AT THE ROOTS OF PLANT NEUROBIOLOGY: A BRIEF HISTORY OF THE BIOPHYSICAL RESEARCH OF J.C. BOSE

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Sir J. C. Bose (1858-1937) is perhaps best known for his ingenuity and perspicacity in the field of microwave physics. Many of his inventions, including the first solid state semi-conductor diode, are now devices taken for granted in contemporary microwave technology. Bose turned his attention to the world of plants in the early days of the twentieth century, merging the boundaries of what had been quite separate disciplines, botany and physics, and establishing a nascent field of biophysics. The series of insightful experiments into life-processes of plants he began then would occupy him until his death, produce a prodigious body of published work, and see him transformed from a well-respected physicist into a controversial figure, a maverick, in the west. Seeking unifying principals underlying apparent disparities between animal and plant responses, Bose invented original and ingenious instruments that enabled him to simultaneously measure bioelectric potentials and to quantify very small movements in plants. Bose worked with touch-sensitive plants, including Mimosa pudica, with plants that perform spontaneous movements, such as the Indian telegraph plant Desmodium, as well as with 'ordinary' plants that made no obvious rapid movements.

The conclusions he drew from his experiments flew in the face of the emerging Victorian mechanistic materialist philosophy of science. Plants and animals share essentially similar fundamental physiological mechanisms. As do animals, plants co-ordinate their movements and responses to the world through electrical signaling. Rather than belonging to the category of passive automata, to which they had been consigned, Bose argued that plants are sensate, active, intelligent explorers of the world. He identified a fundamental physiological motif that interlinked measured pulsations or oscillations in cellular electric potentials with oscillations in cell turgor pressure, cellular contractility, and growth. All plants respond to the world and to other living things through this pulsatile motif, this electromechanical pulse.

Bose's conclusions that all plants possess a nervous system, a form of intelligence, and a capacity for remembering and learning, was poorly received by prominent electrophysiologists of the time. One hundred and fifty years after Bose's birth, concepts of kin-recognition, complex foraging strategies, intelligence, learning, and long-distance electrical signaling in plants are featured in the mainstream literature. Recent advances in both neurobiology and plant cell biology are uncovering some surprising similarities between plant cells and the neurons of animals. A relatively new discipline, plant neurobiology, now recognises plants as knowledge-accumulating systems that enact many of the same behaviours as do animals, despite lacking eyes, ears, or an obvious brain. Plant neurobiology now aims to understand how plants perceive, remember and process their experiences, coordinating their behaviours via integrated information networks, including molecular, chemical, and electrical levels of signaling.

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Introduction: The Roots of Plant Biology

In 2010 the field of research, called evocatively and perhaps provocatively 'plant neurobiology', aims to explain how plants perceive, remember and process their experiences of the world. From the perspective of plant neurobiologists, there is little doubt that plants, like animals, coordinate their responses to the world via integrated information networks, incorporating electrical, hydraulic and molecular levels of signalling[1] Plants are regarded as neuronal, knowledge-accumulating systems[2], organisms that recognise their kin[3,4], forage using trial-and error strategies rivalling those of certain animals[5], make choices and anticipate the future[6], modifying their behaviours according to past experience. 'Intelligence' may be hard to define, but few would disagree that it implies a capacity for sensing changes in the environment (information), for subsequently processing, integrating and evaluating sensory perceptions, and then, making choices regarding a course of action. In his series of eloquent, comprehensive and thoughtful reviews, Trewavas [7,8,9,10,11] builds a powerful case that, within these criteria, plants must be regarded as intelligent. The common assumption that plants are passive, insensate automata is wrong. Plants not only behave: their behaviour is intentional.

Over a century ago, Jagadis Chandra Bose (1858-1937, Figure 1), planted the seeds of contemporary plant neurobiology in contentious soil. After some years of researching plant behaviour and responsiveness, he stated "*…these trees have a life like ours…they eat and grow…face poverty, sorrows and suffering. This poverty may…induce them to steal and rob…they also help each other, develop friendships, sacrifice their lives for their children…*" (p46)[12].

Over a decade of research had established for Bose an enduring reputation as an inventor and physicist of extraordinary originality and perspicacity. Not only had he discovered millimetre waves, using ingenious devices of his own invention to generate them, but he laid bare most of their properties, and invented the 'eye' ('coherer') or receiver that would see them[13]. In the process, Bose published increasingly daring, original and inspired papers[13] in prestigious journals including *Proceedings of the Royal Society*, the "*Philosophical Magazine*" and "*The Electrician*"[13,14,15,16,17,18,19].

This research, applauded in its time, continues to inspire today. Concepts from Bose's 1897 Royal Society paper have been incorporated into the design of a 1.3 mm multibeam receiver, part of a 12 m telescope at the National Radio Astronomy Observatory in Tucson, Arizona. Bose's one patented invention, the Detector for Electrical Disturbances, was the first solid-state semiconductor diode detector, a galena crystal detector sensitive to microwave/ millimetre and optical waves[13,16,20]. Without semiconductors, today's world is truly unimaginable.

In around 1900, J.C. Bose began his plant electrophysiological research, becoming in the process one of the earliest biophysicists. He pursued this research until his death in 1937. His hard-won reputation as a physicist of surprising originality and insight was almost immediately overwritten, in Western botanical and electrophysiological circles, by a kind of notoriety, an image as mystic, maverick and outsider.

If there were two scientific Wests at this time- the first materialist, mechanistic, and colonial, and the second, vitalist, ecological[21] or organicist, the world of plant physiologists had polarised along these lines by the late 1920's into 'Bosephiles' and 'Bosephobes'[22]. The respect of 'Bosephiles' resulted in Bose being knighted in 1917, and elected a Fellow of Royal Society in 1920. The deep philosophical schism between the two scientific Wests contributed to the spread of 'Bosephobia' in other electrophysiological quarters.

We recall that late Victorian mechanistic materialism was developing as a philosophy at this time, and as a philosophy it impelled reductionist agenda, such that all living phenomena could be reduced to the laws of physics - as they were understood then. An analytic-summative philosophy of science became prominent along with the rise of industrialization, and it imbued biology with an idea that living things were machines - the *Bete Machine* of Descartes.

The schism between the scientific philosophies of the two Wests was later demonstrated in the famous debate between Bertrand Russell and Alfred North Whitehead, with Russell arguing, "life is matter-like" and Whitehead, that "matter is life-like"[23]. Similar philosophical views to Whitehead's were deeply rooted in the East, but stood in opposition to the mechanistic materialist philosophy that was beginning to underpin much of Victorian science. Whiteheadian process philosophy is still argued today, for example in the contexts of quantum physics and neuroscience[24].

In lectures at the Royal Institution and the Royal Society, Bose drew analogies between semi-conducting electric responses in metals, plants and muscles. Humans, animals and plants are members of a continuum of existence, he said, and this includes the inorganic world. There is no sharp demarcation between the realms of living and non-living[25]. Life did not emerge from lifeless matter. Rather, matter has life-like properties. As I have argued elsewhere[26] this philosophy was entirely compatible with Whitehead's process philosophy, but it was anathema to the mechanistic methodologies and philosophies that prevailed at the time.

In the audience were prominent electrophysiologists of the time, Sir John Burdon-Sanderson and Auguste Waller. Exponents of mechanistic materialist philosophy and methods, they aimed to make medicine scientific. Both were advocates of animal experimentation. During this lecture, both would become became powerful 'Bosephobes'.

