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OPINION

Are plants sentient?

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Abstract

Feelings in humans are mental states representing groups of physiological functions that usually have defined behavioural purposes. Feelings, being evolutionarily ancient, are thought to be coordinated in the brain stem of animals. One function of the brain is to prioritise between competing mental states and, thus, groups of physiological functions and in turn behaviour. Plants use groups of coordinated physiological activities to deal with defined environmental situations but currently have no known mental state to prioritise any order of response. Plants do have a nervous system based on action potentials transmitted along phloem conduits but which in addition, through anastomoses and other cross-links, forms a complex network. The emergent potential for this excitable network to form a mental state is unknown, but it might be used to distinguish between different and even contradictory signals to the individual plant and thus determine a priority of response. This plant nervous system stretches throughout the whole plant providing the potential for assessment in all parts and commensurate with its self-organising, phenotypically plastic behaviour. Plasticity may, in turn, depend heavily on the instructive capabilities of local bioelectric fields enabling both a degree of behavioural independence but influenced by the condition of the whole plant.

1 | INTRODUCTORY BACKGROUND

Probably, 95% of plant biologists would reject any association of sentience with plant life. So did the authors of this article initially. But an investigation of older literature combined with present understanding led us to a more agnostic position; the question mark in the title remains—at present (Calvo, 2016, 2017; Trewavas & Baluška, 2011).

This article is mainly concerned with electrical (and bioelectrical) communication in plants. This is nothing new; it has been known for over a century that electrical signals are conducted and, in certain cases, initiate visible responses. What is more recent is that electrical signals are in part mediated by cytosolic Ca^{2+}. The aequorin method, for example, enabled cytosolic Ca^{2+} kinetics to be easily determined (Knight, Campbell, Smith, & Trewavas, 1991). Aside from demonstrating that many signals to which plants respond also generate cytosolic Ca^{2+} transients, finding that the latent period of response is usually less than a second was also salutary (Trewavas, 2011). Although changes in behaviour to the signal were very much slower than the visible movement common in animal responses, the initial signal detection via Ca^{2+} was often at rates similar to those in animals (Trewavas, 2011). Cytosolic Ca^{2+} signals are mediated by hundreds of proteins and protein kinases (Luan, 2011; van Bel et al., 2014). Many of the same signals inducing cytosolic Ca^{2+} transients also induce action potentials in plants; the two are probably intimately related.

Likewise, what is more recent, at a higher level of description, is that plants prioritize between signals in the order of response. Animals prioritize their signal responses using sentience. Plants currently have no known mental state to prioritize theirs, and yet they use groups of coordinated physiological activities to deal with defined environmental situations. The phloem is the pathway for electrical communication, with the plant nervous system based on action potentials transmitted along vascular conduits stretching throughout the whole plant body. In this article, we report that this communication network is highly cross-linked through anastomoses and other transverse links, forming a truly complex network. We cannot discard among the emergent properties of such system, the potential for overall assessment as mediated by mental states. Whether the excitable network of plants form, a mental state is unknown, but it does not escape us that it might in principle be exploited to distinguish between different and even contradictory signals to the individual plant and thus determine a priority of response. This is commensurate with its self-organizing, phenotypically plastic behaviour. We shall suggest some future investigations and the potential involvement of bioelectric fields in plant learning and memory. In what follows, we start with the basics and build up progressively to the more controversial aspects of this article.

Action potentials in plants are carried by the phloem (Bose & Guha, 1922). Sir J. C. Bose, FRS, an Indian physicist who worked initially with John Strutt (Lord Rayleigh) and was the first to use semiconductor junctions to detect radio signals, was not the first to characterize action potentials in plants that is usually identified with Burdon-Sanderson (1873, 1899) in the Venus fly trap. But Bose contributed very much more to plant electrophysiology. He did experience extensive criticism from Burdon-Sanderson, among others (Shepherd, 2012), who claimed, wrongly, that only plants with visible movements used electrical signals. Bose demonstrated that many species did likewise and furthermore provided a wealth of information on the nature of the electrical signal. Although we do not like the terminology, Bose was the Father of plant electrophysiology, and he is considered one of the Fathers of radio science too. His contribution needs better recognition, and we attempt to repair this situation here (see also Shepherd, 2012).

In 1926, Bose published *The Nervous Mechanism of Plants*. Surprisingly, we have seen it seldom referenced in modern publications. Maybe the term “nervous” worried some who think it smacks too much of trying to make plants green animals. To address that reasonable criticism, we have used the terms phytoneurone to refer to sieve elements carrying an electric current and phytoneurology for this general subject area. Bose however was very clear; plants had “a system of nerves that constituted a single organised whole” (Bose, 1926, p. 121).

