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Plant neurobiology: an integrated view of plant signaling

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Plant neurobiology is a newly focused field of plant biology research that aims to understand how plants process the information they obtain from their environment to develop, prosper and reproduce optimally. The behavior plants exhibit is coordinated across the whole organism by some form of integrated signaling, communication and response system. This system includes long-distance electrical signals, vesicle-mediated transport of auxin in specialized vascular tissues, and production of chemicals known to be neuronal in animals. Here we review how plant neurobiology is being directed toward discovering the mechanisms of signaling in whole plants, as well as among plants and their neighbors.

The concept of plant neurobiology

To contend with environmental variability, plants often show considerable plasticity in their developmental and physiological behaviors. Some of their apparent choices include: when and where to forage for nutrients and where to allocate those nutrients and derived organic molecules within the organism; when and what organs to generate or senesce; when to reproduce and the number of progeny to create; how to mount a defense against attack and in what tissues or organs; and when and where to transmit chemical signals to surrounding organisms. All these responses must occur within the context of a changing environment, including periodic and meteorological variation regarding light, nutrients, water, wind, temperature and attack. They must be made within the multicellular confines of the complex biological unit of the plant body and, thus, require coordinated cell-to-cell signaling, which requires a sophisticated information storage and acquisition system.

Plant neurobiology (Box 1) is a newly initiated field of research [1] aimed at understanding how plants perceive their circumstances and respond to environmental input in an integrated fashion, taking into account the combined molecular, chemical and electrical components of intercellular plant signaling. Plant neurobiology is distinct from the various disciplines within plant biology in that the goal of plant neurobiology is to illuminate the structure of the information network that exists within plants. Hence, much of the emphasis in plant neurobiology is directed towards discovering and understanding the action of unknown and known systemic signals. These signals are both fast and slow, and are derived from electrical, hydraulic and chemical sources. They include recent discoveries of intercellularly transported macromolecules that regulate development and/or defense pathways, including transcriptional activators [2], RNA molecules [3,4] and peptide hormones [5], as well as decades-worth of information on phytohormones. These and yet to be discovered signals will be brought into a composite view of complex plant behavior with emphasis on the symplastic and apoplastic infrastructure that supports long-distance signaling as well as the downstream gene networks that synthesize this information. New advances in genomics and bioinformatics from a systems-biology approach should further help sift through the complexity of cellular and intracellular information circuitry.

In animals, and particularly in humans, the concept of neurobiology is tightly coordinated with behavior. However, neurobiology also covers the coordinated behavior of communities, whether these be communities of organisms or communities of genes. At the level of unicellular bacteria, special gene circuits coordinate the behavior of inter- and intra-specific bacterial communities; this system has been termed quorum sensing [6]. Therefore, it might not be surprising that multicellular organisms such as plants have developed gene circuits that could regulate the behavior of the community. The field of plant neurobiology will ultimately have to account for how individual plant gene circuits and signals are able to coordinate community interactions. It is becoming accepted that plants in natural environments can regulate the microbial community in their rhizosphere and that functional groups of plants are linked in natural landscapes [7,8]. In the past, pathways and gene circuits

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Box 1. The etymological origin of the word neuron

In Plato, the word ‘neuron’ is used with the connotation of ‘vegetal fibre’. In the dialogs ‘*Cratylus*’, ‘*Theaetetus*’, ‘*Sophist*’ and ‘*Statesman*’: he wrote ‘…and we removed the entire manufacture of cloth made from flax and broom-cords and all that we just now called vegetable fibres (νευρον)…’ [109]. In Athens, a cobbler was a neurorrhaphos or one who sews with vegetal fibers [110]. Thus, in the ancient Greek language, neuron is normally used to indicate a vegetal fiber and for analogy anything of fibrous nature such as a tendon as in Homer’s Iliad: ‘…and he drew the bow, clutching at once the notched arrow and the string of ox’s sinew (νευρον)’ [111]. Indeed, this is the meaning of the word ‘neuron’ as given in the classical *Greek–English Lexicon* by Henry Liddell and Robert Scott [110]. ‘Neuron’ means anything of a fibrous nature.