Comparing his researches on properties of semi-conducting metals and plants, Bose reached a radical conclusion: "*…how can we draw a line of demarcation and say 'here the physical process ends and there the physiological begins?' No such barrier exists...the responsive processes in life have been foreshadowed in non-life …*" [25] and "*.... At the source of both the inner and outer lives is the same Mahashakti who powers the living and the non-living, the atom and the universe*" (p29)[12]. With respect to his pioneering studies on mechano-perception in plants, he made a generalisation: "*…every plant, and even the organ of every plant, is excitable and responds to stimulus by electric response…*"[25].

First, Burdon-Sanderson objected to the use of the word *response* in connection with metals[22]. Then, he insisted that ordinary plants did not have electrically mediated responses. Such responses were restricted to exceptional insectivorous plants, such as the Venus Flytrap, in which Burdon-Sanderson had himself discovered the plant action potential at Charles Darwin's behest. Auguste Waller did not comment, but not long afterwards, he published his own paper on electrical behaviour in plants, claiming priority for the discovery of "vegetable electricity". This resulted in a long-standing enmity between Bose and Waller, which has been insightfully reviewed [22].

Later, Burdon-Sanderson scathingly reviewed and recommended rejection of a *Mimosa* paper submitted by Bose to the *Proceedings of the Royal Society*. Despite Bose's formidable reputation as a physicist and inventor of enormous originality, Burdon-Sanderson was particularly critical of the unique and delicate instruments Bose had designed and used in his *Mimosa* work. Describing the incident, Paul Simons[27] writes of Burdon-Sanderson, "*Why he was so antagonistic amazes me. Was it professional jealousy because he himself had not investigated the Mimosa? Was it because Bose did not cite Burdon-Sanderson's paper on the Venus Flytrap*?"

Doubt was cast on Bose's professional competence and technical skill, Simons explains. Bose had controversially said that there was no demarcation between life and non-life, and in stark contrast to the prevailing mechanistic philosophy of the day, maintained that plants and animals possess essentially the same fundamental physiological mechanisms.

The Victorian science establishment in England simply could not abide those they perceived as mavericks. Burdon-Sanderson and Waller also had their hands full with the activities of the anti-vivisectionists, who claimed that using no anaesthetics failure to use aneasthetics during animal experiments was cruel[28]. Burdon-Sanderson's work may have contributed to the introduction of the Cruelty to Animals Act of 1876.

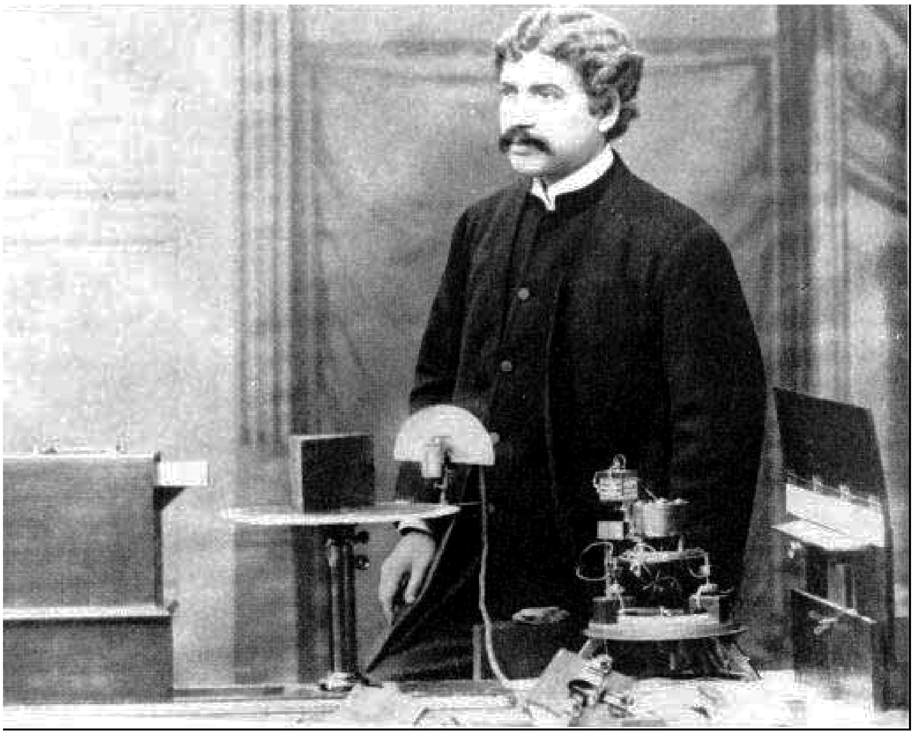

Figure 1. J. C. Bose at the Royal Institution, London, with his radio equipment. The date is 1897, prior to his plant research.

Yet, here was Bose, proclaiming "…. *the complex mechanism of the animal machine that has long baffled us, need not remain inscrutable for all time, since the intricate problems of animal life would naturally find their solution in the simpler vegetable life"*, which would mean "*very great advance in the sciences of general physiology, of Agriculture, of medicine and even of psychology*"[29].

Failure to accept Bose's *Mimosa* experiments as valid stalled research into plant electrical signalling for many years, according to Simons[27]. The discovery of chemical signaling via auxins in plants in the 1930's contributed to further reluctance to accept the coordinating role of electrical signals in plants. This reluctance did not begin to give way until the 1990's.

The Biophysics of Plant Behaviour and Responses

Bose argued that all plants co-ordinate their movements and responses to the environment through electrical signals and possess the equivalent of a well-developed nervous system. All plants have an electromechanical pulse, a kind of vegetable heartbeat, and are capable of intelligent behaviour, memory and learning.

Of the hundreds of intricate experiments using original and ingenious apparatus, reported in books, research papers and essays, I confine myself to those studies where Bose cleverly coupled specific plant behaviours with electrical and hydraulic signals.

Bose sought to establish that plants and animals share many behaviours in common. He carefully chose certain plants that enabled him to compare and contrast three kinds of responses. These were:

1. **Contractility (plant movements, following a stimulus) :** The *Mimosa*, or "touch-me-not" plant folds its leaflets and dips the entire leaf as a response to being touched.

2. **Rhythmicity (plant movements taking place automatically, analogous to a heartbeat[30]) :** The Indian Telegraph Plant *Desmodium* (Bon Charal or "forest churl") has a trifoliate leaf, whose two small lateral leaflets make mysterious spontaneous gyrations of regular period. In *Biophytum*, Bose found an instance of both 1 and 2. Stimulus-induced and spontaneous movements both took place in the same plant, depending on the strength of the stimulus and the individual's history (p289)[30].

3. **Conductivity (transmission of electrical excitation associated with plant movements) :**

As a contrast to the dramatic behaviours of motile or rhythmic plants, Bose also investigated quiescent vegetables- ordinary plants that made no obvious dramatic movements. These included *Chrysanthemum*, trees such as *Ficus*, *Nauclea*, the mango, monocotyledons including the banana (*Musa*), palms, and fruits and other organs, such as the tomato, turnip, carrot and potato.