The term “system” has a direct meaning. Systems are composed of networks; they act as integrated entities because of the connections and cross linking between the elements. Systems have emergent properties, and these properties depend on the behavioural characteristics, number and density of the linkage between the elements (Trewavas, 2007). In this case, the elements are phloem or sieve elements that are cross-linked. What is surprising is that those who work in the electrophysiological area and those who examine phloem anatomy have not managed to put these two features together. Either the emphasis is laid upon phloem anastomoses regarded as an “emergency system” for the sake of fast, alternative response pathways (Aloni & Peterson, 1990) or upon the role of plasmodesmata and not anastomoses, in cell–cell transport and communication (van Bel & van Kesteren, 1999). The only holistic cross linked, excitable networks, as such, familiar to us in biology are those found in animals. Whether this plant version has equivalent properties remains to be seen, and thus, the uncertainty expressed above. The potentially unique qualities of this network and how it pertains to critical aspects of plant life need to be investigated more thoroughly. The relationship and interaction with bioelectric fields need better understanding and investigation too. We suggest below some potential experimental ways forward that might clarify some of its overall behaviour.

In many animals, physiological and behavioural events are grouped which are activated by particular signals. They use mental states and processes to prioritize which response groups need to be attended to first. Plants also group together physiological and morphological events in response to particular environmental circumstances. It is suggested that prioritizing signals, when commonly presented with many sources of stimulation, will be one function of the phytoneurological system in plants (Calvo & Friston, 2017).

2 | THE NATURE OF ANIMAL FEELINGS AND SENTIENCE

Sentience has long been regarded as the capacity to feel, in contrast to reason or logic. A recent extensive review summarizes current understanding in animals (Damasio & Carvalho, 2013). Feelings such as sadness, anger, fear, joy, compassion, pain, and others are thought to be mental experiences of body states but are recognizably subjective. Is the internal experience of any feeling the same between different individuals (Calvo, 2017)? Even more difficult is the question of animal sentience and is hugely controversial (Boyle, 2009). Commonly, this discussion hinges around pain and the activities of nociceptors. These transmit information to the brain on tissue damage and the detection of noxious or potentially noxious circumstances eliciting the pain sensation. Those signals that cause pain in animals (damage, heat, cold, etc.) do actually induce action potentials in plants (see later).

Feelings in humans, like most other human characteristics, are present because they plausibly served a role in selection and subsequent evolution. They represent mental states that are connected to groups of physiological and metabolic activities, focussed on required individual behaviours. Perhaps, the most familiar feeling to the reader is that of flight or fight, which can vary enormously in intensity between human individuals. The threat signal generates a mental state involved in energizing the familiar group of physiological responses: increased cardiac and respiratory activity, elevated blood flow rates and blood sugar, dilated pupil, and increased secretions of adrenalin and cortisol, amongst others. By providing the necessary assessment of a potential or potentially threatening future, the brain prioritizes, amongst a plethora of potential competing information, which ones need to be attended to first (Calvo & Friston, 2017).

Feelings are thought to originate in the brain stem, and thus, their evolution is probably ancient. They do use unmyelinated nerve cells, and thus, the route of transmission is open to surrounding circumstances (Cook, 2006). The membrane potential is considered more of a relevant guide to the involvement of particular nerve cells than supposed connections. What came first was the grouping of physiological responses together in response to defined environmental perturbations; only later, it is suggested, were these coordinated by nervous activity. The incorporation of mental states helped provide the organism with a potential guide to adaptive behaviours including forms of perception that underwrite purposeful, anticipatory behaviour, learning, and memory. An illustration of the way plants respond selectively to salient features of the environment, proactively sampling their local environment to elicit information with an adaptive value, is provided by the hierarchical deployment of distinct vascular cell populations, encoding expectations in plants, and functionally analogous neural architectures in the case of animals, with cross linked and bidirectional (forward and backward) communication pathways (Calvo & Friston, 2017; Friston, 2013).

3 | COULD PLANT BE SENTIENT?

Sentience is rejected for plants for the following reasons (Animal Ethics Inc, n.d. www.animal-ethics.org/beings-conscious; Grinde, 2013):

1. Plants are simple. They do not move and thus do not need a nervous system.
2. The capacity to feel arose in evolutionary terms solely from its usefulness in motivating animals; it does not make sense for plants that cannot run away from a threat or forage for a food they enjoy.
3. The supposed absence of a mechanism for transmission of information similar to the animal nervous system.
4. Plants do not have brains, the supposed seat of feelings.

