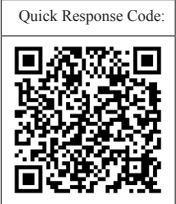


Review Article

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Jagdish Chandra Bose & plant neurobiology

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When Jagdish Chandra Bose, a renowned physicist, devoted himself entirely to research in the field of plant physiology post his superannuation at Presidency University, Kolkata, India (earlier known as Presidency College, Calcutta), it came as a surprise to many. The research on plant nervous system by JC Bose during this period was pioneering in nature, being recognized by recent plant biologists globally as the first in the field. His findings were so revolutionary at the time of their proclamation that these aroused disbelief and contradiction. Surprisingly, not many at that time took up such investigations and once accepted with reluctance, there was practically very little activity in the field for the next several decades. More than a hundred years later, recent advances in molecular biology, genomics, ecology and neurophysiology have led to renewed interest resulting in a flurry of activity, confirming most of Bose's observations. The present review describes this pioneering scientist's work and his immense contribution in the emergence of the discipline now designated as 'Plant Neurobiology'.

Key words Intelligence - Jagdish Chandra Bose - learning - plant memory - plant nerve - plant neurobiology

Introduction

Between 1900 and 1935, Jagdish Chandra Bose working in Calcutta (now Kolkata), India, initially at the Presidency College (now Presidency University) and later at the Bose Institute, established by him after his retirement from the former institution, dedicated himself to research solely in the field of plant physiology. This, no doubt, was something unexpected and unusual for a distinguished physicist who had already attained international recognition for his work on the optical properties of radiowaves and wireless transmission ahead of Guglielmo Marconi. Owing to his philosophical and overall scientific belief in 'Unity of Life' and evolution, he initially studied the

effect of such waves on inorganic matter. Finding the response similar to animal muscle, he initiated his studies on plants. His observations and findings transformed him into a plant physiologist (an explorer of plant nervous system). In this quest, he devised a number of ingenious instruments enabling him to record the plant responses to a variety of stimuli. Notwithstanding some opposition, ridicule, disbelief and criticism initially, his observations in the early 1900s ultimately found general acceptance by eminent biologists and plant physiologists globally. He forcefully presented his claim through lecture-demonstrations across the UK and Europe that the nerve impulses in all types of plants were similar to those in animals.

Action potentials (APs)

From general electrical response of different parts of the plant, he proceeded to record responses from individual cells using microelectrode recording system devised by him. In those early years, prior to the 1920s, such microelectrode studies had not yet been initiated on single neurons in animals. On the basis of a large number of studies, Bose concluded that plants - small or big - have a nervous system akin to one in the lower animals. He reported, "Plants also have receptors for stimuli, conductors (nerves) which electrically code and propagate the stimulus and efferent or terminal motor organs" and further "The _____ physiological mechanism of the plants is identical with that of the animal"¹. He established the nervous impulse and its transmission in plants, responsible for the control of many physiological functions including growth, ascent of the sap, respiration, photosynthesis, motor activity and response to the environment - light, heat, trauma, shock, and drugs and toxins. The action potential (AP) follows the all or none character and unipolarity of transmission in plants similar to that observed in animals. He localized the nervous tissue in the phloem which conducted the afferent or the sensory and the efferent or the motor impulses. He even measured the speed of the nervous impulse within the petioles and found it to be as high as 400 mm/sec¹. In addition to the APs generated in response to an external stimulus, he observed automatic or spontaneous rhythmic or pulsatory movements in plants like heart beat in animals.

Bose became the first to use the term 'Plant Nerve'². Though nervous impulse in insectivorous plants was already reported a few years earlier than Bose by Burdon-Sanderson³ and Darwin⁴, the types of details of the nervous system provided by Bose, in a large number of papers and a series of monographs (Bose, 1906, 1907 and 1926-1929)⁵, were not available from any other source. Though Augustus Waller from London claimed that he had reported 'the phenomenon of vegetable electricity' earlier than Bose, a detailed discussion by Dasgupta⁶ on this controversy could not take away the credit from Bose. In any case, the continued elaboration of the diverse aspects of this phenomenon by Bose for the next three decades has no parallel in the history of plant nervous system research. While there were some references on plant nervous system and activity in the 1930s^{7,8}, there were limited reports on the subject till after the 1950s. However, later publications in the field confirmed most of his findings and acknowledged

Bose's contributions in this field as the most important pioneering work⁹⁻¹⁴.

