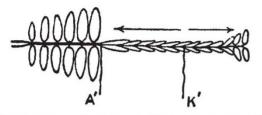


FIG. 2.-Effect of stronger current. Block at stronger anode A'.

secondary petiole (1) at S, by tetanising electric shock of moderate intensity (Fig. 3), gives rise to an ingoing or afferent impulse, which reaches the pulvinus and causes the fall of the leaf. After a short while, the existence of an efferent or outgoing impulse is detected by the serial fall, from base towards apex, of the leaflets on the secondary petiole (2). There is a marked difference between the velocities of the ingoing afferent and of the outgoing efferent impulses. Bose found it to be about seven times greater. In the experiments which I carried out I found it to be six to eight times quicker.

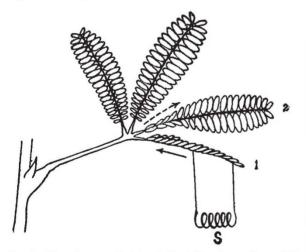


FIG. 3.—The reflex arc. Peripheral stimulation of secondary petiole 1 at S causes afferent impulse (continuous arrow), which after reflection at pulvinus gives rise to efferent impulse (dotted arrow) in secondary petiole 2.

As all the characteristic effects of the transmitted impulse in *Mimosa* are in every way similar to those of the nervous impulse in the animal, the most natural inference is that the process of transmission is of the same nature in both. Physiologists will therefore be inclined to agree with Bose's conclusion, that if the impulse be called 'nervous' in the animal, there is equal reason for applying the same term in the case of the plant.

Bose Institute, Calcutta, Jan. 29. HANS MOLISCH.

Growth-gradients and the Development of Animal Form.

D'ARCY THOMPSON in his "Growth and Form," Chapter xi., deals lucidly with the properties of logarithmic spirals, and the reasons for their frequent occurrence in organisms. He points out that for them to arise, (1) parts of the growing edge must be growing at different rates, the growth-rates of any two points on the edge preserving a constant ratio of growth-rates for so long as a regular logarithmic spiral is produced; (2) the growth-rate must fall off more or less steadily from one end of the growing sur-face to the other; (3) the products of growth must be laid on as so much dead matter, or at least matter incapable of further growth. In his own words (p. 500) the logarithmic-spiral form of an organic structure can be explained "if we presuppose that the increments of growth take place at a constant angle to the growing surface, but more rapidly at the 'outer edge ' than at [the ' inner edge '], and that this difference of velocity maintains a constant ratio. Let us also assume that the whole structure is rigid, the new accretions solidifying as soon as they are laid on."

It is, I think, worth pointing out that this and the type of growth which Champy (C. Champy, "Sexualité et Hormones," Doin, Paris; 1924) and I (J. S. Huxley, *Biol. Zentralblatt*, Bd. 47, p. 151; 1927) have called heterogonic (in which the size-relations of organs x and y can be represented by the equation $y = bx^k$) are both special cases of the same phenomenon, namely, of constant differential growth-ratios in different regions of the organism. The sole difference is that in logarithmic-spiral growth the increments produced take no further part in growth, but are locked up as so much rigid structure, while in hetero-gonic growth the increments are added to the mass of living tissue capable of continued growth. The difference is similar to that between two sets of sums of money growing at different rates of simple interest and at different rates of compound interest respectively.

There is a further interesting similarity between the two types of differential growth. In logarithmicspiral growth, the growth-rates fall off more or less evenly from one margin of the growing surface to the other. I have succeeded in showing (*l.c.* and unpublished work) that in markedly heterogonic organs such as crustacean chelæ (*Uca, Maia, Homarus, Eupagurus,* various prawns, etc.) the most rapid growth-rate is that of the penultimate joint, the growth-rates of the other joints falling off regularly as the body is approached. Similar facts appear to be true for the limbs of ungulates, according to my friend Mr. J. C. Hammond, and the abdomen of female spider-crabs (M. E. Shaw, *Brit. J. Exp. Biol.*, 6, 145; 1928). When, on the other hand, growth is isogonic, all the parts (joints of female chela, *Uca, Maia*; joints of male abdomen, *Inachus*) grow at the same rate.

As I previously pointed out, and as has been stressed by Pearsall (W. H. Pearsall, "Growth Studies." 6. "On the Relative Sizes of Growing Plant Organs," *Ann. Botany*, vol. 41, No. 163, pp. 549-556; 1927) in his analysis of similar heterogonic relations between the parts of plants, heterogony is really the simplest type of differential growth, occurring, namely, when the ratio of two growth-rates remains constant over long periods. It is interesting to find that one of the other most generally distributed modes of growth, that in the form of a logarithmic spiral, is deducible from the same principle. Various shells depart slightly from the strict logarithmic spiral; and various disharmonically-growing organs depart slightly from the accurate heterogonic formula. But this does not obscure the basic nature of the differential growthratio.

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