In animal cell biology, neurons are excitable animal cells that propagate electrical action potentials. Neurons are polarized and equipped with voltage-gated channels and a vesicular trafficking apparatus that is sensitive to calcium signals, mediated via synaptotagmins, induced by electrical signals. This transfer of signals occurs at electro-chemical synapses, allowing direct cell-cell coupling. At the molecular level, plants have many, if not all the components found in the animal neuronal system. There are action potentials (see Box 2), voltage-gated channels, a vesicular trafficking apparatus sensitive to calcium signals, including synaptotagmins and other components of the neuronal cell infrastructure. Plants use plasmodesmata for direct cell-cell transport; these cytoplasmic connections have a poorly described role in electrical coupling between adjacent polarized plant cells [112]. It is also hypothesized that plant cells can become specialized for vesicle trafficking-mediated, polarized hormonal transport.

have been studied at the single plant level, usually at the cellular or subcellular level. However, the ecological significance of these gene responses – in terms of competition and interaction between plants of the same species and other species and with the natural community at large have been overlooked and should be reconsidered.

Plant neurobiology is as new as it is old for it touches upon the controversial question of ‘plant intelligence’. Consider what Virginia A. Shepherd [9] wrote about the work of the eminent plant electrophysiologist Jagadis Chandra Bose (1858–1937): ‘he was the first to recognize the ubiquitous importance of electrical signaling between plant cells in coordinating responses to the environment.’ Bose provided direct evidence that long-distance, rapid electrical signaling stimulated leaf movements in *Mimosa* and *Desmodium* and also showed that plants produce continuous, systemic electrical pulses.

Bose’s 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 hundred years later, concepts of plant intelligence, learning, and long-distance electrical signaling in plants have entered the mainstream literature.

Recently, plant neurobiological aspects have regained an audience, both among the lay press [10–12] and the general scientific community [1,13–15]. Nevertheless, the concept of plant intelligence generates a considerable amount of controversy. Some scientists do not view plants as intelligent organisms and so restrict the concept of intelligence only to animals or even to a specific subset of animals such as chordates or humans. One recent, rather broad definition of plant intelligence is ‘adaptively variable growth over the lifetime of a plant’ [16]. An alternative definition of plant intelligence is an intrinsic ability to process information from both abiotic and biotic stimuli that allows optimal decisions about future activities in a given environment.

This Review article touches on several aspects of plant neurobiology to present some examples of emergent topics in the field. One is the cryptic function of long-distance electrical signals and their poorly understood role in regulating plant responses. The second examines the role of homologous molecules from plants that are similar to neuroreceptors and neurotransmitters in the nervous system of animals. The final aspect discussed is the neurotransmitter-like characteristics of the phytohormone auxin. These examples are intended to show how different topics have overlapping themes within the field of plant neurobiology. Moreover, they also document how information generated in other areas of plant biological research, from molecular and cellular aspects of signal transduction to physiology and even community ecology of plants, might eventually be brought together toward understanding how plants acquire and integrate information so as to coordinate responses affecting the whole plant body.

Early evidence of electrical signals in plants

In 1791, Luigi Galvani provided the first evidence of an electrical signal being behind the ‘mysterious fluid’ that was previously believed to mediate muscle contraction [17]. Stimulated by this discovery, Alexander von Humboldt carried out ~4000 experiments with both animals (including himself) and plants [18]. He concluded that the bioelectrical nature of animals and plants is based on the same principles [19]. Later, Emile du Bois-Reymond [20] used a galvanometer to measure the electrical potential between the intact surface and the cut end of nerve fibers (the first crude recording of a membrane potential). He found that mechanical and electrical stimuli caused a rapid negative signal (‘negative Schwankung’). These experiments represent the first instrumental recording of what he then called an ‘action potential’. Within the next 30 years, action potentials were also measured in two sensitive plants: *Dionaea muscipula* (Venus fly trap) [21] and *Mimosa pudica* [22–24].