Modern era

Baluska *et al*¹⁴ not only confirmed Bose's major observations referred to above, but also advanced these further by utilizing tools and techniques of modern molecular and cellular biology, chemical ecology and genomics. Though molecular biology was not yet a distinct discipline during Bose's time, in 1918, in his lecture on 'Control of Nervous Impulse', he stated, "The propagation of nervous impulse is a phenomenon of transmission of molecular disturbance"¹⁵. It is not clear what he meant by this term because in none of his papers, before or after, there is any indication of investigations on the molecular basis of the nervous impulse in plants in the modern sense.

Plant neurobiology

The advances in this field have led to the introduction of the term 'Plant Neurobiology' as a distinct discipline^{11,12}. Plant neurobiology attempts to elaborate "of what structural elements is the plant nervous system constituted and what is the form of the, information which this system is supposed to convey? Further, how is this information initially gained from external signs, and then encoded and imported into a plant nervous system, where it is transmitted and finally decoded so that a response can be brought about?"¹¹ Stahlberg¹¹ provided a 'Historical Overview on Plant Neurobiology'. Two recent books, 'Communication in Plants'¹⁶, and 'Plant Electrophysiology'¹⁷, as well as a host of other papers, describe various ways in which cell-to-cell propagation of the nerve impulse takes place and the manner in which the AP is transmitted to long distances.

Electrical studies

According to Brenner *et al*¹², "Plant Neurobiology is a newly initiated field of plant biology that aims to understand how plants perceive their circumstances and respond to environment input in an integrated fashion taking into account the combined molecular, chemical and electrical components of intercellular plant signaling". In addition to the APs already described in detail by Bose, another long-distance signal the slow wave potentials (SWPs) or variation potentials (VPs) has been documented¹¹. The long-distance signalling - APs - similar to those in the animal nervous system are more common in higher plants and are propagated in vascular bundles of the phloem along the plant axis as already established by Bose⁵. The

long-distance potentials (SWs or VPs) were found to be unique to plants^{11,12}. The SWs follow hydraulic pressure changes that use the vascular bundles (xylem) for propagation over long distances along the plant axis. Some lower plants such as *Dionaea* flytraps and *Aldrovanda vesiculosa* were also found to possess omnidirectional APs similar to cardiac myocytes as also described by Bose⁵ (Bose in his talk at Guildhouse in London on June 30, 1929 poetically described this phenomenon, ‘In many other ways we are able to find that plant has a heart that beats continuously as long as life remains’)^{12,18}. These APs have been reported to be associated with plant respiration, photosynthesis, phloem transport, recognition of herbivora attack, light-induced phototropism and systemic deployment of plant defences. However, the precise mechanisms responsible for these functions still need to be established^{18,19}.

Molecular studies

“At the molecular level, plants have many, if not all, components found in the animal neuronal system. There are voltage-gated channels, a vesicular trafficking apparatus sensitive to calcium signals including synaptotagmins and other components of the neuronal cell infrastructure”¹². Trewavas²⁰ while discussing the communication within the plant cells observed the role of cytosolic Ca²⁺, in particular, to act as a cellular second messenger with ubiquitous roles in signal transduction and intracellular communication. He pointed out that, ‘Many different environmental signals (e.g., touch, wind, cold, gravity and disease) modify Ca²⁺ and are responsible for phenotypic plasticity’. It is now becoming clear that Ca²⁺ signal, though important, is just one of the large numbers of such signal transduction molecules. It is once again tempting to quote Bose (1918) from his paper ‘The Voice of Life’²¹, “My investigations show that all plants, even the trees, are fully alive to the changes in the environment, they respond visibly to all stimuli, even to the slight fluctuations of light caused by a drifting cloud”. Molecular biology investigations now provide the changes at the cellular level associated with this behaviour. Information about the ion channels and transporters can be obtained from genomic investigations and electrophysiological characterization of their activities^{12,22}.

