ON THE NERVOUS MECHANISMS OF PLANTS

V.A. SHEPHERD*

Science has under-estimated plants. Neurons, a large brain, and the ability to rapidly move are widely regarded as requisites for intelligent and adaptive behaviour. The sessile, slow-moving plants lack these structures and capacities. Nonetheless, plants share neural homoplasies with animals, including a simple form of nervous system and integrative centres or root-brains. Plants employ long-distance electrical signals (action potentials) transmitted via phloem tissues, and local electrical signals (variation potentials) when responding to the environmental exigencies to which they are captive. Evidence is growing that plants possess distributed swarm intelligence, embodied cognition, and purposive, intentional behaviours. Sir J. C. Bose (1858-1937) was a pioneer of this field. He invented unique instruments for measuring bioelectric potentials and for quantifying subtle movements of plants. He concluded that plants have a form of nervous system, and coordinate responses to the environment through electrical and hydraulic signalling. He identified pulsatile rhythmic oscillations in electric potential, turgor pressure, contractility, and growth as motifs elemental to plant behaviour. He recognised that phenotypic plasticity is the key to the adaptive behaviour of plants. He regarded plants as possessing simple intelligence, memory and purposeful behaviours. On the centenary of the establishment of the Bose Institute, this article reviews Bose's legacy in the field of plant signalling and behavior — a legacy that continues to grow— and situates his work in the context of current research.

Introduction

Science has under-estimated plants : Until recently, science has treated plants as insensate automata. As motile animals, we solve problems by moving away from them. We have assumed that neurons, a large brain, and the ability to rapidly move are requisites for intelligent and adaptive behavior. Measuring plants against our own structure and capacities, we have found them wanting.

However, sessile plants are obligate problem solvers. Both roots and leaves actively forage for resources. Roots succeed in mining for water and mineral nutrients in the same place for hundreds or thousands of years[1]. Through photosynthesis, plants are the major portal by which energy enters our biosphere, around 50% of which occurs in the oceans. On land, leaves position themselves to harvest light energy. A tree crown changes its shape if overgrown, implying that the cambium possesses a map of the outside[2]. Plants deploy both electrical and hydraulic signals between roots and leaves to regulate photosynthesis according to the amount of water accessible to roots[3], solving problems of perception, integration and cost-benefit analysis.

Plants are supracellular. The cytoplasm, continuous through plasmodesmata, constitutes an interconnected body-wide network contained within cellulose walls. Vacuoles generate turgor pressure by swelling or shrinking against the cell wall. Regulation of turgor pressure by electrical signals including action potentials (APs) and variation potentials (VPs) drives the osmotic motors that enable the plant movements and growth integral to much behaviour. Plants lack neurons. Neither do they have the aggregated

* Faculty of Science and Health Science, Western Sydney University, Nirimba Campus, Quakers Hill NSW, 2763, Sydney, Australia. email : v.shepherd@westernsydney.edu.au

mass of firing neurons that is the structural basis of a brain. Yet, plants employ electrical, hydraulic and chemical levels of signaling appropriate to their body plans and mode of life.

Plants have a modular construction. They are assembled from many repeating and self-similar parts. This is due to meristems, cells that are able to differentiate into new cell types. Of these, the root pericycle produces new lateral roots, the cambium of trees produces new vascular elements (xylem and phloem), and the apical or shoot meristems produce new shoots and leaves. Modular construction enables replacement of damaged parts, whereas a damaged organ could be fatal for an animal. Meristems confer on sessile plants a morphological plasticity, an ability to respond to the environment through spatial and temporal regulation of growth patterns. The functions we attribute to our single or double organs are distributed throughout the entire modular plant body. Plant intelligence is likewise distributed.

That wild plants possess a 'green intelligence', with the capacity for remembering, learning, predicting the future and responding adaptively, has become the focus of new research[2,4]. The distributed intelligence of plants involves complex networks that control their own behavior via feedback and feedforward controls. Trewavas[5,6] has likened this intelligence to the swarm intelligence of insect colonies. Both modular plants and social insect colonies"…*gather information, evaluate, deliberate, form a consensus, make choices and implement decisions*…" without the necessity for a central controller or single large brain.

As with a colony of bees, the world for plants is a perceptual mosaic that includes resources for foraging. Each of the interconnected modules has its own ability to sense and respond to its local environment. Short and long-distance electrical (nervous) and hydraulic (fluid) signals between interconnected modules coordinate adaptive responses by the whole plant in the mosaic of its entire environment[7]. Sessile plants perceive, integrate and respond to a growing list of environmental signals (at least 22 different types[8]) and to some with greater sensitivity than animals. Plants sense and respond to the touch of the wind or a feather, the passage of clouds overhead, subtle geomagnetic disturbances, the lunisolar gravitational force, the gravity vector, temperature, light and seasonal changes in photoperiod, electric fields, wireless signals, pH, salinity, water, oxygen levels, possibly sound, and finally their whole form. Plants recognise self and kin, aggressively compete with non-kin, employ trial-and error strategies when foraging, make choices[9] and possibly show anticipatory behaviours, a hallmark of intelligence (Calvo and Baluka 2016). Plants enlist or manipulate other organisms in complex behaviours[2,10]. The behaviour of plants is intentional and purposive.

Philosophers have now entered the literature of plant intelligence, arguing that plants display minimal embodied cognition[11], and arguably some levels of consciousness[12,13].

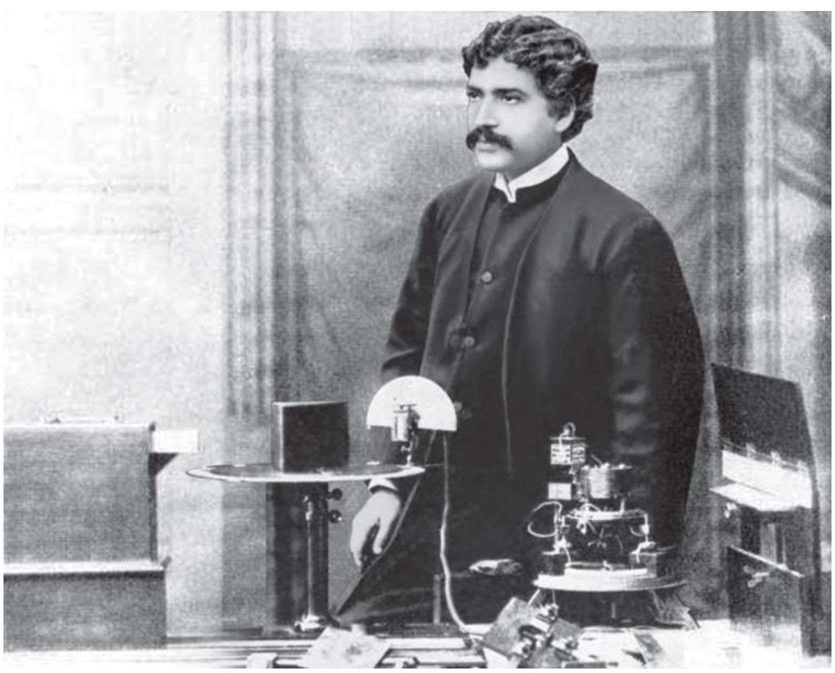

Figure 1. J. C. Bose at the Royal Institution, London, with his radio equipment. The date is 1897, prior to his plant research.