These discoveries suggested that the excitability of plant cells could be a means of intercellular communication in plants [24–28]. Despite the repeated demonstrations of electrical long-distance signals in plants, the concept of a plant nervous-analog system lost popularity in the scientific community in favor of a chemical diffusion mechanism of signaling coinciding with the discovery and effects of plant hormones. Moreover, the early anatomical studies revealed particularities of plant cells, such as turgidity and thick cell walls, which were considered incompatible with electrical transmissions. This turn of events was so complete that electrical signals themselves were thought to be caused and mediated by chemicals [29]. Most biologists began to view plants as passive organisms without a need for rapid electrical signals. Later, publicity from pop culture in the 1970s, generated by the controversial book ‘*The Secret Life of Plants*’ [113] (including paranormal claims that plants are attuned to human emotional states), stigmatized any possible similarities between plant signaling and animal neurobiology. Many plant biologists, wittingly or unwittingly, practiced a form of self-censorship in thought, discussion and research that inhibited asking relevant questions of possible homologies between neurobiology and phytobiology. The prohibition against anthropomorphosizing plant function, perpetuated ignorance of the work of outstanding researchers such as Sir John Burdon-Sanderson, Charles Darwin, Wilhelm Pfeffer, Georg Haberlandt and Erwin Bünning, and so prevented the investigation of the roles of electrical long-distance signals. Not surprisingly, the importance of I.I. Gunar's and A.M. Sinykhin's [29] discovery that action potentials exist not only in a few specialized plants such as *Dionaea* and *Mimosa,* but also in cucurbits and other 'normal' plants, escaped mainstream plant science. Barbara Pickard summarized the knowledge of plant action potentials in 1973 [30].

A modern view of the long-distance electrical signals of plants

Since Burdon-Sanderson first measured electrical signals [21], considerable data have been collected measuring and characterizing electrical signaling in plants. Notably, the study of the electrical activity of characean cells, and more recent experiments on guard cells using patch clamp methods have created a strong base for understanding plant electrophysiology at the cellular level. Information about ion channels and transporters is available both from genomic investigations and electrophysiological characterizations of their activities. A big challenge facing plant neurobiologists is connecting this molecular information obtained at the cellular level to understanding long-distance electrical signaling and systemic responses in plants. Plants can propagate two principal types of electrical signals (Box 2). Traps of *Dionaea* flytraps and *Aldrovanda vesiculosa*, as well as of some lower plants, possess omnidirectional action potentials (APs) similar to cardiac myocytes [31]. More common among higher plants are APs that are directionally propagated in vascular bundles along the plant axis. The second type of electrical long-distance signals is slow wave potentials (SWPs) also known as variation potentials (VPs) [32]. SWPs are unique to plants; they follow hydraulic pressure changes that use the vascular bundles (xylem) for propagation over long distances along the plant axis. Studies suggest that both APs and SWPs can be triggered by natural factors (in particular light and shade) [31,33,34]. Aside from affecting cytoplasmic calcium levels, peroxidation, respiration, photosynthesis [31,35,36] and plugging phloem transport by forisomes [37], APs have also been associated with such signaling processes as blue light-induced phototropism [34,38], flower induction [39] and recognition of herbivore attack. Electrical signals have been linked with changes in rates of respiration and photosynthesis [30,35], observed in response to pollination [40,41], phloem transport [42–44], and the rapid, systemic deployment of plant defenses [45–50].

A thorough understanding of how electrical signals are related to these diverse responses is still in its infancy. Novel approaches are necessary to understand the mechanistic particularities of propagating action potentials in plants over much longer distances than the length of an axon in animal nerve cells. Such approaches must be directed towards explaining the role of sieve tubes, companion cells, forisomes and plasmodesmata [51] in propagating these signals. To understand these plant electrical responses fully, such as the photoelectric response of photosynthetic cells, [52], APs [31] and SWPs [32], we will also need to define the molecular basis behind ion-channel function involved in these processes, as well as the many different ligands that trigger these responses.