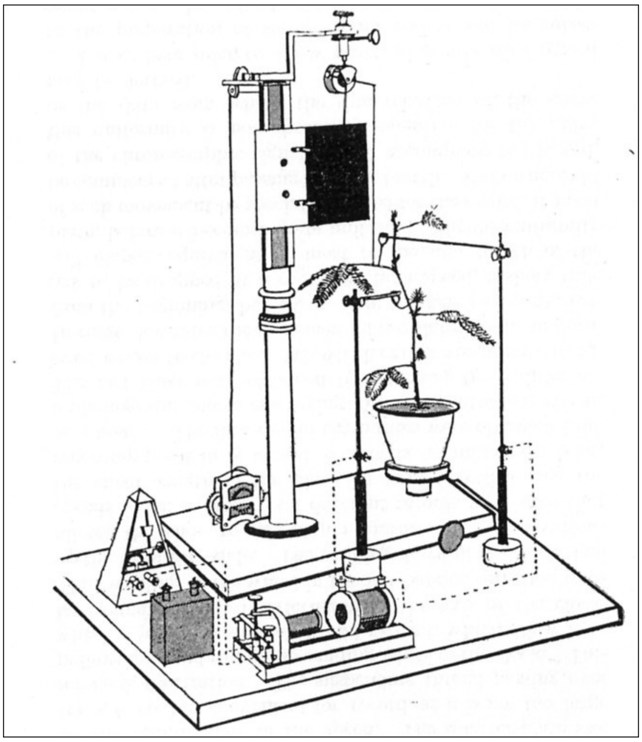

Figure 2. Some of Bose's equipment and some measurements he made with it

Fig 2 (a). The Resonant Recorder (reproduced from Fig. 4, Bose [30]). This device had "frictionless" jewelled bearings, a fine lightweight horizontal lever connected to the pulvinus or leaf, and a vertical lever for writing the response on a smoked glass plate, which moved at a uniform rate using a clockwork mechanism. In this configuration, the duration of an "induction shock" applied to *Mimosa* was determined by a metronome, which completed the electric circuit. The illustration shows a *Mimosa* plant ready for measurement of leaf movements.

Bose invented unique instruments for simultaneously measuring bioelectric potentials and for quantifying very small movements in plants (Figure 2 a-d, 3a-d). Many of these are still in working order, in the Bose Institute Kolkata. With its frictionless jewelled bearings, and lightweight aluminium lever connected to the leaf, The Resonant Recorder used a vertical lever to write leaf movements (plant response) on a smoked glass plate that moved at a regular rate using clockwork. The problem of friction of the writer against the smoked glass plate was solved by having the writer vibrate or resonate, making intermittent contacts with the plate (p55)[31]. Leaf movements were recorded with precision (~1/100th of a second intervals)- and "*the record is thus its own chronogram*" (p22)[30].

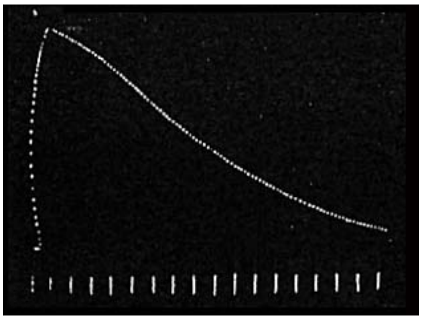

Fig. 2 (b). The record shows the leaf-dropping response in *Mimosa* made with the Resonant Recorder (reproduced from Fig. 14, Bose[30]). Dots are at 1/10 sec. intervals during the "contractile" or leaf-dropping phase and at 10 sec. intervals during recovery. Vertical marks, 1 min. intervals.

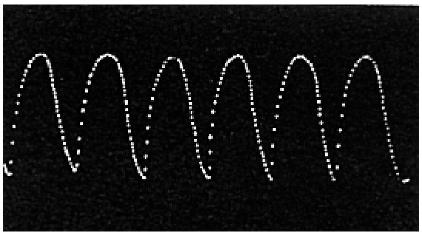

Fig. 2 (c). The rhythmic gyrations of the leaflets of the telegraph plant *Desmodium* (reproduced from Fig. 145, Bose[30]). Individual dots are 2 sec. apart. This leaf was measured in summer and the whole period is about a minute, although in winter this increased to 4-5 minutes.

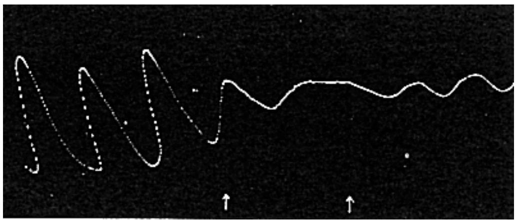

Fig. 2 (d). Arrest of spontaneous movements in *Desmodium* by a cut applied at the first arrow. The pulsatile movement was revived by an electric shock at the second arrow. An electrical stimulus could substitute for a mechanical one. (Reproduced from Fig. 145, Bose[30]).

Other extraordinary delicate instruments included the High Magnification Crescograph, with which one could measure tiny increments of growth at intervals of a second, the Electric Probe, an early intracellular microelectrode, the tip of which was in circuit with a galvanometer, and which could be advanced into plant tissue at extraordinarily fine intervals of 0.1 mm, and early microelectrodes. Electrical stimulation of different intensity were produced with an induction coil, using a slide (potentiometer) to generate feeble (0.5-8 μA) or strong (100 μA) currents. Plants appeared to be highly sensitive to electrical currents. For example, *Biophytum* responded to a feeble stimulating current of about 0.5 μA (p 27)[30], which was too feeble for his own tongue to detect[32]. The "*sensitiveness of Mimosa to electrical stimulation is high and may exceed that of a human subject*" (p51)[30].

His numerous experimental set-ups enabled Bose to perform complex experiments, which would be challenging to execute today. Bose could simultaneously measure plant movements and electric potentials, measure very small electrical oscillations, apply mechanical stimuli and electrical stimuli, vary hydrostatic pressures, apply chemical inhibitors or poisons (e.g. KCN, HCl, NH_4, H_2S, NO_2, SO_2, anesthetics such as chloroform and ether), suddenly modify temperature, vary light conditions, and measure tiny growth increments over very short time intervals.

Such experiments would be the envy of any well set-up plant physiological lab today, and the ingenuity with which they were executed makes us marvel no less than those earlier experiments into millimetre waves that had won Bose fame[13].

Plant Nervous System – The Mimosa and Desmodium Work

Intimate coupling of hydraulic and electrical signaling

Using this suite of techniques, Bose produced evidence that plants possess the equivalent of a well-defined nervous system.

Plants have receptors for stimuli, conductors (nerves), which electrically code and propagate the stimulus, and effectors, or terminal motor organs. The "*...physiological mechanism of the plant is identical with that of the animal*"…(p ix)[31]. "…*All plants and their organs are excitable, the state of excitation being manifested by an electric response of galvanometric negativity* [relative depolarisation]" (p95)[31]. "*It can only be in virtue of a system of nerves that the plant constitutes a single organised whole, each of whose parts is affected by every influence that falls on any other*" (p121)[30].

The motor organ in both *Desmodium* and *Mimosa* is the pulvinus, a structure subtending the leaf. Increase or decrease of turgor pressure in pulvinar cells causes the leaf to collapse or rise. One of Bose's remarkable discoveries was that an electrical or excitatory response decreased turgor pressure in the *Mimosa* pulvinus, followed by collapse of the leaves. Certain stimuli (touch, sudden temperature change, initiation or cessation of a constant current, induction shock) induced electrical excitation. Importantly, an electrical stimulus could substitute for a mechanical (touch) stimulus. From these results, Bose concluded that electrical signals (including action potentials) controlled leaf movements. The excitation was bipolar,

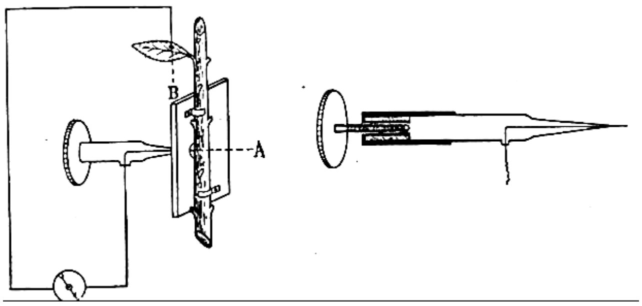

Fig. 3 (a). The Electric Probe (reproduced from **Fig. 75**, Bose[32]). The tip of the Probe was in circuit with either a sensitive or Einthoven galvanometer, and the device could be driven, by small (0.1 mm) increments into the tissue by turning the screw. Bose achieved remarkable precision of measurement-a deflection of 1 mm PD between electrodes was equivalent to a one mV deflection of the galvanometer. In some cases, he measured potentials as small as 0.1 mV. The tip of the probe enters at A, and a reference contact is made with a distant or dead leaf. The micrometric screw enables the probe to be gradually introduced.