Who Was Sir J.C. Bose?

Sir J.C. Bose was one of the first modern Indian scientists. His life and contributions to microwave physics have been reviewed in[14] and in Sen Gupta (this issue). In plant biology, Bose has been viewed both as the "… *lonely Indian David fighting a Goliathal British establishment …the pitting of the colonised against the coloniser*…"[15], and as having over-stated, misinterpreted, or at least carelessly executed, his research (Nandy 1995). Plant researchers had polarised along similar lines into "Bosephiles" and "Bosephobes" by the late 1920s[15]. In the 21st century, Bose's plant research has achieved recognition. In his comprehensive volume 'Plant Behaviour and Intelligence',Tony Trewavas, FRS, cites J.C. Bose alongside

Nobel prize-winner Barbara McClintock and Charles Darwin as systems thinkers who inspired his own integrative studies of plant signaling and behavior : "…. *Bose was one of those early, superb scientists that with almost no facilities to hand, constructed equipment that produced a wealth of scientific information far ahead of his times.*"[2].

Bose believed that he had proven the "*...unity of physiological mechanism in all life… 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*"[16]. Poorly received in its day and in succeeding decades, Bose's conclusion that the slow-moving wild plants coordinate their responses to the world through both electrical (nervous) and fluid (chemical) signals was indeed pioneering. In a prolific output of books, research papers, essays, lectures and public presentations, Bose argued further that plants show meaningful, adaptive behaviours if we know how to look for them. Plants have agency, simple intelligence, the ability to learn and to respond adaptively. All plants sensitively explore the world, responding to it rhythmically through coupled oscillations in electric potential, turgor pressure, contractility, and growth. Of trees, J.C. Bose wrote "…*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*…"[18].

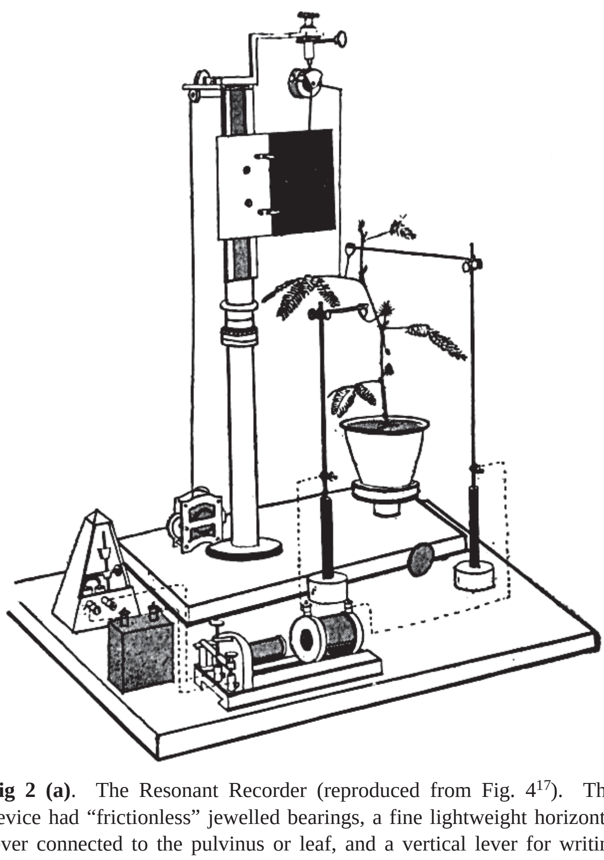

Fig 2 (a). The Resonant Recorder (reproduced from Fig. 4[17]). This device had "frictionless" jewelled bearings, a fine lightweight horizontal lever connected to the pulvinus or leaf, and a vertical lever for writing the response on a smoked glass plate, which moved at a uniform rate using a clockwork 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.

Today, the International Society for Plant Signalling and Behaviour (http://www.plantbehavior.org/) focuses on the fascinating field in plant biology, which seeks the physiological and neurobiological basis of adaptive behavior in plants. In his inaugural address to the Bose Institute, Bose had said "…*this alternating yet rhythmically unified interaction of biological thought with physical studies*…" would enable researchers to "…*winnow old knowledge with finer sieves, to research it with new enthusiasm and subtler instruments*"[19]. The Bose Institute was to inspire scientists from all over the world, especially the young, to devote themselves to research in this biophysical and integrative vein.

Beginnings: Bose in Context—Background and Philosophy

I have previously reviewed aspects of J.C. Bose's biophysical research, and told something of his story[20-23]. Clearly, interest in J.C. Bose has not flagged. Plant electrophysiology has come a long way, yet the pioneering concept that plants have a form of nervous system still provokes resistance[24] whilst stimulating the investigative imagination of scientists[25].

Jagadish Chandra Bose (1858-1937) was born into turbulent times. In 1857, the Government of India Act brought India under direct British rule, and this Raj persisted for another 90 years,ending in partition, leaving in its wake 11 famines with up to 35 million dead from starvation, a population in which 84% of people were illiterate, and India reduced to penury[26]. A leading figure in the Bengal Renaissance, Bose studied physics, botany and physiology at Christ's College Cambridge, the first College to admit Indians.Mentored by teachers including Lord Rayleigh and Professor Sidney Vines, he returned to India in 1884 as Junior Professor of Physics at Presidency College, Kolkata. Presidency College lacked research facilities and, as an Indian, Bose was expected to accept a reduced salary. After ten years of teaching, Bose converted a tiny room into a laboratory, and began experiments into microwave optics[27,14] and in this issue. Bose proved to be an extraordinary inventor and experimenter. Respected by physicists of stature (e.g. Rayleigh and J.J. Thompson), he invented the first solid-state semiconductor diode detector[28]. Some of his turn-of the-century inventions later found application in the design of a radio telescope[29] .

Why did he turn his attention to plants? Mechanistic materialist philosophies had begun to influence physiology with the physicalist doctrine that organisms are deterministic machines, ultimately reducible to purely physico-chemical phenomena. Research was to deconstruct organisms to the laws of physics and chemistry — as these were understood then. Humans alone were conscious, imbued with mind, agency (some more than others) and able to experience pain. This reflected an even older concept. The inviolable 'great chain of being' was a hierarchical ordering of earth and universe, with God at the top, and successively lower rungs occupied by angelic beings, rulers, descending ranks of humans, down through animals to plants and then metals, minerals and rocks. At the borderland between the living and non-living, plants grew and reproduced but lacked agency, whilst metals, minerals and rocks simply existed.

Bose did not believe in the sharp demarcation between the living and non-living. Humans, animals and plants were part of a continuum of existence that included the inorganic world. Matter had life-like properties; "…*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* …"[19]. This monistic philosophy treated the world as a single unified entity[30], where mind was not separate from matter, intelligence was a continuum, and where electrical signaling was fundamental — "… *this characteristic of exhibiting electrical response under stimulus is not confined to animals, but extends also to vegetable tissues. In these the same electrical variations, as in nerve and muscle were obtained* ….