Box 2. Electrical long-distance signals of plants

Electrical long-distance signaling in plants is well established [31–36,38,39,45,51]. There are two types of electrical long-distance signals in plants: action potentials (APs) and slow wave potentials (SWPs) or variation potentials (VPs) [31,32]. Both appear as transient depolarizations in the membrane potential of affected cells, both signals share a refractory period, a time interval necessary before another signal can be induced or propagated. However, whereas APs are induced after the membrane potential of a cell drops beyond a certain threshold value (implying a crucial role of voltage-gated ion channels), SWPs (VPs) are induced by rapid turgor increase. APs follow an all-or-nothing principle in producing constant, full amplitudes, whereas SWPs (VPs) are graded signals of variable size. While calcium, chloride and potassium channels are involved in the ionic mechanism of plant APs, VPs are thought to involve the transient shut down of the P-type H^+ ATPase in addition to the possible involvement of unidentified ion channels [31,32]. In general, the depolarization reverts more slowly in SWPs than in the short-lived APs and, hence, the term slow in SWPs (VPs).

Animal neurotransmitters and receptor homologs found in plants

A minor sensation was caused in the plant biology community when the first ligand-peptide hormone systemin was identified [53]. Systemin can activate defense responses throughout a damaged leaf within an hour of wounding and throughout the entire plant after a couple of hours [54]. Since then, several peptide hormones have been isolated in plants with roles involving not only defense but also development [5]. Plant peptide hormones are conserved with animal defense or developmental systems that rely on a variety of ligands that activate an ancient system of leucine-rich repeat-containing receptors [55]. Systemin-induced pathways induce depolarization of leaf cells [56]. Whether this action is the direct effect of systemin or mediated through electrical long-distance signals has not been determined [45,50,57]. Among the metabolic neurotransmitters, acetylcholine, catecholamines, histamines, serotonin, dopamine, melatonin, GABA (γ-aminobutyric acid) and glutamate are the most common in the animal nervous system, playing roles in sensing, locomotion, vision, information processing and development. It has long been noted by scientists that each of these compounds are present in plants, often at relatively high concentrations [13]. However, it is unclear whether these compounds play a metabolic or a signaling role in plants despite numerous studies [1,58,59].

Among all these neurotransmitters, strong evidence now supports glutamate as a signaling molecule in plants, particularly with the discovery of a likely target of glutamate in plants – the glutamate receptors [60]. Glutamate causes rapid membrane depolarization in roots coupled with calcium flux in *Arabidopsis* [61], which acts synergistically with glycine to control ligand-mediated gating of calcium channels [62]. Genes that are similar to genes for glutamate receptors in the animal nervous system have been found in plants, including 20 such genes in *Arabidopsis* alone [63]. Physiological evidence indicates a role in growth – potentially as a response to light [60,64], calcium sensitivity [65], nitrogen sensing [66], root growth [67], and aluminum-sensitivity mediated via microtubules [68]. Glutamate receptor agonists found in plants include kainate from seaweed, β-*N*-oxalylamino-L-alanine (BOAA) in grass pea (*Lathyrus sativus*), quisqualic acid from *Quisqualis*, and S(+)-β-methyl-α, β-diaminopropionic acid (BMAA) from cycads (reviewed in Ref. [69]). It is not known if these native plant agonists have protective, metabolic or signaling roles. BMAA has served as a useful compound to understand plant glutamate receptors because it alters morphogenesis in plants by enhancing hypocotyl elongation [64]. Direct genetic evidence has shown that a glutamate receptor in rice is necessary for meristematic function and organization [70], indicating a fundamental role for glutamate signaling in plant growth and development. Plant glutamate receptors are phylogenetically related to GABA receptors in animals [71]. Like glutamate, the role of GABA is undefined. GABA, which is readily produced from glutamate via glutamate decarboxylase and detoxified via GABA deaminase has also been implicated in long-distance sensing as a signal for nitrogen availability [72]. GABA has also been implicated as a maternal signal in the directional growth of pollen tubes to the ovule [73] (the role of GABA in plants is reviewed in Ref. [74]). Besides glutamate and GABA, the neurotransmitter acetylcholine has also gained strong support as a signal in plants recently [75]. Acetylcholine is the only neurotransmitter that is inactivated by enzymatic cleavage via acetylcholinesterase activity. This enzyme is specifically inhibited by neostigmine bromide. Interestingly, neostigmine bromide inhibits the graviresponse of maize roots; this enzyme was cloned in maize recently [75]. *In silico* screening has shown that homologs of maize acetylcholinesterase are widely distributed in plants [75].