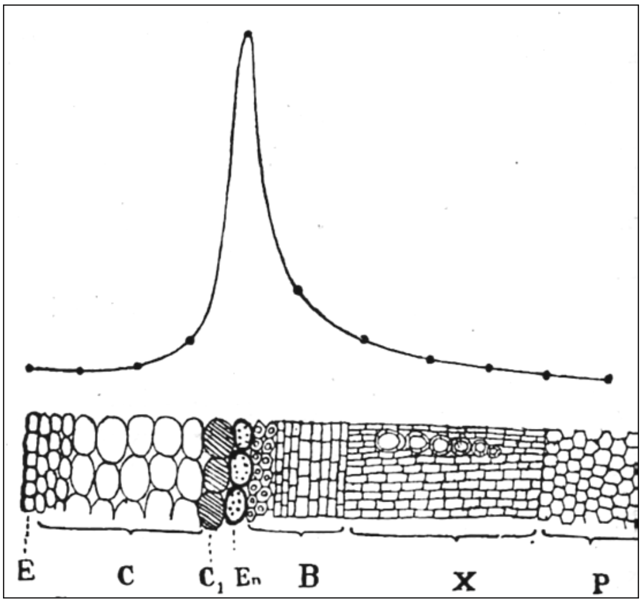

Fig 3 (b). A section of a *Brassica* petiole showing the relative cellular activity in terms of electromechanical pulsations. The pulsations occur mainly in the inner cortical layer abutting the endodermis. Reproduced from Fig. 77, Bose[32]).

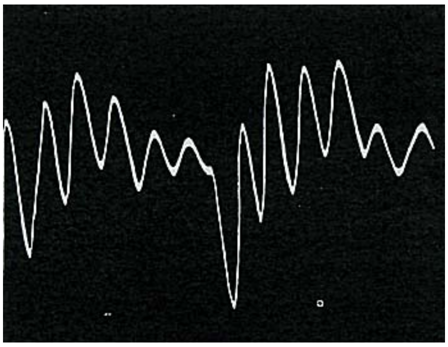

Fig. 3 (c). Periodic groupings of the electrical oscillations in the pulvinus of *Desmodium* (reproduced from Fig. 69, Bose[32]), which accompanied the mechanical oscillations of leaflet position shown in Fig. 2c.

moving both with and against the direction of the transpiration stream. Furthermore, the intensity of the stimulus impacted upon the response. For example, a moderate or short-lived light stimulus applied to the upper half of the leaf caused turgor pressure to increase, and leaves to lift. However, a strong light stimulus had the opposite effect, producing loss of turgor and an abrupt fall of leaves.

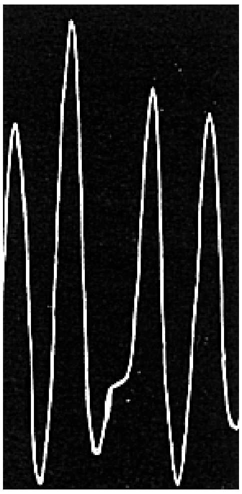

Fig. 3(d). Regular electromechanical pulsations in the cortical cells of *Musa*, the banana. Bose used an Einthoven galvanometer to measure the amplitude of these pulsations in *Nauclea* as ~ 0.4 mV, and lasting ~ 13.5 sec. Reproduced from Fig. 71, Bose[30]).

This led Bose to generalise that leaf-lifting was associated with increased turgor pressure, expansion of pulvinar cells, and "galvanometric positivity" [relative hyperpolarisation], whilst leaf collapse was a true excitation, a wave of "galvanometric negativity" [relative depolarisation], associated with loss of turgor pressure and contraction of pulvinar cells.

The hydraulic and electrical systems of a plant cell were therefore intimately coupled, Bose reasoned, and the plant nervous system was complex, with both sensory and motor components. Electrical propagation depended on living cells.

Using the Electric Probe, Bose identified the main conduction pathway or nerve, as the phloem. Staining with safranin and haemotoxylin revealed two phloem bundles, one internal and one external to the xylem (p34)[31]. Bose measured the velocities of excitations moving through the two phloem bundles, and found marked differences. These bundles, he reasoned, were the equivalents of sensory and motor nerves in the animal. The inner phloem conducted the fast motor impulse, and the outer, the slower sensory impulse (p189)[25].

A unilateral stimulus was conducted only on the stimulated side. On repetition of the stimulus, or upon increasing its intensity beyond a critical threshold, the slow sensory impulse was converted to a fast motor impulse in the pulvinus. The ascending impulse was then converted into a descending true excitation after crossing over at the apex of the stem (p42, 204)[31]. Stimulating the stem produced an electrical signal propagated to the leaves. Stimulating the leaves produced an electrical signal propagated to the stem, and then conducted both up and down, causing other leaves to collapse (p40)[32]. Electrical signals propagated preferentially from stem to pulvinus, and moderate stimulation of the pulvinus alone was not accompanied by collapse of the leaves (p44).

Thus, Bose reasoned, there must be the equivalent of a synapse between pulvinus and the stem. He wrote: "*The typical experiments…prove that conduction is irreciprocal. They also indicate the existence of a synapsoidal membrane, which by their valve-like action, permit propagation* [small to moderate stimulus] *in one direction only*" (p48)[31].

That the electric signal was a propagated protoplasmic excitation, as in the nerve of an animal (p20)[31], was demonstrated by employing a blocking current. Two electrodes were placed 5 mm apart in between the pulvinus and the point of stimulation, and a constant current was maintained between them (p29)[31]. This arrested signal transmission. Bose wrote: "… *in the contractile cells of the pulvinus…a wave of excitatory contraction passes from cell-to-cell at a rate slower than the nervous impulse. I distinguished this as cellular propagation of excitation. The phenomenon is not unlike the propagation of a wave of contraction from cell-to-cell in the muscles of the animal heart* (p91)[30].

Applying similar methods to the spontaneous leaf-movements in *Desmodium*, Bose found that these mysterious gyrations were due to rhythmic alternations between "galvanometric negativity" [relative depolarisation] and "galvanometric positivity" [relative hyperpolarisation] of pulvinar cell electric potential. These electrical oscillations or pulsations were of identical period to the changes in cell turgor pressure and coupled with it. When turgor decreased, "galvanometric negativity" (depolarisation) was recorded and leaves drooped. When turgor increased, "galvanometric positivity" (hyperpolarisation) was recorded, and the leaves lifted. There could be no more convincing demonstration that the hydraulic and electrical systems of the leaflets were coupled to drive *Desmodium*'s curious behaviour.

The leaflet gyrations were strongly temperature dependent, with a period of ~ four minutes in winter, and much faster, with a period of about one minute, in summer. The pulsations were "*…alternately rendered active or inactive above and below the critical temperature*" (p69)[32], influenced by light-levels, depressed or arrested if turgor pressure was reduced, inhibited by strong or repeated stimulus, arrested by large doses of anesthetic or poisons. Repeated stimuli led to fatigue and loss of response. Furthermore, the pulsations were arrested by short-length Hertzian waves; radio waves, possibly microwaves (p106)[32].