There were two scientific Wests — the first, materialist, mechanistic, and colonial, and the second, vitalist, and ecological[30]. Some Western contemporaries held related philosophies, not necessarily vitalist. Alfred North Whitehead, mathematician and process philosopher, argued that 'matter is life-like' and even protons had a level of experience. Henri Bergson, process philosopher and vitalist, reasoned that consciousness was in principle coexistent with life. Charles Sanders Peirce argued that matter itself is a condensed form of mind[31]. In a sequence logical to his monistic world-view, Bose investigated microwave physics, responsiveness in metals, and the responsiveness of plants.

Falling Afoul of the Mainstream

Bose began his plant research in 1900 and continued until his death (1937). He fell afoul of leading physiologists of the day, Sir John Burdon-Sanderson and Auguste Waller. Both belonged to the materialist, mechanistic tradition, and both attended a fateful meeting of the Royal Society in June 1901, where Bose pronounced that metals responded to stimuli, and furthermore claimed discovery of 'vegetable electricity'. "…*every plant, and even the organ of every plant, is excitable and responds to stimulus by electric response*…"[17]. As a pioneer of plant electrophysiology Burdon-Sanderson objected that electrical signals are restricted to rare and unusual plants, and metals do not 'respond'. Shortly afterwards Waller published a paper also claiming priority for the discovery of 'vegetable electricity'.

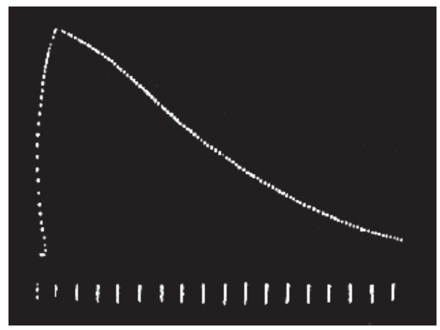

Fig. 2 (b). The record shows the leaf-dropping response in *Mimosa* made with the Resonant Recorder (reproduced from Fig. 14[17]). Dots are at 1/10 sec. intervals during the "contractile" or leaf-dropping phase and at 10 sec. intervals during recovery. Vertical marks, 1 min. intervals.

Dasgupta[15] gives a balanced review of the clash between Waller and Bose. A committee of the Linnaean Society granted Bose priority, but Bose had made professional enemies. Doubt was cast on his competence and he was branded an unreliable mystic[32] — this was after all the heyday of the British Raj. In his Inaugural address,[19] said, "…*I had unwittingly strayed into the domain of a new and unfamiliar caste system… offended its etiquette…an unconscious theological bias was also*

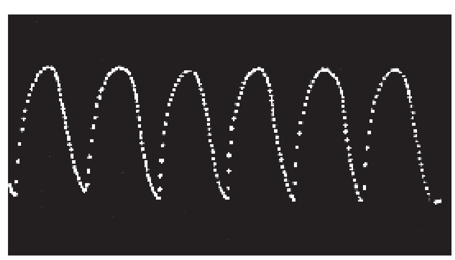

Fig. 2 (c). The rhythmic gyrations of the leaflets of the telegraph plant *Desmodium* (reproduced from Fig. 145[17]). Individual dots are 2 sec. apart. This leaf was measured in summer and the whole period is about a minute, although in winter this increased to 4-5 minutes.

present…. To the theological bias was added the misgivings about the inherent bend of the Indian mind towards mysticism and unchecked imagination…. no conditions could have been more desperately hopeless than those which confronted me for the next twelve years…' Nonetheless, Bose had supporters, and was knighted in 1917, and in 1920, elected a Fellow of the Royal Society.

Inventing Unique Instruments, Selecting Experimental Plants

Bose was a keen observer of wild plants. He built ingenious instruments enabling measurement of the subtle movements of plants, their increments of growth, and the transmission of electrical signals. He focused on three main themes in plant responsiveness.

(i) contractility (movement following a stimulus),

(ii) conductivity (transmission of electrical excitation) and

(iii) rhythmicity (movements taking place automatically, analogous to a heartbeat).

The Resonant Recorder enabled precise measurement of leaf movements (at intervals of 1/100th of a second) – and "*the record is … its own chronogram*"[17]. The High Magnification Crescographenabled measurements of tiny increments of growth, as small as 1 in 27,000.The Electric Probe, an early microelectrode, was advanced into plant tissue at fine intervals (0.1 mm) and in circuit with a sensitive galvanometer, measured electrical signals in specific tissues.

Bose sought evidence for rhythmic, contractile and excitation phenomena in both remarkable and 'ordinary' plants. The seismonastic *Mimosa pudica* responded to touch with dramatic collapse of the leaves. The Indian telegraph plant *Desmodium* made mysterious spontaneous rhythmic movements. Trees such as *Ficus*, *Nauclea*, the mango; monocotyledons such as the banana (*Musa*), made no obvious rapid movements.

From a prodigious output, I will distil some major findings, and relate these to current advances in plant neurobiology.

Wild, Rather than Domesticated Plants Show Adaptive and Intelligent Behaviors

From Bose's time onwards, plant physiologists have standardised experimental conditions, pooling data and statistically analysing results, assuming both that identical plants grow from a single batch of seed, and averaged measurements are meaningful. Bose was interested in the individually variable behaviour of each plant, recognizing that its history and environment could influence its responses. He was aware of phenotypic plasticity. Growing seedlings from the same batch of seed under different environmental conditions, he applied a poison, and observed one batch die, the second recover, and a third batch be stimulated. He regarded environmental change as essential for plant behaviour to show itself : "*…the continuance of normal functions depends on external stimulus…deprivation of stimulus reduces plants to an atonic condition in which all life-activities are brought to a standstill…rhythmic activities are maintained…by stimulus…*"[16]. This also meant that experiments on different plants would not give identical results.

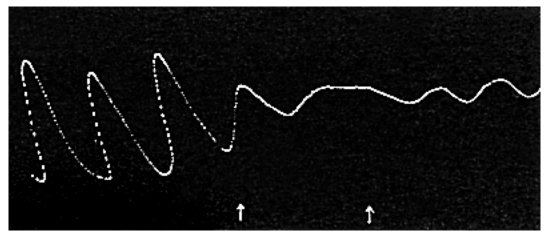

Fig. 2 (d). Arrest of spontaneous movements in *Desmodium* by a cut applied at the first arrow. The pulsatile movement was revived by an electric shock at the second arrow. An electrical stimulus could substitute for a mechanical one. (Reproduced from Fig. 145[17]).

Plants Have Nervous Mechanisms

Mimosa – a Fast-moving Plant : The *Mimosa* displays fast movements — dropping its leaves after a touch stimulus. The motor organ enabling this is the pulvinus, a joint-like structure subtending the petiole[17] proved that leaf dropping was triggered by excitation (an action potential) transmitted from the petiole to the pulvinus, resulting in loss of turgor pressure and collapse of the pulvinus. Sudden temperature change, initiation or cessation of a constant current, and induction shock initiated similar responses. Critically, an electrical stimulus could substitute for a mechanical (touch) stimulus[17]. The bipolar excitation was transmitted through the living phloem, which Bose identified as the plant nerve. The nervous system of *Mimosa* was complex, with both sensory and motor components that could be transformed to one another, forming a reflex arc. "*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*"[17]. Thus, there must be the equivalent of a synapse between pulvinus (motor) and the stem. "*The typical experiments…prove that conduction is irreciprocal. They also indicate the existence of a synapsoidal* *membrane, which by their valve-like action, permit propagationin one direction only*"[33].