Plant roots: Role in sensing the environment

In his book, ‘The Power of Movement in Plants’, Darwin²³ proposed, “It is hardly an exaggeration to say

that the tip of the radicle thus endowed (with sensitivity) and having the power of directing the movement of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense organs and directing the several movements”. Bose²⁴ also pointed out the sensory functions of the roots as, ‘Fine rootlets in contact with the soil are stimulated by friction and the presence of chemical substances. The cells thus undergo contraction forcing their liquid contents into others higher up’. Bose attributed the ascent of sap to this sensory-motor activity of the rootlets.

It is difficult to understand the implications of the use of the term ‘root brain’ by one of the most outstanding scientists of his era, Charles Darwin. It is no surprise that neither Bose, nor any other plant physiologist, referred to it until recently when Baluska *et al*¹⁴ tried to revive and justify this concept. According to them, “In 1990, we reported upon a unique zone within the root apex of maize which is interpolated between the apical meristem and the elongation region. Recently, the term ‘basal meristem’ has been used for this same zone. In future, terms ‘command centre’ or ‘cognitive centre’ might prove even better”¹⁴. They further added, “Growing root apices are well known to screen the numerous abiotic and biotic parameters of their environment and to respond to them with either positive or negative tropisms. Sensory areas are typically at the apices of organs whereas the responsive motoric areas are located basally which implicates long-distance transmission of sensory signals. This, in effect, is an animal-like sensory-motor circuit which allows adaptive behavior, and it was remarked upon for the first time by Charles and Francis Darwin”. While this function of the plant roots reflects the existence of a sensory-motor circuit capable of serving a reflex action, the present author considers it nowhere near the complex function the brain performs in animals. Of course, Bose never used the term brain for any part of the plant nervous system.

Synapses - neurotransmitters

In a paper published in January 1928²⁵, Bose pointed out, “The nerve tissue _____ consists of elongated tubular cells, the dividing membrane of which acts alike a synapse in the animal nerve; the membrane functions as a valve and allows the impulse to travel with greater facility in one direction than the opposite”. While in the broadest sense this function of the synapse

is correct, it appears that Bose used the term nerve for nerve cell (or neuron) because the nerves do not have synapses. It may be pointed out that the term 'neuron' had not yet been coined, and the synaptic hypothesis was announced by Sherrington only in 1898²⁶.

With advances in molecular biology and electron microscopy, the existence of synapses in the plant cells was unequivocally established. Cell-cell propagation of impulses makes use of or is the result of structures akin to synapses similar to those in animal nervous system¹⁶. Barlow¹³ further elaborated this as, "Plant 'synapses' share certain characteristics with animal synapses, in particular, presence of a calcium-sensitive vesicle trafficking apparatus". The role of molecules such as auxin, actin, myosin and acetyl choline in the process of impulse transmission has been investigated^{13,27}. It is now established that plants synthesize and presumably utilize a wide range of chemicals which have known neuronal attributes in animals. These include synaptic neurotransmitters such as acetylcholine, glutamate and γ -aminobutyric acid (GABA)^{13,28}. Lam *et al*²² claimed to have discovered the gene encoding putative ionotropic glutamate receptors (GluRs) in plants and presented preliminary evidence for their involvement in light signal transduction. The membrane topology was found to be analogous to animal ionotropic GluRs and their role in rapid synaptic transmission. The existence of other neurotransmitter receptors is surmised. However, a lot more research is necessary to ascertain the existence and precise role of the neurotransmitters and their receptors.

Plant memory, learning and intelligence

In a review of Bose's lifelong research contributions, Shepherd¹⁰ observed, "His overall conclusion that plants have an electromechanical pulse, a nervous system, a form of intelligence, and are capable of remembering and learning, was not well received in its time. A century later, some of these concepts have entered the mainstream literature". Trewavas²⁸ in his commentary on, 'How plants learn' described a large number of protein kinases involved in signal transduction discovered in plants. On the basis of these molecular studies, he concluded that the signal transduction network (in plants) shared properties with neural networks (in animals). Neural network learns by increasing the number of connections. "The increased information flow that results represents a kind of cellular learning. This cellular learning coupled with the memory built into signal transduction systems suggests an unexpected form of cellular intelligence"²⁸.