The excitatory response in *Mimosa*, and rhythmic leaf movements in *Desmodium* were both blocked by metabolic poisons such as KCN, $CuSO_4$, by sudden temperature change, and by anaesthetics such as chloroform. Just as strong electric stimulus of the pulvinus made *Mimosa* leaves dip, without mechanical stimulation, a cut in the *Desmodium* stalk prevented the rhythmic leaf movements, but these were restored by an electric current passing through the pulvinus (Fig. 2d).

The Electromechanical Pulse of Mimosa and Desmodium : From this comprehensive suite of experiments, Bose (p94)[30] generalised that all forms of significant direct stimulation produced a decrease in turgor pressure, a contraction of cells, a transient diminution of growth rate, a negative mechanical response (such as dropping of leaves) and a "galvanometric negativity" [relative depolarisation]. Subtle stimuli, on the other hand, produced directly opposite effects. Turgor pressure increased, cells expanded, and the growth rate transiently increased and a "galvanometric positivity" [relative hyperpolarisation] was measured.

Remarkably, growth itself was pulsatile. The High Magnification Crescograph showed that *Desmodium* grew with alternating spurts, and these spurts corresponded to the electrical pulsations, and a "galvanometric positivity" [relative hyperpolarisation].

Such was Bose's creativity and capacity for perceiving the holistic dimension, that he was able to synthesise his conclusions regarding *Mimosa* and *Desmodium* at a meta-level where electromechanical pulsations became a central motif at the heart of all plant behaviours. The key to this intuitive leap seems to be the two major findings:

1. Strong stimulation (of leaf or stem) in *Mimosa* induced a wave of protoplasmic, electrotonic excitation (electrical depolarisation), transmitted through the phloem to the pulvinus, where it caused turgor pressure to decrease, and the leaves to subsequently fall. However, subtle stimulus had the opposite effect, causing turgor pressure

to increase, and leaves to lift. There existed two nervous systems, a sensory (slow) conduction pathway, and a fast, motor pathway.

2. In *Desmodium*, subtle light stimulus induced rhythmic leaf gyrations, through alternate contraction and expansion (turgor pressure changes) of the pulvinar cells, associated with a corresponding electrical pulsation or oscillation.

Bose reasoned that the expansive phase was hydraulic, and the contractile, depolarising phase was nervous and electrical, a true excitation. The two were antagonistic (p255)[32]. As did animals, plant employed sensory and motor conduction pathways. Of these two forms of signalling, the first was essentially hydro-mechanical, and the second, a true, propagated excitation. The first could be converted into the second by a strong enough stimulus.

All Plants have an Electromechanical Pulse : Extraordinary plants such as *Mimosa* or *Desmodium* make striking and dramatic movements that easily catch the attention of a human observer. However, Bose concluded that *all* plants have an electromechanical pulse. All plants employ electromechanical pulsations in their active responses to the world. Thus, "*…the characteristics of the transmitted impulse as ascertained from the mechanical response of motile, sensitive plants find an exact parallel in the electric response of ordinary non-motile plants. They are in fact common to all plants…*" (p103)[30].

Bose found that cortical cells abutting the endodermis of ordinary plants (those not making obvious and dramatic movements) also exhibited electric pulsations or oscillations (p219)[32]. Using the Electric Probe, he measured electrical pulsations in field-grown tomato, vines, and potatoes, *Chrysanthemum*, banana, *Canna*, and trees including the mango and the Cadamba, *Nauclea* (p225)[32].

He found "*periodic mechanical pulsations corresponding to electric pulsations, as in Desmodium*" (p214)[32]. These pulsations he recorded on a photographic plate driven by clockwork, resulting in a galvanograph (Fig. 3c, 3d). The "galvanonegative" part of the pulsation Bose associated cellular contraction and turgor decrease, whilst the "galvanopositive" part was accompanied by cellular expansion and increased turgor.

In an extraordinary experiment, Bose connected the Electric Probe (and reference electrode) to trees 30 metres tall, wiring the signals to a sensitive Einthoven galvanometer, and measuring electric fluctuations of about 0.4 to several mV in amplitude in *Nauclea*. The period of the pulsations changed from 13.5 sec (for a complete pulsation) to 3 min., with increasing temperature (p214)[32]. The pulsations were subtle on cold mornings, maximal at noon, and changed in amplitude during the course of a day.

As with *Desmodium*, periodic mechanical pulsations, expansion and contraction, were directly coupled with periodic electrical pulsations or oscillations.

What was the explanation for these electric and hydraulic pulsations in plants making no obvious behavioural movements? The tension-cohesion hypothesis proposed by Dixon and Joly in 1894 remains the most widely accepted explanation of the ascent of sap. However, Bose did not believe that xylem water-columns could sustain the necessary tensile strength without forming air-bubbles (p2)[32]. He found, instead, the rationale for the electromechanical pulsations of cortical cells in the ascent of sap. This, he argued, depended on the activities of living, pulsating cells. All plants, including trees, had a kind of pulse, a rhythmic electrical oscillation accompanied by turgor increase and decrease in living cells, which propelled water upwards in the xylem. The xylem was a reservoir into which water was injected or from which it was withdrawn, according to the conditions, time of day, and temperature (p222)[32].

Fluid was injected into the xylem by expulsive contraction of cortical cells, but this could not happen if all the cells pulsed together at the same time. There had to be a phase difference of pulsations along the length of the stem. That is, the electromechanical pulsations must be peristaltic. The physicist Bose approached the problem by making a fixed electric contact with a stem, and then bringing the Electric probe progressively closer to it. Indeed, he found there was a certain distance apart at which the potential difference between electrodes was maximal, and another distance between electrodes where the PD was cancelled out. The distance at which the maximum PD was found equated to half the pulse width. Thus, the pulse width was about 100 mm in *Chrysanthemum*, 50 mm in banana, and 40 mm in *Canna* (p225)[32].

The pulse width depended on environmental conditions. It increased with sudden irrigation, when warm water was applied to the banana plant, and changed with passage of a constant electric current. The pulsation amplitudes increased with increased hydrostatic pressure, moderate constant current and increased temperature. They were arrested by a large dose of chloroform (which also arrested the ascent of sap), plasmolysis of the roots, a large drop in temperature, and poisons such as KCN.

Again, Bose made a generalisation on a meta-level. He wrote: "…*any agent affecting the pulsations induced corresponding effects in the ascent of sap*…" (p258)[32]. His theory of the ascent of sap, put simply, stated that successive periodic hydraulic waves (propagated waves of contraction preceded by waves of expansion) squeezed water upwards.

Thus, Bose argued, all plants employed a universal mechanism involving coupled electrical and mechanical oscillations, protoplasmic contraction and expansion.

He summarised his results, " …*expulsion of sap by cells of the pulvinus on stimulation is an essential part of its motile mechanism, and this applies also to the pulvinule of the leaflet of Desmodium in its 'spontaneous oscillation'…evidence has been accumulated…. that the active expulsion of sap by living cells is an essential part, not only of the mechanisms of movement, but also ...for the distribution of fluid throughout the plant*…" (p144)[32].

This implied cellular polarity. Comparing a tree to a bar magnet, with two poles at root and shoot, and an apparently neutral region in between, Bose reasoned that polarity operated at all functional levels of a plant. If a bar magnet is divided, the two parts both then show a north and south pole. So it was with plants, all the way down to the individual pulsating cell. All cells pulsed, and each "*must exhibit polarity, [one] end absorbing water, [the other] end excreting it*" (p192)[32].