Most of the above arises from a common perceptual fallacy. We, ourselves, are animals and thus tend to judge all of nature from an animal perspective only. If it does not appear to move, for example, it does not behave. Our ability to see any movement has quite severe constraints on detection, and time lapse has illustrated that failing. The cell wall, necessary to contain osmotically active photosynthetic products, was the primary constraint on preventing easy movement and, in turn, through its multicellular use as a skeleton and fitness competition responsible for tip growth and branching of trees. In addition, using established criteria of complexity, angiosperms and mammals could not be distinguished (Trewavas, 2014, chapter 7). Earth is a planet dominated by plants. If oxygen and carbon dioxide reflect the abundance of photosynthesis to respiration, then 99% of the life is plant. The forms of behaviour in plants such as phenotypic plasticity and chemical changes are the biologically dominant kind, not movement visible to us in our time frame (Trewavas, 2009, 2014).

4 | THE “NERVOUS” SYSTEM IN PLANTS

The major contention of the above is the supposed lack of a nervous system. The familiar anatomical animal neurone has no equivalent in plants but that was known several centuries back. However, the lack of obvious anatomical neurones does not preclude a functional, excitable equivalent, a phytoneurone, capable of electrical transmission, which most certainly is present.

In the early 20th century, Bose investigated the electrophysiology of plants in detail on returning to India, publishing both journal papers and the better-known books.[1] His electronic expertise enabled him to construct many pieces of extremely elegant electrical equipment, well before others. Amongst many, he could, for example, monitor electrical activity and determine latent periods of electrical response (within 0.005 s) and the velocity of transmission of action potentials (Bose, 1914). He also constructed a device (a crescograph) that enabled plant growth to be detected and measured every 15 min (Bose, 1920). His books describe others.

In 1926, he published *The Nervous System of Plants*, which contradicts the above claim that an analogous system is absent in plants. The book contains some 100 experiments on various plants; some of which are to be found in his published papers. His previous studies are summarized in the preface: “The most important fact established in plant response was the nervous character of the impulse transmitted to a distance.” The electrical transmission is an all-or-nothing action potential. “The response of the isolated plant nerve is indistinguishable from that of the animal nerve, through a long series of parallel variations of condition” (all page viii). He reported the “transformation of the afferent or sensory into an efferent or motor impulse in the reflex arc of *Mimosa*” (page ix). He identified the phloem as the phytoneurone (Bose & Guha, 1922). This tissue therefore has dual functions, that of organic transport and electrical excitation transmission.

4.1 | Modern investigations support many of Bose conclusions

Numerous modern investigations (e.g., Favre & Agosti, 2007; Fromm & Lautner, 2007; Pickard, 1973; van Bel et al., 2014; Volkov & Ranatunga, 2006; Yan et al., 2009; Zimmermann, Mithöfer, Will, Felle, & Furch, 2016; and references therein) have confirmed the validity of some of these early claims of electrical communication by Bose. Because the phloem is to be found throughout any higher plant, the potential for very long distance communication in large plants exists, incidentally, at considerable speeds (Fromm & Bauer, 1994; Fromm & Lautner, 2007; Galle, Lautner, Flexas, & Fromm, 2015; Yan et al., 2009; Zimmermann et al., 2016). Action potentials in plants can move from 0.5 to 40 cm/sec, and the distance covered may be helped by the recently described system potentials (Choi, Hilleary, Swanson, Kim, & Gilroy, 2016; Zimmermann et al., 2016). In young trees, damage or cold shock to one leaf is experienced by other leaves remote from the signal (Gurovich & Hermosilla, 2009; Lautner, Grams, Matyssek, & Fromm, 2005; Oyarce & Gurovich, 2010).

In addition to action potentials, variation potentials have also been characterized, and the properties are reviewed in van Bel et al. (2014). These variation potentials are at least 20 fold slower in transmission and may last up to 30 min, influencing surrounding cell behaviour during this time period. Variation potentials are also dose dependent and more localized near to the site of stimulation. These two phytoneurological signals (action and variation potentials) rapidly separate from each other following signal initiation. Specific information may thus be conveyed by the separation of distance between these two phytoneurological signals, as well as amplitude, duration and profile, which appear also to be signal specific.