The pulvinus contains four major vascular bundles, or effector regions. Stimulating one of these resulted in torsional movements. Each bundle/ effector or plant-nerve was specific to a quadrant of the pulvinus, producing directional torsions that enabled navigation towards light. "*It is by the particular innervation of the motor organ that the leaf undergoes the purposeful movements by which it places itself at right angles to incident light so as to absorb the largest amount of radiant energy*"[34]. This was how leaf blades made heliotropic movements, or 'followed the sun'.

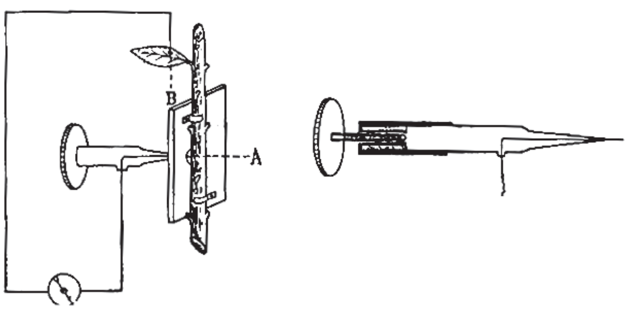

Fig. 3 (a). The Electric Probe (reproduced from Fig. 75[16]). The tip of the Probe was in circuit with either a sensitive or Einthoven galvanometer, and the device could be driven, by small (0.1 mm) increments into the tissue by turning the screw. Bose achieved remarkable precision of measurement : a 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.

The excitation response to stimulus was calibrated differently during changes in light and temperature. For example, *Mimosa* showed a transient reduction in its excitation response as a cloud moved overhead[35]. The velocity of the transmitted electrical excitation depended on the tonic condition of the plant. A plant in optimum condition conducted excitation rapidly, and excessive stimulation resulted in fatigue, whilst a sub-tonic plant conducted excitation slowly, and excessive stimulation enhanced its response.

Did the movements of *Mimosa* have a purpose? When a cow trampled or nibbled *Mimosa* leaves then "*Nothing could be more startling than the rapid change by which large patches of vivid green thus become transformed into thin lines of dull grey unnoticeable against the dull background of the soil. Like the kitten hiding under the sofa, the plant escapes danger by making itself invisible!*"[35].

Desmodium – a Plant Making Spontaneous Rhythmic Movements: *Desmodium motorium* (*Codariocalyx motorius*, The Indian Telegraph plant) has a trifoliate leaf. Two small lateral leaflets make mysterious spontaneous gyrations of regular period, whilst a large leaf makes sleep movements (nyctinasty). The pulvinus is also the motor organ of *Desmodium*, driving leaflet gyration. The spontaneous leaflet movements reflected electromechanical pulsations in the pulvinus, rhythmic alternations between "galvanometric negativity"[relative depolarisation] and "galvanometric positivity" [relative hyperpolarisation] of pulvinar cell electric potential, coupled respectively with reduced turgor(leaflets dipped),and turgor increase (leaflets lifted). The gyrations in the leaflets were temperature dependent, with a period of about four minutes in winter, and much faster (up to one minute) in summer. The pulsations were "*…alternately rendered active or inactive above and below the critical temperature*"[16]. Movements slowed with reduced turgor pressure, were inhibited by strong or repeated stimulus, and arrested by anesthetics. Furthermore, the electromechanical pulsations were arrested by short Hertzian waves, microwaves[16].

In both *Mimosa* and *Desmodium*, the expansive, hyperpolarising or 'leaf lifting' phase was hydraulic, and the contractile, depolarising, 'drooping' phase was nervous and electrical. The nervous system of these plants contained two, antagonistic,sensory and motor pathways[16]. The slow hydraulic (sensory) signal was converted into a fast electrical (motor) signal by a strong enough stimulus, completing the reflex arc. The inner phloem conducted the fast motor impulse, and the outer, the slower sensory impulse[33].

Electromechanical Pulsations in Ordinary Plants: Using the Electric Probe, reference electrode, sensitive galvanometer and a moving photographicplate to record data, Bose recorded electromechanical 'pulsations' in trees (the mango, and the Cadamba, *Nauclea*). He discovered 'pulsations' (rhythmic depolarisation and hyperpolarisation) in cortical cells abutting vascular tissue[16] : "*periodic mechanical pulsations corresponding to electric pulsations, as in Desmodium*"[16]. Pulsations had a small amplitude — about 0.4 mV to several mV in *Nauclea*— and their rate varied, from 13.5 sec for a complete pulsation, to 3 mins., with changing temperature[16]. The pulsations were feeble on cold mornings, maximal at noon, and changed in amplitude over a day.[16] noted, "*The cellular activity undergoes a periodic variation, in response to changes in the environmental condition during twenty-four hours. This causes a very interesting diurnal periodicity of the pressure exerted by the sap, as indicated by a self-recording manometer attached to the tree*". The "galvanonegative" (depolarising) phase of the pulsation was accompanied by cell contraction and turgor loss, whilst the "galvanopositive" (hyperpolarising)phaseaccompanied expansion or swelling of the cells.

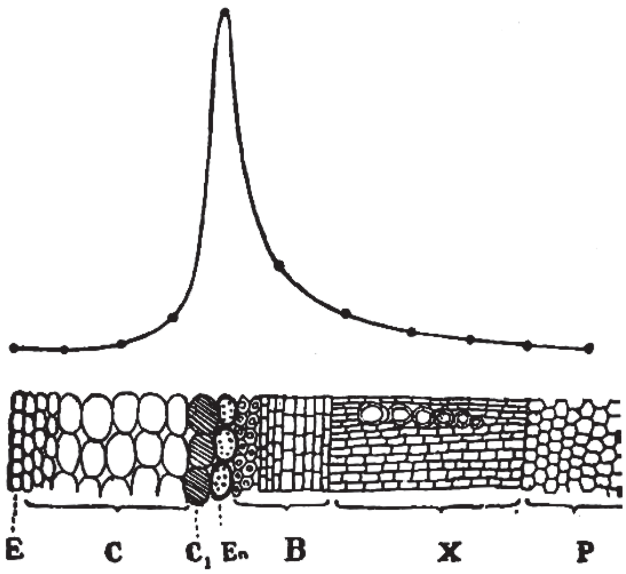

Fig 3 (b). A section of a *Brassica* petiole showing the relative cellular activity in terms of electromechanical pulsations. The pulsations occur mainly in the inner cortical layer abutting the endodermis. (Reproduced from Fig. 77[16]).

Unlike the widely accepted Dixon-Joly tension-cohesion theory of the ascent of sap, Bose maintained that the ascent of sap was propelled by pulsations of living cortical cells : "…*any agent affecting the pulsations induced corresponding effects in the ascent of sap*…"[16]. Contraction of cortical cells expelled fluid into the xylem, whilst cellular expansion withdrew fluid according to the time of day and temperature[16]. Pulsations varied diurnally, as did the 'sap pressure' of trees (e.g. the raintree) with minimal sap pressure at thermal noon and maximal pressure in the early morning and evening. Bose attributed this variation to diurnal temperature variation[35].