Several tryptophan derivatives have been investigated for their role in signaling, including serotonin, which has been the subject of numerous studies in plant development but whose role remains elusive [13]. Melatonin has also been detected in plants and has been shown to have a role in a variety of complex processes such as flowering [76,77]. Interestingly, in this respect, the most important signaling tryptophan derivative in plants is auxin, which has a basic regulatory role in plant growth and development. Auxin, which is transported cell-to-cell, also has some characteristics reminiscent of neurotransmitters as described below.

Neurotransmitter-like cell-cell transport of auxin

Polar transport of auxin is inherently linked to signaling-based regulation of growth and polarity of plants. For instance, the plant body is shaped in response to environmental gradients, particularly of light and gravity [78,79]; these factors influence auxin transport such that the hormone is delivered to tissues induced to grow. Auxin is transported across the whole plant body via effective cell-cell transport mechanisms involving both the symplast and the apoplast. However, it is not clear why auxin bypasses the cytoplasmic channels of the plasmodesmata crossing through the apoplast, whose diameter could easily accommodate several auxin molecules. This suggests the presence of an active mechanism that prevents auxin entering the plasmodesmata [80] and implies a functional benefit for including an apoplastic step in the polar transport of auxin.

Transcellular auxin transport is accomplished via a poorly understood vesicle-based process that involves the putative auxin transporters, or transport facilitators, recycling between the plasma membrane and the endosomes [58,81,82]. Both PIN proteins [83,84] and certain ABC transporters have been shown to function in the polar transport of auxin [85]. Importantly, cell-cell transport of auxin is based on continuous vesicular trafficking because classical inhibitors of exocytosis, such as Brefeldin A and monensin, inhibit the polar transport of auxin within minutes in treated suspension cells [86] and intact root apices [87]. Moreover, auxin is enriched within endosomes and the cell wall region between cells across which the transcellular transport of auxin takes place [88]. Importantly, mutated PIN2 (pin2Gly97) expressed in budding yeast cells localized exclusively to intracellular compartments but was still functional in auxin transport. This particular finding strongly suggests that PIN2 can act as a vesicular transporter [84].

All these features suggest a similarity between auxin and neurotransmitter release from neuronal cells [58,81,89,90]. Considering that auxin is known to induce fast electrical responses when applied extracellularly [91–93], the role of auxin can be seen in a new light when viewed from the plant neurobiology perspective [58]. One hypothesis is that auxin molecules, secreted via auxin-enriched vesicles [88], elicit electrical responses in adjacent cells within a few seconds [93]. Such electrical activation would be reminiscent of signaling molecules with neurotransmitter-like properties [81]. These fast electrical responses at the plasma membranes encountering extracellular auxin molecules might be mediated via the ABP1 (auxin binding protein)-based signaling cascade [93,94] or some other receptors. This signaling cascade is likely to be distinct from the auxin-induced responses with a lag-time of many minutes to hours, which are based on auxin receptors and generally involve changes in gene expression [95] via auxin-mediated activation of transcriptional regulators known as auxin response factors [96]. Furthermore, secreted auxin molecules interact with cell wall peroxidases, inducing the formation of reactive oxygen species within the cell wall [97]. These highly reactive molecules act as potent signaling molecules in plants [98,99]. Moreover, auxin signaling is also closely linked to nitric oxide [100], which has numerous roles at neuronal synapses [101]. Further examination of the dynamic signaling properties of intercellularly transported auxin is an important topic that falls well within the realm of plant neurobiology.

Last but not least, *Arabidopsis* cells express and use large batteries of neuronal molecules supporting endocytosis, vesicle trafficking and regulated secretion [102–108], driving the cell-cell communication at chemical neuronal synapses. This robust vesicle trafficking apparatus of *Arabidopsis* fits well with the predictions made by plant neurobiology.

Outlook

Recent advances in plant biology, including molecular genomics and cell biology, as well as in chemical and biochemical ecology, will now allow us to study plants as behavioral organisms with a capacity to receive, store, share, process and use information from the abiotic and biotic environments. How plants acquire information from their environment, both abiotic and biotic, and integrate this information into responsive behavior is the focus of the emerging field of plant neurobiology. Understanding this complex plant behavior within the field of plant neurobiology will require the combined efforts of plant scientists from diverse backgrounds and from all disciplines.

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