Voltage-gated (Ward, Mäser, & Schroeder, 2009) and mechanosensitive channels (Hamilton, Schlegel, & Haswell, 2015) are present in the phloem (Volkov, 2012). Action potentials are initiated through specific chloride channels followed by activation of calcium and potassium channels, as membrane potential declines. Plasmodesmata transmit the excitable state and variation potentials

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[1] We could find no biological publication bibliography for Bose, and he was not eager to refer to his own publications in his books. We have included what we could find in the reference list as Bose, 1902, 1903, 1914, 1915, 1920, Bose & Das, 1916, 1919, 1925, and Bose & Guha, 1922. One long paper of 130 pages submitted in 1904 to the *Proceedings of the Royal Society B* was the source of unresolved contention and remains unpublished in their library archive. Its contents have been provided to us by the librarian but would need expensive photography for a copy. The contents cover details of experimental material found later in his nine books that are listed at https://en.wikipedia.org/wiki/Jagadish_Chandra_Bose.

to other surrounding nonphloem cells. Transient increases in cytosolic Ca^{2+} are one important consequence, not only in the phloem but also in surrounding cells, where they can initiate cytosolic Ca^{2+} waves (Choi et al., 2016; Furch et al., 2009). Numerous calmodulins, hundreds of calcium-sensitive proteins, and protein kinases continue to relay the signal through the metabolism of recipient cells (Luan, 2011).

The initiating signals currently known to induce action potentials include herbivory and physical damage, leaf and fruit removal, rapid stressful temperature variations, light–dark changes, mechanical stress from bending, amongst others (Fromm and Lautner, 2007; Galle et al., 2015; Pickard, 1973; Trebacz, 1989; Yan et al., 2009). The balance between photosynthesis and respiration is often diminished. Repair and resistance mechanisms, both short and long term, are induced. These help prime the plant by the synthesis and release of both hormones and defence chemicals. Specific turgor and transcriptional changes are induced, as well as wall hardening, natural pesticide synthesis, the production of gums or attraction of parasitoids specific to the herbivore, by volatile chemical release (Frost, Mescher, Carlson, & de Moraes, 2008).

5 | THE NERVOUS SYSTEM OF PLANTS CONSISTS OF COMPLEX NETWORKS OF EXCITABLE TISSUES CARRYING ELECTRICAL SIGNALS

The closing line of *The Nervous System of Plants* reads: “No structure corresponding to the nerve-ganglion of an animal has, indeed, been discovered in the pulvinus of *Mimosa pudica*, but it is not impossible that the physiological facts may one day receive histological verification.” (Bose, 1926, p. 218).

Although Bose failed to find an analogous equivalent, the “glomerulus” composed of a complex stack of interconnected phloem bundles and several millimetre in length suggests one might well exist (Behnke, 1990). This phytoneurological system is highly cross-linked. Figure 1 (fig. 54 from Bose, 1926) shows the vascular system of *Papaya* to consist of vascular elements cross-linked extremely frequently by numerous, irregularly distributed and tangential connections. A network of excitable phloem cells is clearly present. “How reticulated they (the vascular bundles) may often be, even in the trunk of a tree, is shown in the photograph of the distribution of vascular bundles in the main stem of *Papaya* …. This network of which only a small portion is seen in the photograph girdles the stem throughout its whole length and in this particular case, there were as many as twenty such layers one within the other” (Bose, 1926, p. 121).

In very young plants, such as *Helianthus* seedlings, phloem anastomoses (cross links), up to 7,000/stem internode in number, have been reported. How common this cross linking might be remains unknown (Aloni & Barnett, 1996; Aloni & Sachs, 1973). It is speculated that auxin might be responsible for their formation, and that they might have a function in xylem regeneration. Computer-assisted tomography has been used to identify a complex network of xylem vessels (Brodersen et al., 2011). However, xylem does not differentiate in the absence of phloem, although the converse is not true (Roberts, Gahan, & Aloni, 1988, p. 47). The observed vessel network probably indicates the phloem network too.

FIGURE 1 Distribution and network of vascular tissue in a single stem layer of *Papaya*. According to the text in the script, there are 20 such layers of vascular tissue, one inside the other (like Russian dolls) and surrounding the whole trunk. The bundles are connected through enormous numbers of tangential connections and perhaps anastomoses to form a complex excitable structure. “The existence of a system of nerves enables the plant to act as a single organised whole” a requirement perhaps for selection on fitness. Figure and quote taken from fig. 54, page 121, Bose (1926) [Colour figure can be viewed at wileyonlinelibrary.com]

In more mature stems and trunks, with the appearance of additional secondary and supernumerary cambia, and other features of secondary growth, plant vascular architecture becomes extremely complex. Tangential connections and anastomoses between numerous bundles become very frequent as do radial connections between different stem layers (Carlquist, 1975; Dobbins, 1971; Horak, 1981; Wheat, 1977; Zamski, 1979). These anastomoses do not occur simultaneously in the xylem and phloem but construct a “complex net-like structure” already observed in some related 20 families of plants (Zamski, 1979). The complexity of the excitable phloem network is nothing like the simple structures of vascular tissue presented in text books that are usually limited to seedlings. Woody tissues, often xylem, are sometimes penetrated by interxylary phloem. Starch is deposited in the xylem that is then mobilized on a seasonal basis.