The files of cortical cells contracted one after another producing peristaltic waves whose lengths varied between plants (e.g., 100 mm in *Chrysanthemum*, 50 mm in banana, and 40 mm in *Canna*)[16]. Pulsations also occurred in field-grown tomato, vines, and potatoes. Pulsations were enhanced by increased hydrostatic pressure, moderate constant current and increased temperature. They were arrested by a large dose of chloroform (which also halted the ascent of sap), plasmolysis of the roots, temperature decrease, and poisons such as KCN. Bose compared the file of pulsing cells to an elongated 'heart'.

Thus, propagated electromechanical waves of contraction preceded by expansion, squeezed sap upwards."…*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*…"[16].

The Sleep of Plants: Bose claimed that plants sleep, in the true sense of the word : "…*the plant goes through a daily cycle of sensibility and insensibility which may be aptly described as waking and sleeping*…"[35]. A *Mimosa* plant stimulated hour by hour over a 24-hour period showed maximum excitability between 1 and 3 pm, and minimal excitability at 6 am, independent of nyctinastic leaf movements.

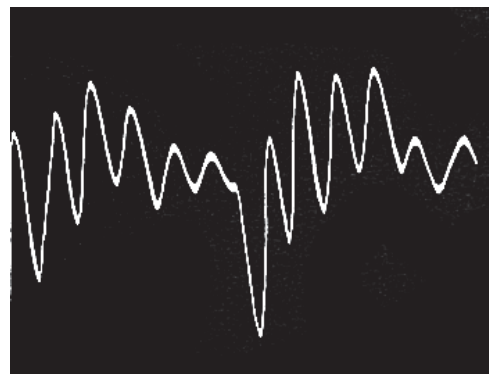

Fig. 3 (c). Periodic groupings of the electrical oscillations in the pulvinus of *Desmodium* (reproduced from Fig. 69[16]), which accompanied the mechanical oscillations of leaflet position shown in Fig. 2c.

The Rhythmicity of Plants- a Fundamental, Pulsatile, Motif

How did a slow-moving plant, encased in cell walls, negotiate with and navigate its environment? J.C. Bose proposed that plants are fundamentally rhythmic. They have a developed nervous system, and coordinate theirbehaviourvia long-distance electrical signaling. In addition to transporting sugars, the phloem constitutes a system of nerve-equivalents, transmitting sensory (hydraulic) and motor (electrical) signals in response to environmental stimuli. Intense stimuli provoke motor responses by completing a reflex arc between sensory and motor nerve equivalents.

Vascular bundles embedding these nervous tissues enable navigation in relation to the four compass points. Depolarisation and turgor loss accompany a faster electrical response, whilst hyperpolarisation and turgor increase constitute a slower sensory response, and this forms a fundamental pulsatile motif. Cortical cells surrounding vascular bundles pulse persistently, alternating between depolarisation/turgor loss and hyperpolarisation/turgor increase, analogous to a heartbeat that is responsive to the time of day and temperature. Sleep or reduced responsiveness exists in the true sense of the word.

Bose advanced the view that plants are intelligent, capable of learning from experience and displaying adaptive behaviours.As to the question of consciousness, Bose allied himself with the philosopher Henri Bergson, who reasoned that consciousness is in principle coextensive with life, even in organisms lacking a large brain[35]. If consciousness is equated with presence of a nervous system, sense organs, and spontaneous or voluntary movements, all these characteristics exist in simpler forms in plants[35].

Some Current Concepts in Plant Neurobiology

Neural Systems are Ancient and are Manifest as a Continuum Throughout Organisms: The field provocatively called 'plant neurobiology' aims to explain how plants perceive the world, and deploy electrical and chemical signals to respond adaptively. Terms such as 'nervous system', 'brain', 'synapses' and 'intelligence' applied to plants have provoked misunderstanding and controversy[24]. There are problems of terminology.[36] Applies Living Systems Theory (LST) to reconcile neural homoplasies between plants and animals. In LST, each level of biological organisation (e.g. cell, tissue, organ, organism, ecosystem) is supported by critical subsystems, performing equivalent tasks but constituted from different elements. At the organism level, the 'channel and net' subsystem 'transmitting electrical signals' fits both plant phloem and animal nervous tissues[36]. Neural systems are ancient, and are not exclusive or specific to animals or humans — even prokaryotes display neural aspects such as chemical quorum sensing[37], and 'wired' networks of electrical communication through pili[38]. Some researchers prefer to apply the terms nervous system and neuronal to plants. For example, "*plants are neuronal, knowledge-accumulating systems*"[39].

Adaptive Behavior is Characteristic of Wild Plants: Domesticated plants have been selected for traits found desirable by humans. We breed the phenotypes we like best, supply them with nutrients, light and water, protect them from predators and enable their reproducion. As Bose had realised, we will not find evidence for variable adaptive behaviours in domestic plants because we eliminate variability of phenotype. Phenotypic plasticity "…*enables the phenotype to accurately occupy local space, change its phenotype as it grows, forage accurately for resources, competitively exclude neighbours and construct, within genetic/ environmental limitations, its own niche*…"[9]. Phenotypic plasticity results from perception and integration of signals, translated into adaptive growth patterns and movements.

The Neural System of Plants: Action Potentials and Variation/Slow Wave Potentials: Action potentials (APs) are transmitted electrical signals involving voltage-gated ion channels or pumps. Stimuli such as changes in temperature or light or osmolarity, wounding and touch, provoke APs[40]. An AP involves depolarisation, Ca^{2+} release, activation of Cl^{-} channels and voltage-dependent K^{+} channels, resulting in efflux of Cl^{-} and K^{+}[41,42], turgor loss[43], and a transitory contraction of the cell[44]. APs are multi-functional electrical signals[45,46].

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[17]).

Wounding activates proteinase inhibitor genes in distant tissues[47] via slow-wave potentials(SWPs) or variation potential (VPs) resulting from mechanosensory and/or ligand activated ion channels activated bya hydraulic surge or chemicals in xylem[48]. VPs result in transient inhibition of the proton pump and depolarisation[49]. APs can be triggered by changes in membrane potential occurring during the VP[50]. Thus, short-range VPs are triggered by a hydraulic signal in the xylem, and can then trigger long-range APs following intense stimulus.

Are there two nervous systems, sensory and motor, as Bose proposed? Two types of long distance signals have been identified: faster APs, transmitted through the phloem as a true excitation, and VPs/SWPs, a slower localised response to a xylem-transmitted hydraulic wave, involved especially in wounding. Roots show complex foraging behaviours and indications of decision-making, search and avoidance movements, self and kin recognition[51]. The root apex transition zone integrates incoming sensory information and initiates motor responses of adaptive growth, completing sensory-motoric circuits[51]. Synchronous electrical activities occur specifically in this zone[52], which is also active in auxin transport via vesicle recycling and synapse-like cell-to-cell communication[53,54].

As a 'green cable' that transmits action potentials in response to stimuli such as wounding or chilling, phloem is the focus of recent research using aphid stylets to analyse the complexities of long distance electrical signaling[55].