The polar plant was divisible into quadrants. Its movements were not only up and down, but also clockwise and anticlockwise. Inventing a "torsional recorder", Bose investigated heliotropic movements. It seemed that the motor organ had four effectors, one for each of these directions. Plants were exquisitely sensitive to light and temperature, and "*a beam of light falling on the left flank of the pulvinus of Mimosa induces an anticlockwise torsion [and vice-versa]"* (p156)[31]. *Light applied to one side of the stem caused turgor to increase at the diametrically opposite point"* (p165)[31].

The heliotropic movements in the sunflower *Helianthus* are one of the most dramatic plant behaviours, especially viewed under time-lapse. Here, Bose identified the entire petiole as the motor organ. The sun-following movements were due to a fine interplay between contraction and expansion of cells on each side of the plant in relation to the direction of incident light. Of the leaf, Bose wrote "…*the leaf is...thus adjusted in space by the co-ordinated action of four refle*[31].

From his numerous experiments, Bose formulated an holistic concept of plant responsiveness in which all plants actively explore the world, and respond to it through a fundamental, pulsatile, motif. This involves coupled oscillations in electric potential, turgor (hydraulic) pressure, contractility, and growth. Plants coordinate their responses to the world through electrical signalling. All plants have an electromechanical pulse, a nervous system, a form of intelligence, and are capable of remembering and learning.

Advancing the view that plants are active, intelligent, capable of learning from experience and modifying their behaviour accordingly, Bose believed that his experiments had proved the "..*unity of physiological mechanism in all life. For we find, in the plant and in the animal, similar contractile movement in response to stimulus, similar cell-to-cell propagation of pulsatile movement, similar circulation of fluid by pumping action, a similar nervous mechanism for the transmission of excitation, and similar reflex movements at the distant effectors*" (271)[32].

Some Current Aspects of Plant Neurobiology

Plant neurobiology[1,33,34], as a relatively new and somewhat controversial addition to the discipline of plant sciences, aims to provide both a forum and a context for investigating the means by which plants perceive features of the world, transduce this information into electrical, hydraulic and chemical signals, and subsequently respond physiologically, morphologically, and behaviorally.

Rather than the traditional emphasis on differences between animals and plants, plant neurobiology is inclusive, focusing on similarities. Indisputably, animals and plants share major biochemical pathways, some neurotransmitters (including glutamate receptor-like genes), reproduce by similar fusion of gametes, develop immunity, and employ the same molecules and pathways to drive circadian/ chronobiological rhythms[33].

Plant neurobiology goes further still, asserting that the complexity of plants, whose capacities include making integrated responses to the environment, decision-making (e.g. the onset of dormancy or flowering, selection of prey by the parasite dodder), social learning, behavioural inheritance, and employing complex plant-plant, plant-insect and plant-animal communications, implies a far more sophisticated sensory perception than has hitherto been acknowledged[2].

As did Bose over a century ago, current plant neurobiology regards plants as active and exploratory organisms, capable of learning from experience and modifying their behaviour accordingly. Integral to this form of plant intelligence is the equivalent of a nervous system. Bose was the first person to use the term 'plant nerve', locating the nervous route for long-distance electrical signalling in the vascular tissue, specifically the phloem.

The use of terms such as ‘plant nervous system’, ‘plant brain’, ‘plant synapses’, ‘plant intelligence’ by plant neurobiologists has provoked some misunderstanding and controversy[35]. For this reason, Barlow[36] proposes adopting Living Systems Theory as a means for reconciling neural homoplasies between plants and animals. According to Living Systems Theory each level of biological organisation (e.g. cell, tissue, organ) is supported by a set of critical subsystems, which repeat at each level, building a ‘*self-similar organisational hierarchy*’[34].

The subsystems and the information they contain together assemble a particular level of biological organisation. At each of these levels the tasks of the subsystem is the same, but the elements that make up the subsystem and the means by which the tasks are accomplished are different, becoming more complex the higher the organisational level. Most of the twenty information processing subsystems are appropriate to plants, and at the organism level, the ‘channel and net’ subsystem, with its criterion of transmitting electrical signals (action potentials) throughout the body, is appropriate to plant phloem tissues (Bose’s ‘nerves’) and animal nervous tissues.

As Trewavas has pointed out, plant behaviour involves active phenotypic changes rather than the movements made by animals, although it is the latter that we have come to exclusively associate with intelligence. In his thoughtful reviews, Trewavas[7,8,9,10,37] shows us how biased is this concept of intelligence. Adopting a definition of intelligence from D. Stenhouse (*adaptively variable behaviour during the lifetime of an individual*), Trewavas gives numerous examples of plant intelligence involving growth and development. For example, roots navigate the maze of the soil, constructing a perspective of local space.

Plant roots recognise kin[3]. Plant roots actively forage, using strategies similar to those used by foraging animals. Whilst an animal is a single foraging unit with one mouth, the roots of an individual plant are repeated foraging units, capable of performing different behaviours simultaneously[5]. Plant mouths, as it were, are numerous and can act independently[5]. Plants learn through trial and error, have goals, assess and modify their growth behaviour. A kind of memory enables plants to anticipate difficulties, and to grow around them. As said earlier, plant behaviour is intentional.

In the presence of attacking herbivores, many plants ‘cry for help’ (reviewed, Dicke[38]) and enlist other organisms in complex behavioural strategies. For example, egg deposition by the pine sawfly induces the gymnosperm plant to release volatile chemicals that attract an egg parasitoid wasp[39]. Plants also communicate with each other via airborne chemicals, as in the now well-known example of prey selection by the parasitic vine dodder[6]. In the context of adaptive plant behaviours, the phytochrome pigments are now regarded as central organisers in phenotypic decision-making during shade avoidance[40]. Photosensory systems sensitive in the blue and red regions of the spectrum involve phototropin, cryptochrome and phytochrome pigment systems, and illumination with these wavelengths results in action potentials of 0.3 ms duration and 60 mV amplitude[41].

Plants are modular, constructed from multiple repeated units. Trewavas underlines the similarities between social insect colonies and plants. Both, he says, “…*gather information, evaluate, deliberate, form a consensus, make choices and implement decisions*…”. Trewavas[8,9] draws a powerful and profound analogy between the intelligence of plants and the swarm intelligence of a bee colony, a colony of mind[42,8,9]. A bee colony as a cognitive entity collects up-to-date information about the world, assesses this in relation to its own internal state, (thereby performing simple reasoning), and makes decisions promoting its well-being[42]. The argument that only animals with brains can be intelligent is, then, a form of brain chauvinism, argues Trewavas, and it endows animal nerves with a kind of vitalist quality.

More than a hundred years after Bose’s seminal work had fallen into disrepute, concepts of plant intelligence, learning, and long-distance electrical signalling are established in the mainstream literature of plant science.

In the rest of this paper, I will briefly outline some contemporary research that has since rediscovered or supported the aspects of Bose’s research discussed in this paper.

1. All Plants Employ Electrical Signalling as a Means of Transmitting Information about the World, and Responding to it : At the time of Bose’s death in 1937 electrical signalling in plants had become a marginalised topic. Why would plants, which lack eyes, ears, and obvious brain, and make subtle or very slow movements, require a nervous system? It was widely assumed that plants were simple automata, whose needs could easily be met by simple diffusion. Went’s identification of auxin (indole-acetic acid) in 1928 focussed attention on diffusive chemical signalling, the slowness of which matched the slow movements and passivity expected of plants.