5.1 | Importance in establishing the presence of a network.

Even very simple networks of some five interconnected nerve cells using all-or-none action potentials exhibit a capability for memory, error correction, time sequence retention, and a natural capacity for solving optimisation problems (Hopfield, 1982; Hopfield & Tank, 1986; McCulloch & Pitts, 1943). Some of these capabilities are present in plants although they are not specifically identified with the phloem system (Trewavas, 2017). Thus, knowing the complexity of this phloem based network might improve understanding of these behavioural properties of plants.

Is this network and its behaviour sufficiently complex in behaviour and memory to be analogous to mental states? Again, we cannot comment until the network complexity is better understood, and the frequency and particular qualities of the cross linkages investigated.

6 | LEAF EXCITABLE PHLOEM NETWORKS

The vascular tissue of dicotyledonous leaves forms a highly branched network that penetrates throughout the blade. There are at least four orders of vein based on diameter with the smallest covering over 80% of the vein length (Sack & Scoffoni, 2013). The higher orders are constructed of larger conglomerates of vascular elements. The extent of phloem cross linking here remains unknown but evidence suggests there may be some segregation in electrical function.

1. Leaf movement and action potentials.

The leaf blades of many seedlings and trees are usually positioned at right angles to the primary or average light direction (Koller, 1986; Trewavas, 2014, and references therein). The motor organ is either the pulvinus or the petiole that moves the leaf blade according to perceived light signals. The epidermal cells of leaves frequently have a hemispherical structure, or other more detailed structure such as an ocellus, that focuses light on the basal epidermal membrane (Haberlandt, 1914). When the blade is out of position, the focussed light hits a different basal membrane region and sets in motion torsional adjustments in the motor organ, to bring the blade back into an optimal light-collecting position. If the intensity of light is damaging, the motor organ in many species will move the blade to reduce exposure. In some species such as *Simmondsia*, the highly turgid leaves are placed edge on to the light direction during the hottest part of the day (Sultan, 2015). The leaf epidermal cells act therefore as a sensory epithelium. Phytochrome and cryptochrome, the light sensitive pigments here, both initiate changes in membrane potential and subsequent rapid cytosolic Ca^{2+} transients, and there is crosstalk between the two sensory systems (Baum, Long, Jenkins, & Trewavas, 1999; Shacklock, Read, & Trewavas, 1992).

Action potentials, generated in the leaf by light exposure, can excite the different regions of the motor organ to change their degree of torsion thus moving the blade (Bose & Guha, 1922). The generated action potential is a holistic construct from millions of epidermal cells. When action potentials were induced separately in either side of the leaf, these signals had separate twisting torsional effects on the two opposite sides of the motor organ, enabling a change in leaf blade position by a push or pull mechanism. Even though the leaves of the *Helianthus* plants in these experiments join the central vein, the electrical information seems insulated between the two sides.

2. Leaves generate action potentials in response to mechanical damage from caterpillars.

Leaves are the targets of many insect herbivores. Wounding of one leaf is transmitted to others via sensing through glutamate receptors (Mousavi, Chauvin, Pascaud, Kellenberger, & Farmer, 2013). Although there are glutamate receptors in plants and glutamate induces cytosolic Ca^{2+} transients, these receptors are also activated by numerous amino acids suggesting that they may be directly activated by tissue damage and broken cells (Forde & Roberts, 2014). The action potential generated by damage transmits information elsewhere to induce numerous defence reactions locally (Fromm & Bauer, 1994; Zimmermann et al., 2016). Expression changes lead to increased circulation and synthesis of salicylate and emission of volatile compounds such as jasmonic acid and ethylene. These volatile signals not only generate local defences but can be sensed by more remote weakly connected areas of the plant and importantly adjacent plants that remember the perceived signal for many days (Ali, Sugimoto, Ramadan, & Arimura, 2013).