J.C. Bose did not interpret electrical signals as due to the activities of ion channels, but his overall conclusions were later confirmed. The propagated folding of *Mimosa* leaûets is triggered by an AP transmitted at a rate of 20–30 mm s^{-1}, slower than in animal nerve (up to 100 m s^{-1})[56]. Excitation is propagated in the phloem. The fundamental motif includes electrical depolarisation,turgor loss in the pulvinus, expulsion of Cl^- and K^+, and sudden sucrose unloading[56,57]. Collapse of *Mimosa* leaflets and spontaneous movements of *Desmodium* both require the contractile actin-myosin system[58,59] repeated Bose's results, and re-identified Bose's "inner phloem" as elongated protoxylem parenchyma cells. Both elongated phloem and protoxylem parenchyma have more negative membrane potential and conduct APs. "*The electrical features of these cells are essentially similar to those of nerve and muscle cells*"[59]. Do these movements have a purpose? They discourage predators from attacking the leaves.

Gyration of *Desmodium* leaflets is due to rhythmic oscillations of turgor pressure and membrane potential difference in pulvinar cells[60,61]. During down-stroke, pulvinar motor cells depolarise, apoplastic K^+ concentration increases, cells contract and lose turgor. During up-stroke, motor cells hyperpolarise, apoplastic K^+ concentration declines, cell expand, and turgor increases. The period of leaflet oscillations increases with increased temperature, and an anesthetic (enflurane) abolishes the movements[62]. Pulsed radio-frequency fields transiently alter the amplitude, period

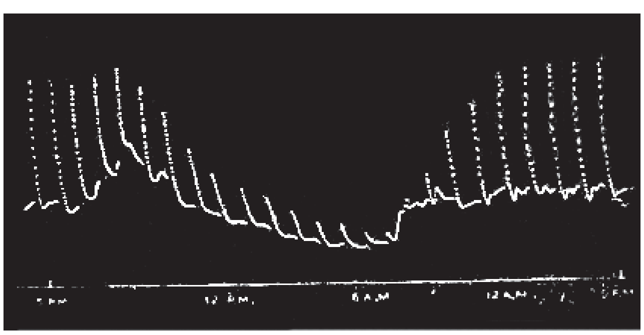

Fig. 3(e). The sleep of plants. Excitability in *Mimosa* changes over the course of a day.

The response to excitation was recorded every hour for 24 hours.Maximum excitability was found between 1 and 3 PM, and this declined from evening to morning. The baseline shifts are due to nyctinastic movements. (Reproduced from Fig. 31[35]).

and phase of the leaflet rhythms[63]. Do these movements have a purpose? They mimic the movements of a butterfly's wings, and can discourage another butterfly from laying eggs on the plant[64].

Rhythmic Electromechanical Pulsations- the Lunisolar Tidal Force: Intriguing new research into the coupled fluctuations of tree stem diameters and electric potential difference (EPD) provide new insight into the rhythmic hydro-electric pulsations Bose measured. Daily variations in the stem diameter of *Picea alba* and other trees correlate with variations in the lunisolar tidal acceleration, and maximal stem diameters coincide with lunar peaks[65]. Diurnal rhythmic variations of electric potential (EP) in the bole of trees are associated not only with daily photoperiods but with lunar periodicities[66]. Fourier analysis of EPD rhythms show oscillations with a period corresponding to the synodic lunar month. There is good evidence that a lunar-rhythmic character of wood-water relations — as traditional knowledge had stated, "*soft wood in a waxing moon, hard wood in a waning moon*"[67] — is a real phenomenon[68].

Barlow and co-workers report correlations between variations in the lunisolar tidal force and variations in EPD and stem diameters[69], leaf movement rhythms[12] and root growth kinetics[70,71]. Diurnal leaf movements, well-known in bean plants, follow a lunar clock rather than an internal molecular clock, initiating APs travelling via phloem and potentially setting the timing of critical physiological events[69]. Circumstantial evidence for an influence of the Moon on bioelectric potentials, water relations and the movements of plants is strengthened by experiments conducted in space. *Arabidopsis* leaf movements in the International Space Station synchronise with in-orbit lunar solar tides rather than those on Earth[72].

How plants are sensitive to the lunisolar tidal accelerative force, and how this rhythmically influences both water status and EPD, is unknown[69]. Lunisolar turning points may match times when the flow of water, into or out of cells, is reversed[13]. This sensitivity provides plants with an ever-present external time-keeper and results in rhythmic behaviours.

Intelligence, Cognition and Behavior of Plants: Philosopher of science and scuba diver Peter Godfrey-Smith proposes that intelligence has evolved more than once, in both invertebrate and vertebrate lineages[73]. Intelligent octopuses show embodied cognition — each tentacle independently assesses and responds to its environment, and tentacles have more neurons than the brain[73]. Neurons and the fast electrical signals (APs) they transmit are integral to the intelligent behavior of such fast-moving animals.

Do plants have a neural system too? The root- shoot polarity is fundamental to plant life. Complex social interactions between plants, plants and fungi and plants and bacteria, are mediated primarily through exploratory roots[53,74] whilst shoots perform respiratory and reproductive functions. The neural system of plants integrates this polarity and embraces the vascular tissues; phloem, through which long-distance APs are transmitted, more slowly than in animals, and xylem, which transmits hydraulic or chemical signals stimulating VPs[77]. The controversially named 'root-brain' is an integrative centre at the root apex transition zone[53] where synchronised electrical spikes are emitted[52], auxin vesicle recycling is active, and sensory-motoric circuits are completed[51].

Are plants intelligent too? As complex modular networks that control their own behaviour in relation to problems posed by the environment, plants possess 'green intelligence'[2,5,6]. Compares this to the swarm intelligence of a bee colony, a cognitive entity or colony of mind[75] that collects information about the world, assesses it in relation to its own internal state (performing simple reasoning), and makes decisions promoting its well-being.

Are plants cognitive entities as well? If cognition is the capacity to perceive, acquire and respond to information, then plants certainly are cognitive[11] postulate embodied cognition as integral to the modular construction and sessile life-style of plants.

Are plants conscious too? Consciousness is ubiquitous, argue[76], and only 'wild' behaviour enacted in the natural environment is meaningful for observing conscious, intelligent behaviour[13] reflects on whether the recently revised ORCH OR theory of consciousness, proposed by Stuart Hameroff and the quantum physicist Sir Roger Penrose, applies to plants. In this theory 'orchestrated' ('ORCH') coherent quantum processes in microtubules of brain neurons lead to 'objective reduction' ('OR') of the quantum state and mediate moments of protoconsciousness. As demonstrably sensitive organisms, endowed with microtubules (especially in ray cells of trees), displaying embodied cognition, a sense of self or 'one-ness', possessing neural homoplasies with animals, plants arguably also possess simple protoconsciousness[13].

Conclusion

Sir J.C. Bose pioneered the study of plant neurobiology.He was the first person to use the term 'plant nerve'. He identified electrical and hydraulic signals in the plant nervous system as the basis for integrated plant movements, rhythms and behaviours. He regarded plants as sensitive and intelligent agents in the world. Today, plants can no longer be viewed as passive automata but have to be considered as active agents. Rather than the traditional emphasis on differences between animals and plants, plant neurobiology focuses on homoplasies and inter-relationships. The study of plant behaviour will be the most important task of plant biologists in this century[78].