By the 1970's and 1980's some plant electrophysiologists had built strong experimental and theoretical frameworks supporting the ubiquity of electrical signalling in plants. Action potentials, they argued (e.g. Pickard[43], Davies[44,45,46], Wayne[47] and Davies[48]) are multi-functional electrical signals employed by plants in actively constructing responses to the world. However, not until the 1990's, nearly a hundred years after Boses' research, did plant scientists embrace this view[49]. The critical role of electrical signalling was validated by Wildon *et al.*[50] who demonstrated that a flame wound activated proteinase inhibitor genes in distant tissues- not chemically, but electrically. The electrical signal was a slow-wave potential or variation potential, due to a hydraulic surge, rather than an action potential[46,48]. A similar flame-induced electrical signal transiently halts photosynthesis in *Mimosa pudica*[51].

In 2010 it is understood that most, and perhaps all plant cells are excitable, responding to stimuli such as heat, cold, wounding, touch, and changes in extracellular osmotic pressure with electrical signals. Signals may be restricted to a single cell (receptor potentials), transmitted over relatively short distances (variation or slow-wave potentials) or transmitted over long distances (action potentials). Plants, with their sessile habits, are fundamentally tactile organisms. As Bose had asserted over a hundred years ago, mechano-perception underlies many subtleties of plant behaviour, including responses to gravity, temperature, osmolarity, and turgor-controlled growth and development[52,53].

Action potentials are electronically transmitted at rates of at least 10-40 mm s^{-1} [47]. Bose found, in *Mimosa*, that velocity of electrical transmission was modified by "*…individual vigour…temperature, and by the season. In summer, the velocity in thick petioles is 30 mm/sec, in winter, as low as 5 mm/sec…*" (p63)[31]. Even the age of organs was important in determining the response; "*…It is impossible to dissociate from the consideration of the age of a leaf its previous history as regards the stimulus of sunlight…the uppermost or youngest leaf of Mimosa [is] pre-optimum and less sensitive...the sensitiveness…[reaches a] maximum as we descend lower...continuing to descend...excitability [is] progressively decreased…*" (p267)[30]. This individuality, along with aliasing and other experimental errors in sampling rates, may account for variability in reported rates of action potential transmission, as noted by[54]. Indeed, evidence suggests that plant action potentials may be transmitted much faster. For example, the uncoupler FCCP induces action potentials propagated an order of magnitude faster, at 40 ms^{-1} [41].

Today, an action potential is understood to be an abrupt depolarisation, induced by release of Ca^{2+} into the cell cytoplasm, activating Cl^- ion channels and voltage-dependent potassium K^+ channels. The result is an efflux of Cl^- and K^+ [47, 55], water efflux, transitory loss of turgor pressure[56] and a transitory contraction of the cell[57].

This motif (Ca^{2+} influx, K^+ and Cl^- efflux, contraction and turgor change) is fundamental to the osmotic machinery that enables plant movements[58]. In action, it mirrors Bose's electromechanical 'pulsations', which played an intrinsic role in plant behaviour. As Volkov *et al.*[54] put it, voltage-gated K^+ and Cl^- channels are the electrical starter of the osmotic motor in the *Mimosa* pulvinus.

2. Plants have Nervous Systems : Barlow's invocation of Living Systems Theory[34] solves the dilemma of attributing to plants a nervous system and brain. This issue has been contentious (e.g. Alpi *et al.*[2]), but no-one is saying that axons exist in plants or that roots contain tiny brains. From a Living Systems perspective, we can say that plants and animal share certain neural homoplasies.

What of the two nervous systems, sensory and motor, that Bose had proposed? Plant neurobiology acknowledges the existence of three kinds of neural-like pathways. First, as proposed by Bose, there is a pathway comprising phloem sieve tubes and their companion cells[46], through which electrical action potentials are transmitted.

Second, is the pathway comprising (non-living) xylem elements and their accompanying living xylem parenchyma, through which travel the variation (slow-wave) potentials-hydrostatic signals or pressure waves[43]. These, as Bose had argued, can induce electrical depolarisation of living parenchyma cells. Slow- wave potentials are induced by more severe damage (flame wounds, *etc.*). Similarly, the so-called receptor potential is a small depolarisation brought about by mechanosensory ion channels, and occurs in response to touch stimulus[59]. It is graded according to stimulus intensity, and does not travel from cell-to-cell. When a critical depolarisation threshold is reached, the receptor potential initiates an (electrical) action potential, which then moves intercellularly. Reducing turgor pressure alters the magnitude of the receptor potential for a given stimulus, but not the threshold for the action potential[60,61,62].

The third neural-like pathway in plants, as postulated by Baluska *et al.*[63], is the 'plant brain', the transition zone of roots, where actin-enriched fields of cell-to-cell communication channels (plasmodesmata) at the end-poles of cells act as synaptic connections. Synapses in this region confer on the root apex the properties of a 'brain', or command centre, where incoming sensory signals are processed[34,36,64,]. '*Higher plants show neuronal-like features in that the end-poles of elongating plant cells resemble chemical synapses*'[52,53].

We recall that Bose had argued for the necessity of such synaptic polarity in cell-to-cell signalling in plants, comparing a tree to a bar magnet, with two poles at root and shoot. In plant neurobiological terms, plants stand upon their heads[33]. The root apex contains plant command centers, or the 'plant brain', whilst the shoot apex, with its respiratory and reproductive organs (leaves and flowers) is the posterior pole of the body. Complex social interactions between plants, plants and fungi and plants and bacteria, are mediated primarily through the roots[33,64,65.]

Ironically the plant growth regulator auxin (indole-acetic acid) that dominated the field of plant chemical signalling, is now regarded as being a plant neurotransmitter. Polar auxin transport has much in common with synaptic signal transmission in excitable animal tissues[63]. Plants show neuronal-like features in that the end-poles of elongating cells resemble chemical synapses. Thus, auxin is thought to be secreted from cell-to-cell, neurotransmitter-like, via vesicle trafficking. The end-to-end polarities of root apical cells, the enrichment of the end-poles with the cytoskeletal protein actin, and the cell-to-cell communication channels (plasmodesmata) at end pole walls linking adjoining cells, constitute the synapse-enriched brain-equivalent of the root.

3. Plants Remember and Learn- the Basis of Plant Learning : How is it possible for plants, which lack an obvious brain and the capacity for rapid movement, to foresee, remember, plan and respond? The current view is that calcium signalling, involving electrical signals, underlies plant responsiveness. This involves chemical signalling also, for calcium is either an agonist or antagonist of all plant growth regulators, including auxin[66]. Hhow can calcium, a mere divalent ion, control such complex processes? [67,68] and[69] propose a neural net concept of Ca^{2+} signalling as the basis of plant learning and intelligence. Electrical signalling systems (e.g. action potentials) that release calcium confer on plants the potential for computation, learning and memory. Changes in cytoplasmic Ca^{2+} are the basis of the intelligent system, not through Ca^{2+} diffusion, but through propagated waves of Ca^{2+} release. Plant cells potentially compute, remember and learn, through a Ca^{2+}-based neural net system[67,68,69].

Calcium channels, located in plasma membrane, vacuolar and endoplasmic reticulum membranes, are envisaged as a network. Signals initiate a biochemical cascade (the inositol triphosphate or IP_3 cascade). The Ca^{2+} channels are activated only when both IP_3 and Ca^{2+} bind to them. The released Ca^{2+} opens further calcium channels, as in a Mexican wave amongst spectators at a football match. The Ca^{2+} waves are spatially structured. Waves propagate only in specific directions whilst others are inhibited. The IP_3- sensitive channels act as a coincidence counter. Stimulus induces Ca^{2+} oscillations in plant cells[70]. Calcium oscillations reflect co-operative integration of the behaviour of many IP_3-sensitive channels, and each Ca^{2+} channel or cluster of channels is the equivalent of a node in a neural network.