3. Is an action potential induced by temperature change used to coordinate homeostatic responses accordingly?

Leaves of many species maintain an internal temperature of 21.4 ± 2.2° C throughout the growing season whilst the external environment varies from 6 to 30° C (Helliker & Richter, 2008). A variety of mechanisms (blade movement, stomatal aperture control, chloroplast movement, hair number variation, changes in reflective or nonreflective wax and branch local leaf number) are used to either warm or cool the leaf, helping to operate this form of homeostasis (Trewavas, 2014). Some of these changes can take just a few minutes, others, a few days. A leaf-wide action potential, we surmise, might be the initiator of this programme. Cells adjacent to the phloem would either experience an action potential themselves or longer-lived variation potentials. More research is needed; however, before electrophysiological facts can receive confirmation.

7 | POTENTIAL CONTROL OF TRANSMISSIBILITY IN THIS EXCITABLE PHYTONEUROLOGICAL NETWORK

The acquisition of short-term animal memory parallels synaptic strengthening that lasts from minutes to hours and is mediated through glutamate sensitive Ca^{2+} channels (Kandel, Dudai, & Mayford, 2014). Long-term memory also parallels synaptic strengthening that lasts from days to weeks. The two are distinguished by the fact that long term memory requires protein synthesis. The production of memory from a learning signal results from increased transmissibility of action potentials through specific nervous channels and distinct pathways. Its progress can be modified in transit by surrounding and synaptically connected nervous pathways.

7.1 | Sieve plate-controller of electrical transmissibility?

This excitable plant network consists of sieve tube elements, companion cells, and finally sieve plates that separate adjacent sieve elements. The plate contains pores whose numbers and cross-sectional area can vary from one to several hundred/square micrometre and from hundredths of micrometres to micrometres in size (Bussières, 2014).

The route of an action potential may involve both the companion cell and the sieve element and plate (Oparka & Turgeon, 1999).

The passage of an action potential initiates the release of cytosolic Ca^{2+} (Furch et al., 2009; van Bel et al., 2014). Contractile protein bodies (P-proteins or forisomes in the *Fabaceae*) are located adjacent to the sieve plate and adjacent to ER calcium channels. They undergo immediate geometrical change (<1 s) when cytosolic Ca^{2+} is released, reversibly plugging the sieve plate pores (Peters, Van Bel, & Knoblauch, 2006). Recovery of the forisome in its undispersed form takes some 10 min or so. If the sieve plate was not blocked by the action potential, then back flux of K^+ from the next sieve element in line could block further transmission of the action potential. The sieve plate may then control differential transmissibility analogous to controlling synapses in animal electrical systems. Actin is closely associated with the pore (van Bel et al., 2014) and filaments contract when Ca^{2+} increases. An additional mechanism of pore blockage may thus be present.

7.2 | Differential electrical transmissibility in the phloem.

Figure 2 shows that differential electrical transmissibility results from thermal or electrical stimulation in the phloem. These data have been selected from a number of similar responses (e.g., Bose, 1907, 1926). The after-effect of a short thermal signal administered to the main phloem bundle of a *Helianthus* leaf results in increasing transmissibility of successive but equal shocks measured with a galvanometer (Figure 2a). Figure 2b reports the after-effects of successive equal strength shocks increasing transmissibility in the phloem of the fern, *Adiantum*. Figure 2c reports that successive equal shocks reduce transmissibility in *Mimosa* as an after-effect of previous repetitive stimulation. Bose separated successive shocks by some 15 min and showed that more frequent administration of shocks reduced transmissibility. In animals, the reduction in transmissibility is associated with habituation (Kandel et al., 2014). Habituation of mechanical response has been observed in *Mimosa* (Gagliano, Renton, Depczynski, & Mancuso, 2014).

As well as these examples, transmission changes may also be primed by small directional currents applied with or against the direction of transmission (Bose, 1915). Conductivity was reduced when in the direction of the small current and enhanced when against it. Transmission is clearly alterable in the phytoneurological network, one fundamental requirement for a learning capability.

8 | FURTHER EXPERIMENTAL INVESTIGATIONS NEEDED

1. Numbers of anastomoses or phloem cross linking.

There is a dearth of measurement of anastamose numbers in phloem tissues. Measurements are needed particularly with changes in development and environmental variation. Rapid advances in microscopy such as two photon laser scanning and other multiphoton