References

1. W. Frommer, Grand opportunities in physiology to address the grand challenges facing the planet. *Front. Physiol*. **1**:1-3, (2010).
2. A. Trewavas, *Plant Behaviour and Intelligence.*Oxford University Press, Oxford, United Kingdom, (2015).
3. J. Fromm and H. Fei, Electrical signalling and gas exchange in maize plants of drying soil. *Plant Sci*. **132** : 203-213, (1998)
4. A. Trewavas, The green plant as an intelligent organism. In *Communication in Plants: Neuronal Aspects of Plant Life.* (eds. F. Baluška, S. Mancuso and D. Volkmann), pp. 1-18. (Springer-Verlag Berlin Heidelberg), (2006).
5. A. Trewavas, Plant intelligence. *Naturwiss.***92**: 401-403, (2005).
6. A. Trewavas, The green plant as an intelligent organism. *Trends Plant Sci.***10**: 413-419, (2005).
7. H. De Kroon, E.J.W. Visser, H. Huber, C. Mommer, M. J. Hutchings, A modular concept of plant foraging behavior: the interplay between local responses and systemic control. *Plant Cell Environ*. **32**: 704-712, (2009).
8. A. Trewavas, *Aspects ofPlant Intelligence.*In: *The Deep Structure of Biology: Is convergence sufficiently ubiquitous to give a directional signal*? (ed. S. Conway Morris), pp. 68-111, (2008). Templeton Foundation Press, West Conshohocken, Pennsylvania, USA.
9. A. Trewavas, What is plant behaviour?*Plant Cell. Environ.***32**: 606-616, (2009).
10. M. Dicke, Behavioural and community ecology of plants that cry for help. *Plant Cell Environ*. **32**: 654-665, (2009).
11. P. Garzón and F. Keijzer, Plants: Adaptive behaviour, root-brains, and minimal cognition. *Adapt. Behav*. **19**: 155-171, (2011).
12. P. W. Barlow, Leaf movements and their relationship with the lunisolar tidal force. *Ann. Bot.***116**: 149-187, (2015a).
13. P. W. Barlow, The natural history of consciousness, and the question of whether plants are conscious, in relation to the Hameroff-Penrose quantum-physical 'Orch OR' theory of universal consciousness. *Comm. Integ. Bio.*, **8**:4, e1041696, DOI:10.1080/19420889.2015.1041696, (2015b).
14. D. P. Sen Gupta, Jagadish Chandra Bose: The Man and His Time. In: Sen Gupta D.P., Engineer, M.H. and Shepherd, V.A. *Remembering Sir J.C. Bose*. IISc Press, WSPC Publications, Singapore, (2009).
15. S. Dasgupta, Jagadis Bose, Augustus Waller and the discovery of 'vegetable electricity'. *Notes Rec. Roy. Soc. Lond.* **52**: 307-322, (1998).
16. J.C. Bose, *The Physiology of the Ascent of Sap.* Longmans, Green and Co. London, (1923).
17. J.C. Bose, *Researches on Irritability of Plants.* Longmans, Green and Co. London, (1913).

18. Nandy, A. *Alternative Sciences. Creativity and Authenticity in Two Indian Scientists.* (Oxford University Press, Delhi), (1995) p.46.

19. J.C. Bose, The Voice of Life. In: *Acharya J.C. Bose: The Scientific Legacy*, Bose Inst. Kolkata, 2004, pp. 1-11, (1917).

20. V. A. Shepherd, Bioelectricity and the rhythms of sensitive plants- the biophysical research of Jagadis Chandra Bose. *Curr. Sci.* **77**: 189195, (1999).

21. V. A. Shepherd, From semi-conductors to the rhythms of sensitive plants: The research of J.C. Bose. *Cell. Mol. Biol*. **51** : 607-619, (2005).

22. V. A. Shepherd, Reflections on the Many-in-One: J.C. Bose and the roots of plant Neurobiology. In: Sen Gupta D.P., Engineer, M.H. and Shepherd, V.A. *Remembering Sir J.C. Bose*. (IISc Press, WSPC Publications, Singapore), (2009).

23. V. A. Shepherd, At the roots of plant neurobiology. In:*Plant Electrophysiology: Methods and Cell Electrophysiology* (ed. A. G. Volkov), pp. 3-43. (Springer-Verlag Berlin Heidelberg), (2012).

24. A. Alpi. et al., Plant neurobiology: no brain no gain. *Trends Plant Sci*. **12**: 135-136, (2007).

25. A. Trewavas, Response to Alpi et al: Plant neurobiology— all metaphors have value. *TrendsPlant Sci.***12**: 231-233, (2007).

26. S. Tharoor, *Inglorious Empire. What the British did to India.* Scribe, Melbourne, Australia, (2017)..

27. M. Engineer, The Millimetre Wave Researches of J. C. Bose. In: Sen Gupta D. P., Engineer, M.H. and Shepherd, V.A. *Remembering Sir J.C. Bose*. IISc Press, World Scientific, Singapore, (2009).

28. J.C. Bose, Patent for Detector for Electrical Disturbances. reprinted in *Trans. IEEE.* 1998, **86:** 230-234, (1904).

29. D. T. Emerson, Jagadis Chandra Bose: millimetre wave research in the nineteenth century. *IEEE Trans. Microwave Theory Tech.* **45** : 2267-2273, (1997).

30. P. Chakrabati, *Western Science in Modern India: Metropolitan Methods, Colonial Practices*. Orient, Longman, (2004).

31. N. Guardiano, The intelligibility of Peirce's metaphysics of objective idealism. *Cognitio Sâo Paulo*. **12**: 187-204, (2011).

32. P. Simons, *The Action Plant. Movement and Nervous Behaviour in Plants.* (Blackwell, Oxford, Cambridge), (1992).

33. J. C. Bose, *The Nervous Mechanisms of Plants.* Longmans, Green and Co. London, (1926).

34. J.C. Bose and G. P. Das, Physiological and anatomical investigations on *Mimosa pudica*. *Proc. Roy. Soc. Lond. Ser. B.* **98**: 290-312, (1925).

35. J.C. Bose, *Plant Autographs and Their Revelations.* Longmans, Green and Co. London, (1927).

36. P. W. Barlow, Charles Darwin and the plant root apex: Closing a gap in living systems theory as applied to plants. In *Communication in Plants: Neuronal Aspects of Plant Life.* (eds. F. Baluška, S. Mancuso and D. Volkmann), pp. 37-51. Springer-Verlag Berlin Heidelberg, (2006).

37. F., Baluška, and S. Mancuso, Deep evolutionary origins of neurobiology: Turning the essence of 'neural' upside-down. *Comm. Integ. Bio*. **2**: 60-65, DOI: 10.4161/cib.2.1.7620, (2009).

38. G. Reguera, When microbial conversations get physical. *Trends. Microbiol.* **19**: 105-113 (2011).

39. F. Baluška and S. Mancuso, Plant neurobiology as a paradigm shift not only in the plant sciences. *Plant. Sign. Behav.* **2**: 205-207, (2007).

40. J. Fromm and S. Lautner, Electric signals and their physiological significance in plants. *Plant Cell Environ.* **30**: 249-257, (2007).

41. K. Oda, Simultaneous recording of potassium and chloride efflux during an action potential in *Chara corallina.Plant Cell Physiol*. **17**: 1085-1088 (1976).

42. R. Wayne, The excitability of plant cells: with a special emphasis on characean internodal cells. *Bot. Rev.* **60**: 265-367, (1994).