Each is a switch which can direct the flow of information, block or pass signals that arrive at the same time, and behave as an AND/OR logic gate. Trewavas argues that this Ca^{2+}-based neural net is a means for computing, remembering and learning that is unique to plants. It accelerates information transfer and it can be reinforced. Repeated signals make the path more sensitive whilst too many signals inhibit it. A similar Ca^{2+} signal can have different effects in different cells, which thereby remember previous experience, and know where, and what, they are.

4. Mimosa and Desmodium Literature Today : That the phloem tissue is the major conduction pathway for action potentials is now strongly supported by contemporary *Mimosa* researchers[54]. The classic papers of Fromm and Eschrich[71,72,73] demonstrated conduction of excitation within the phloem, and furthermore, that decreased pulvinar turgor is accompanied by phloem depolarisation and expulsion of Cl^- and K^+ as well as a sudden unloading of sucrose [71,72,73]. The contractile actin-myosin system is indeed involved in the collapse of the leaves, and in the spontaneous movements of *Desmodium*[74]. Motor cell movements in *Mimosa* are inhibited by drugs that affect the actin-myosin system involved in cytoplasmic streaming in plants, and in muscle contraction. The contraction in *Mimosa* is similar in some ways to muscle contraction[27].

In the 1990's, elegant experiments of Antkowiak *et al.*[75], Antkowiak and Kirschfeld[76] and Antkowiak and Engelmann[77] proved *Desmodium* leaflet gyration is indeed coupled with rhythmic changes pulvinar cell turgor pressure, and these in turn are coupled with rhythmic oscillations of membrane potential difference[77]. Using ion-sensitive H^+ and K^+ extracellular microelectrodes as well as intracellular microelectrodes, they showed that the leaflet downstroke was coupled with depolarisation of pulvinar motor cells, and increased apoplastic K^+ concentration. The cells contracted, losing turgor. Leaflet lifting occurred when pulvinar motor cells were hyperpolarised, apoplastic K^+ concentration declined, the external PD was positive, the cell expanded, and turgor pressure increased[75,77]. Like Bose, Antkowiak *et al.*[75] found that increased temperature shortened the period of the oscillations, and an anesthetic (enflurane) abolished the movements[76]. Pulsed radio-frequency fields do transiently alter the amplitude, period and phase of the leaflet rhythms in *Desmodium*[78].

Many researchers have confirmed the links between rhythmic changes in cell volume, influx and efflux of water, and rhythmic changes in cell electric potential difference. Mitsuno and Sibaoko[79] found that inhibiting oxidative phosphorylation in *Desmodium* arrests its pulsations, as Bose had found. Vanadate, an inhibitor of the electrogenic ion pump, also inhibits the pulsations, suggesting that an electrogenic pump is rhythmically altering its activity. Furthermore, electric oscillations are coupled to growth oscillations (or pulses) in roots[80], where oscillatory patterns of H^+, K^+, Ca^{2+} and Cl^- influx[81] represent ultradian oscillations in nutrient acquisition. These authors argue that the plant proton pump must therefore operate rhythmically.

Bose's identification of a fundamental motif in plant behaviour, coupled electromechanical oscillations, has thus been amply vindicated.

5. The Hydro-electrochemical Pulse of Plants : What of Bose's conclusion that *all* plants employ this fundamental behavioural motif, and not only those special plants performing dramatic movements? Using a similar experimental set-up to Bose, Gensler and Diaz-Munoz[82] and Gensler and Yan [83] measured electrical pulsations in ordinary crop plants. With a palladium electrode inserted in the stem, and a reference palladium electrode in the root zone of tomato plants, they measured a large stable, and reproducible potential difference (~ -400 mV) and recorded characteristic potential/time fluctuations, which they called electrophytograms[83]. These strongly resemble Bose's galvanographs. The authors commercialised the method as a means for assisting agriculture, enabling the prediction of changes in water status or determining optimum times for watering.

The Gensler pulsations changed according to the condition of the plant, its water status, atmospheric changes, and the time of day, and did appear to be related to the ascent of sap. With an electrode in the stem, and a reference electrode in the root zone of cotton plants, these researchers simultaneously measured apoplastic electropotentials and stem diameter before and after rainfall and irrigation. Stems contracted during the day and expanded at night, coupled with a decrease and increase of electropotential. Following irrigation stems expanded and the electropotential declined.

In mature trees, variations of electric potential in the bole of trees are linked not only with daily photoperiods, but also as 'stem tides', with lunar periodicities[84]. This correlation suggests that the Moon is influencing the flow of water between different parts of the trees [85,86], although it is not known how plants might detect lunar periodicities. The measured electrophysiological oscillations or noise spectra also bear a strong resemblance to Bose's galvanographs.

Recently Wagner *et al.*[87] suggest that a diurnal rhythm in surface potential fluctuations represents integration of the metabolic activities of plants on a hydraulic-electrochemical level. Hydraulic changes at the shoot apex prior to initiation of flowers imply hydro-electrochemical communication between leaves, the shoot, and the root system and a specifically timed electrical signal could substitute for photoperiodic flower induction[87].

Another interpretation of some of the (small amplitude) electrical oscillations Bose measured lies in geomagnetic pulsations. Minorsky[88] relates small amplitude low frequency (~ 0.1 to 0.25 mV, 0.1 to 10 Hz) oscillations in trees to geomagnetic pulsations, for which trees can act as antennae. In this case, they are not generated by the tree but rather the tree receives and expresses them.

Under the terms of the current tension-cohesion hypothesis, there is no obvious explanation for the 'electrophytograph'- type oscillations in electric potential measured by Bose and contemporary authors. The question of whether living cells are involved in the ascent of sap is unresolved, although mainstream opinion on the whole concludes not. Are electro-mechanical pulsations associated with the ascent of sap? According to Laschimke *et al.*[89], water may travel through the xylem in peristaltic waves, and gas bubbles behave as a hydro-pneumatic system that cyclically stores and releases energy.

Conclusion

All science is philosophically informed. A great gulf separated Bose's philosophy of science from that of the leading English electrophysiologists of his day. At least three philosophical movements, mechanistic materialism, vitalism, and organicism, informed the Western science and its experimental methodology at that time. Bose's detractors, Burdon-Sanderson and Waller, were firm adherents of mechanistic materialism. The reductionist experimental methods accompanying this philosophy involved deconstructing biological forms into simple parts, which could then be analysed. From this supposedly ultimate physical level could then be reconstructed the properties of the whole[90]. In such a conceptual framework, a living thing was, in essence, 'nothing but' the sum of its parts- a machine, in other words - Descartes' '*bete machine*'[91]. Crucial to this philosophy was the view that living things are passive, tossed about by the physical and chemical features of their environments like "…*passive flotsam on a physico-chemical ocean…*", in the memorable phrase of Agutter *et al.*[92].

Bose's insistence on the unity of the living and non-living arose from his deeply-held philosophical position[22], *Vedanta* in inspiration, a monism that regarded the world as a single unified entity[21] where mind and matter were aspects of the one thing. As attempts at uncovering this unity, Bose's experiments were holistic investigations that revealed plants as active, exploratory organisms, capable of perceiving the world and integrating their responses to it through electrical signalling networks mediated by a nervous system.

From the perspective of 21st century plant neurobiology, plants are no longer to be viewed as passive automata but as active agents with a capacity for recalling and predicting the world. Over a century ago, J.C Bose advanced the view that plants have a nervous system, as well as a capacity for learning, remembering, and actively responding to the world. According to Ballare and Trewavas[11], the study of plant behaviour has now not only come of age, but understanding its complexity will be the most important task of plant biologists in this century.

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