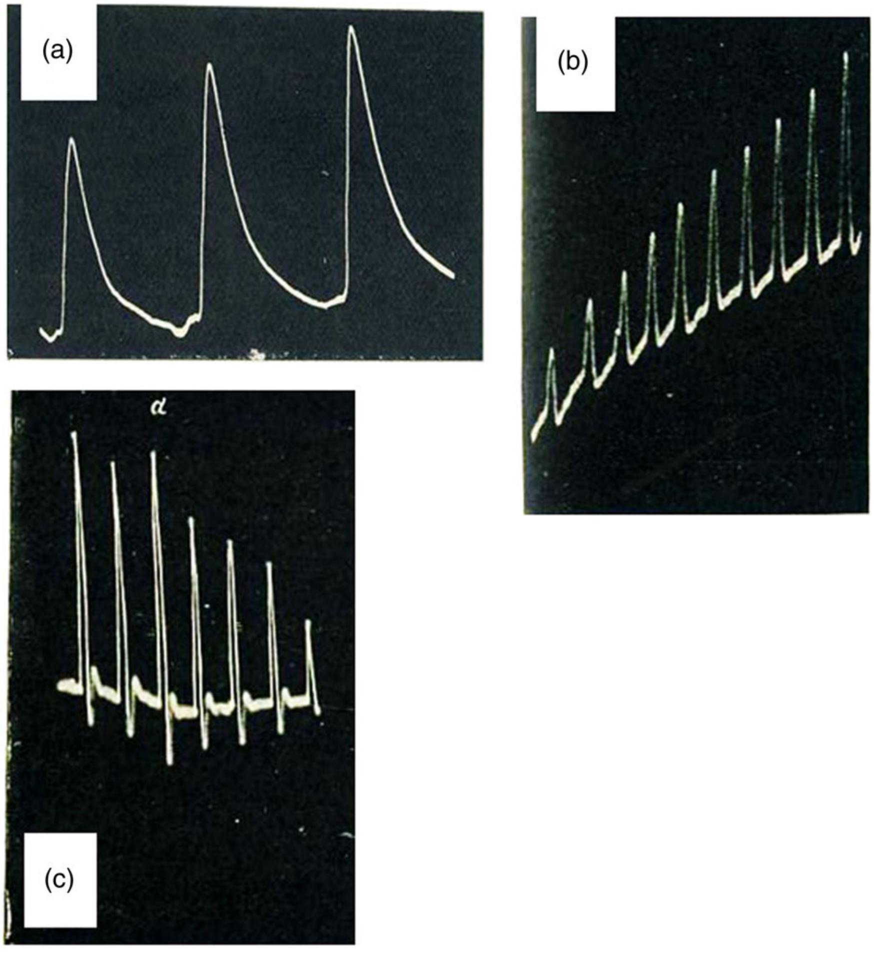

FIGURE 2 The transmissibility of equal electric shocks to some phytoneurones can be facilitated or inhibited. The equipment and circuit diagram used by Bose to administer equialternating shocks is illustrated in chapter 21, Bose (1907) and further circuitry in Bose (1915) and Bose and Guha (1922). **(a)** Increased electric transmission of *Helianthus* leaf midrib phloem as an after-effect of a transient thermal stimulus to one short region of the phloem (fig. 41, Bose, 1926). Relative transmission of single identical shocks increases in two successive measurements. According to Bose, there is an initial block in transmission that is progressively overcome by successive shocks providing a staircase increase whose transmissibility eventually levels off. **(b)** The after-effects of successive electrical shocks on the transmissibility of *Adiantum* phloem, (fig. 55, Bose, 1907). The transmissibility continues to increase with successive shocks. **(c).** The after-effect of previous electrical stimulation on transmissibility in the *Mimosa* petiole (fig. 198, Bose, 1907). Note the slow reduction in transmissibility which Bose claims is fatigue. Bose indicates that similar effects can be obtained by reducing the interval of shocks from 15 to 10 min

procedures have enabled penetration of several millimetre into living tissues (Truong, Suppato, Koos, Choi, & Fraser, 2011). With suitable clearing methods, the claim is up to 8 mm (De Grand & Bonfig, 2015). Methods for phloem imaging and in particular live imaging are available (Cayla et al., 2015; Furch et al., 2009; Truernit, 2014). Using green fluorescent protein (GFP) coupled proteins together with a specific sieve element promoter should greatly simplify examination and ease the assessment of anastomose numbers. A specific sieve element promoter is available, and coupled to GFP coupled proteins enabling fluorescence microscopy should ease collection of data on anastomoses (Froelich et al., 2011). Live imaging of numerous fluorescent GFP-coupled proteins in sieve elements of transformed *Arabidopsis* leaves has been reported (Cayla et al., 2015). Methods are thus available to establish whether anastomoses are truly elements of the phloem.

Computer assisted tomography has been used for xylem network analysis (Brodersen et al., 2011), and a cursory investigation using microscopic techniques might indicate that the xylem branching acts as a surrogate for phloem anastomoses too. There is unfortunately no information from Bose (Figure 1) as to the methods used for the vasculature of *Papaya* although these must have been simple procedures at the time.