43. U. Zimmermann and F. Beckers, Generation of action potentials in *Chara corallina* by turgor pressure changes. *Planta* **138** : 173-179, (1978).

44. K. Oda and P. J. Linstead, Changes in cell length during action potentials in *Chara.J. Exp. Bot.*26: 228-239 (1975).

45. E. Davies, Action potentials as multifunctional signals in plants: a unifying hypothesis to explain apparently disparate wound responses. *Plant, Cell, Environ.***10**: 623-631, (1987).

46. E. Davies, New functions for electrical signals in plants. *New Phytol*. **161**: 607-610, (2004).

47. D.C. Wildon, J. F. Thain, P. E. H. Minchin, I. R. Gubb, A. J. Reilly, Y. D. Skipper, H. M. Doherty, P. J. O'Donnell and D. J. Bowles, Electrical signalling and systemic proteinase inhibitor induction in the wounded plant. *Nature* **360** : 62-65, (1992).

48. E. Davies, Electrical signals in plants: facts and hypotheses. In *Plant Electrophysiology-Theory and Methods* (ed. A.G. Volkov), pp. 407-422, (2012). (Springer-Verlag Berlin Heidelberg).

49. V. A. Vodeneev, E. K. Akinchits, L.A. Orlova and V. S. Sukhov, The role of Ca^{2+}, H^+ and Cl^- ions in generation of variation potential in pumpkin plants**.** *Russ. J. Plant. Physiol*. **58**: 974-981, (2011).

50. B. Stankovic, D. L. Witters, T. Zawadzki and E. Davies, Action potentials and variation potentials in sunflower: An analysis of their relationships and distinguishing characteristics. *Phys. Plant*. **103**: 51-58, (1998).

51. F. Baluška, S. Mancuso, D. Volkmann and P. W. Barlow, Root apex transition zone: a signalling–response nexus in the root. *Trends Plant Sci*. 15: 402-408, (2010).

52. E. Masi, M. Ciszak, G. Stefano, L. Renna, E. Azzarello, C. Pandolfi, S. Mugnai, F. Baluška, F. T. Arecchi and S. Mancuso, Spatiotemporal dynamics of the electrical network activity in the root apex. *Proc. Nat. Acad. Sci*. **106**: 4048-4053, (2009).

53. F. Baluška, S. Mancuso, D. Volkmann and P. Barlow, Root apices as plant command centres: the unique 'brain-like' status of the root apex transition zone. *Biologia, Bratislava.* **59:** Suppl. 13: 1- 13, (2004).

54. F. Baluška and S. Mancuso, Root apex transition zone as oscillatory zone. *Front. Plant Sci*. 4:354. doi: 10.3389/fpls.2013.00354, (2013).

55. R. Hedrich, V. Salvador- Recatala and I. Dreyer, Electrical wiring and long-distance plant communication. *Trends. Plant. Sci.* **21**: 376- 387, (2016).

56. J. Fromm and W. Eschrich, Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. II. Energesis and transmission of seismic stimulations. *Trees* **2** : 18-24, (1998a).

57. J. Fromm and W. Eschrich, Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. III. Displacement of ions during seismonastic leaf movements. *Trees* **2** : 65-72, (1998b).

58. T. Van den Driessche, Nutations in shoots and in *Desmodium* lateral leaflets, nyctinastism and seismonastism in *Mimosa pudica*. Comparison and evolution of morphology and mechanism. *Biol. Rhythm. Res.* **31**: 451-468, (2000).

59. T. Sibaoka, Excitable cells in *Mimosa*. *Science* **137**: 226, (1965).

60. B. Antkowiak, W. E. Mayer and W. Engelmann, Oscillations of the membrane potential of pulvinar motor cells *in situ* in relation to leaflet movements of *Desmodium motorium*. *J. Exp. Bot*. **42**: 901-910, (1991).

61. B. Antkowiak and W. Engelmann, Oscillations of apoplasmic K^+ and H^+ activities in *Desmodium motorium* (Hout) Merril. pulvini in relation to the membrane potential of motor cells and leaflet movements. *Planta* **196**: 350-356, (1995).

62. B. Antkowiak and K. Kirschfeld, Enflurane is a potent inhibitor of high conductance Ca^{2+}-activated K^+ channels of *Chara australis*. *FEBS Lett*. **313**: 218-221, (1992).

63. S. Ellingsrud and A. Johnsson, Perturbations of plant leaflet rhythms caused by electromagnetic radio-frequency radiation. *Bioelectromag.* **14**: 257-271, (1993).

64. S. Lev-Yadun, The enigmatic fast leaflet rotation in *Desmodium motorium*. *Plant Signalling & Behavior*, **8** : 6, e24473, DOI: 10.4161/psb.24473, (2013).

65. E. Zürcher, M-G. Cantiani, F. Sorbett-Guerri and D. Michel, Tree stem diameters fluctuate with tide. *Nature* **392** : 665-666, (1998).

66. K. Holzknecht and E. Zürcher, Tree stems and tides- A new approach and elements of reflexion. *Schweiz. Z. Forstwes*. **157**: 185-190, (2006).

67. E. Zürcher, Plants and the Moon - Traditions and Phenomena. *HerbalEGram* **8** : 1-14, (2011).

68. E. Zürcher, R. Schlaepfer, M. Conedara and F. Giudici, Looking for differences in wood properties as a function of felling date: lunar phase correlated variations in the drying behaviour of Norway spruce (*Picea alba* Karst) and Sweet Chestnut (*Castaneae sativa*). *Trees* **24**: 31-41, (2010).

69. P. W. Barlow, Moon and Cosmos: plant growth and plant bioelectricity. In *Plant Electrophysiology.* (ed. A.G. Volkov), pp. 249-280. Springer-Verlag Berlin Heidelberg, (2012).

70. J. Fisahn, N. Yazdanbakhsh, E. Klingele and P. W. Barlow, *Arabidopsis thaliana* root growth kinetics and lunisolar tidal acceleration. *New Phytol.* **195** : 346-355, (2012).

71. P.W. Barlow and J. Fisahn, Lunisolar tidal force and the growth of plant roots, and some other of its effects on plant movements. *Ann. Bot.* **110** : 310-318, (2012).

72. J. Fisahn, E. Klingele and P. W. Barlow, Lunar gravity affects leaf movement of *Arabidopsis thaliana* in the international space station. *Planta.* **241** : 1509-1518, (2015).

73. P. Godfrey-Smith, *Other Minds: The Octopus and the Evolution of Intelligent Life*. William Collins, London, UK., (2017).

74. H. P. Bais, S. W. Park, T. L. Weir, R.M. Callaway and J. M. Vivanco, How plants communicate using the underground information superhighway. *Trends Plant Sci*. **9**: 26-32, (2004).

75. T. D. Seeley and R. A. Levien, A colony of mind. The beehive as thinking machine. *Sciences (NY)* **27**: 38-43, (1987).

76. A. Trewavas and F. Baluška, The ubiquity of consciousness, cognition and intelligence in life. *EMBO Reports* **12**: 1221-1225, (2011).

77. P. W. Barlow, Reflections of plant neurobiology, *Biosystems* **92**, 132-147 (2008).

78. C. L. Ballare and A. J. Trewavas, Plant behaviour. *Plant Cell Environ.***32**: 605, (2009).