In his detailed review on the 'Aspects of Plant Intelligence', Trewavas²⁰ considered 'various aspects of plant intelligence' and also reviewed 'other aspects of plant learning, memory, individuality and plasticity'. Attributing these functions to signal transduction is entirely similar between nerve cells and plant cells. In this regard, he quoted Bose's continuous recording of the behaviour of petioles, roots, styles and leaflets of *Mimosa* to thermal, mechanical and light stimuli^{5,29}. According to Trewavas²⁰, the concept of intelligence in animals and plants was not identical because plants are sessile and the time scale of behaviour in most plants differs from animals. The importance of time scale photography for this purpose, as first used by Bose, was highlighted. In yet another publication, 'Green Plants as Intelligent Organisms', Trewavas³⁰ referred to intelligence as the ".....capacity for problem solving". He pointed out, "plant intelligence starts with cell molecular networks. Enormous number of molecular connections integrate into an emergent, organized order that is characterized as living". Quoting the work of several authors, he indicated, "There are ~1000 protein kinases in both animals and plants, providing the capability for numerous complex elements of control, switching mechanisms and interacting positive and negative feedback controls". Plant cell signal transduction is performed by this network which constitutes the basis of intelligence. The author mentioned several behaviours of plants such as competing for resources, foraging for food and protection against environmental and physical impediments by changing their architecture, physiology and phenotype³⁰. Based on an extensive review of the literature, Trewavas³⁰ concluded, "...that plants exhibit the simple forms of behavior that neuroscientists describe as basic intelligence", and remarked, "It is obvious that at present we should regard primate intelligence as much more advanced than that exhibited by plants", but future investigations on plant behaviour might need to reassess this conclusion. Barlow¹³ provided another detailed account of 'Modern beginning of plant neurobiology' as concerned with exploring how plants "perceive signs within their environment and convert them into internal electro-chemical signals (which) in turn, permit rapid modifications of physiology and development that help plants to adjust to changes in their environment". The author discussed, 'Living Systems Theory' in relation to plant neurobiology and plant structure. In this connection, the author deals with memory. According to him, "Memory has not been mentioned in relation to plant neurobiology, but would

evidently have a place there”¹³. As an example, he quotes the memory system that operates in the insect-trapping organ of *Dionaea muscipula*. Discussing decision-making in plants, Barlow¹³ pointed out that certain decision in plants may depend on the ability to construct a ‘memory’. In this connection, he refers to a study by Thellier *et al*³¹ who described a logical (discrete) formulation for the storage and recall of environmental signals in plants. Discussing decision-making in plants, Barlow¹³ referred to the phenomenon of hydrotropism and gravity tropism manifested by the roots and suggested “that the root cap could sense at least four tropic stimuli simultaneously (touch, gravity, humidity and light), and it should be possible to uncover more about how decisions or choices are taken in order to implement one type of tropism in preference to other”. It may be mentioned that Darwin²³ and Bose⁵ had already described these functions of roots.

Cognition, consciousness and self- and non-self in plants

In an address before the British Association in Dublin in 1908, Charles Darwin proposed, “It is consistent with the doctrine of continuity that in all living things there is something psychic, and if we accept this point of view we must believe that in plants there exists a faint copy of what we know as consciousness in ourselves”³². Bose in several of his talks referred to human-like emotions and behaviour in plants. Baluska *et al*¹⁴ in a discussion on Darwin’s ‘Root-Brain’ hypothesis remarked, “The numerous data and results which we review here are clearly not compatible with the classical concept of plants which places them outside the realm of cognitive, animated, animal living systems”. They further added, ‘Recent advances in chemical ecology reveal the astonishing communicative complexity of higher plants as exemplified by the battery of volatile substances which they produce and sense in order to share with other organisms information about their physiological state’. They quoted a number of papers in support of this postulation. Already, in 2004, Gruntman and Novoplansky³³ from Israel have made an astonishing claim that plants recognize self from non-self. They provided evidence, “*B. dactyloides* plants are able to differentiate between self and non-self-neighbors and develop fewer and shorter roots in the presence of other roots of the same individual”. Quoting a number of publications, Baluska *et al*¹⁴ pointed out, “Recent advances in plant molecular biology, cellular biology, electrophysiology and ecology that have

unmasked plants as sensory and communicative organisms, characterized by active problem solving behaviour”. “They possess a sensory-based cognition which leads to behavior, decisions and even displays of prototype intelligence”. They went on to postulate a possible cognitive centre in the root apex of maize. It was hypothesized, “The physiological specificity of plants is mediated by internal oscillations of hormones such as auxin and cytokines and/or electricity that is perceived by the roots through the soil. Such signals are known to be highly dynamic in nature and thus individually unique. Such signals can be potentially perceived and monitored both within the plants and outside roots. Accordingly, the perception of ‘self’ is based on resonant amplification of oscillatory signals in the vicinity of other roots of the same plant”³³.

Conclusions

It is now universally accepted that all plants have a nervous system responsible for gathering information from their environment responsible for their survival and growth. This nervous system functions like that in animals. The nerve impulse (AP) responsible for information transmission in plants from one region to the other, often for long distances, is found to be associated with most of the vital functions of the plant - respiration, photosynthesis, light and gravity tropism, transport through phloem and plant defence. The molecular basis of these functions has now been elucidated in some details^{11-14,16,27}. Thus, the seeds sown by Bose have blossomed into an interesting new field of ‘Plant Neurobiology’, so named by Brenner *et al*¹², and Stahlberg¹¹. The idea of designating this field of scientific endeavour with a new name which has resulted in the establishment of an international society has already developed its opponents. Thus, Amedo Alpi from the Department of Plant Sciences, University of Pisa, Italy, along with 32 other botanists, plant scientists and molecular biologists from Europe, the UK and the USA (8 from Germany, 7 from the USA, 6 each from the UK and Italy, 3 from France and 1 each from Switzerland, the Netherlands and Canada) have published a brief but well-argued paper entitled, ‘Plant neurobiology: no brain, no gain’, in 2007³⁴ questioning the necessity for dignifying it with a title. However, they did not challenge any of the findings of Bose. Hence, their observation in this regard is quoted here, “Plant cells do share features in common with all biological cells including neurons. To name just a few: plant cells show action potentials, their membranes harbor voltage-gated ion channels, and there is

evidence of neurotransmitter-like substances. Equally, in a broader sense, signal transduction and transmission over distance is a property of plants and animals. Although at the molecular level the same general principles apply and some important parallels can be drawn between the two major organismal groups, this does not imply *a priori* that comparable structures for signal propagation exist at the cellular, tissue and organ levels³⁴. It must be reiterated that what Bose described functionally has not been faulted with, and what these authors objected to was never claimed by Bose.

Notwithstanding such detailed studies in the overall field of neurosciences, hardly scientists in the general field of animal neurosciences seem to have utilized the gains of these researches in their work. The microelectrode studies of the nervous system in plants utilizing an elegant self-designed equipment by Bose preceded those in the animals by several years, yet one fails to find any reference to these in the works on animal neuroscience. As a matter of fact, the existence of nervous system akin to that in the animals is hardly known to most of the neuroscientists. Neither did one find reference to these investigations in plants in the main field of neurosciences. Much could be gained if there is a channel of communication between the two groups of scientists working in such tight disciplinary compartments.

In addition, important new physiological features such as the existence of synapses, neurotransmitters and voltage-gated channels, like those in the animal nervous system, have been identified. According to Muday and Brown-Harding³⁵, and Toyota *et al*³⁶, besides serving the functions referred to above, it is now observed that plants have memory, intelligence and learning. It is surmised that they have at least some form of cognition, consciousness and even self and non-self-recognition. Undoubtedly, there are only preliminary data in support of these contentions and therefore, a need for further research in the future. Let me quote a statement attributed to Bose, dictated by his predictive endowments, not constrained by his otherwise strict scientific rigour, because this may open doors for further research and wider interdisciplinary participation; “these trees have a life like ours.....they eat and grow.....face poverty, sorrows and sufferings. This poverty may.....induce them to steal and rob.....they help each other, develop friendships, sacrifice their lives for their children³⁷. Having studied a fairly large number of writings of Bose personally, it is not clear to the present author as to the scientific evidence adduced by him (Bose) to arrive at

this philosophical statement, but it can certainly serve an inducement to explore the neuroscientific basis for it. May be a century later, this may find scientific confirmation like his studies in the early 1900.

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