2. Anastomose formation. It has been suggested that auxin is responsible for cross-link formation (Aloni & Sachs, 1973). In that case, measurements of numbers in auxin mutants might clarify this possibility. If cross-link formation is indeed auxin-dependent (or dependent on other hormones or electrical signals), then the numbers might reflect the history of auxin or other inducing signal involvement in development and environmental variation. Other functions need to be distinguished from electrical behaviour.
3. Anastomose function. If these are part of an electrical network, then that capability needs to be demonstrated. One major and helpful advance has been the construction of fluorescent dyes that report action potentials (Miller et al., 2011; Zhou et al., 2015). Together with the microscopic techniques described above, these probes should indicate whether anastomoses transmit action potentials. One piece of evidence suggests this possibility. Lautner et al. (2005) initiated an action potential in the leaf on one side of a young poplar tree and detected its appearance in a leaf on the alternate side, lower down. The ease and distance with which the action potential can be detected in phloem bundles on alternate sides might be relatable to numbers of cross links transmitting the electrical signal.
4. Is an action potential transmitted by all sieve tube members of a vascular bundle? It is feasible that the examples of differential excitability in Figure 2 represent different numbers of sieve elements involved. A remarkable technique, time lapse fluorescence microendoscopy with its miniaturized camera, could be adapted for use enabling observation of numerous sieve members (Barretto et al., 2011). Numerous probes introduced by transformation are available for calcium imaging, with a change in fluorescence acting as a surrogate for the passage of an action potential.

9 | BIOELECTRIC FIELDS AS A BASIS FOR PLANT LEARNING AND MEMORY

9.1 | Learning and memory may reside in bioelectric fields

Learning is the biological process of acquiring new knowledge about the environmental world in which organisms live, and memory is the process of retaining and reconstructing that knowledge over time (Kandel et al., 2014). Until recently, it had been assumed that the basis of memory in neurological systems resided in the holistic bioelectric fields constructed from numerous nerve cells (Adey, 2004). Only, more recently has the synaptic facilitation mechanism described above become more dominant (Kandel et al., 2014). The human brain is certainly electrical in its characteristics and phenomena such as alpha rhythms demonstrate bioelectrical holistic behaviour, the products of millions of cells cooperating together.

The emphasis here is on the notion of field; a composite integrated system of ion movements and membrane charge constructed from the integrated activities of millions of cells that has an instructive role in growth and development. The construction of the field involves an array of ion channels and pumps in membranes eventually modifying one (but not the only) bioelectric element itself: the external plasma membrane potential. Enormous progress has been made in identifying the membrane-bound proteins that are involved together with definition of their individual functions in plants (e.g., Baluška & Mancuso, 2013; Hedrich, 2012). Functioning plasmodesmata are also contributors to eventual field structure because there is an internal flow of ions accompanying external or wall flow. The activities of pumps, channels, and plasmodesmata can all be gated posttranslationally, providing an important further epigenetic control of cell development and one that is largely invisible to the control of messenger ribonucleic acid processing and translation. Bioelectric gradients are a systems level, physiological epigenetic instructive that helps drive growth and differentiation.

Tissue cells can store and process information if their plasma membrane potential is slow to change. In this respect, they act like animal nerve cells that have the same capability. Research on the Venus fly trap is a recent example. The plant can store information bioelectrically for short periods of time and can discriminate the number of stored signals (Bohm et al., 2016; Hedrich, 2012). Variation potentials with relatively long half-lives (and referenced above) could confer cells with that capability. There are many other examples of memory that clearly involve longer-term storage with the capability of using that memory when needed. Some of these are resuscitated by signals such as blue light, known to involve ion flux (Trewavas, 2009). Associative, memory-based, forms of plant learning have recently been reported (Gagliano, 2017; Gagliano, Vyazovskiy, Borbely, Grimonprez, & Depczynski, 2016).

9.2 | The instructive nature of the biolectric fields in plants

Both seedling shoots and roots maintain bioelectric fields around themselves (Lund, 1947; McAulay & Scott, 1954; Scott & Martin, 1962). The fields have a distinct polarity with different regions exhibiting different potential differences (e.g., shoot and root tips are more negative than base). These fields are evidently self-organizing because they oscillate by some 30 mV in size and with frequencies from 4 to 15 min in roots and 10 to 50 min in shoots (Lund, 1947; McAulay & Scott, 1954). Oscillations are usually driven by forms of negative feedback and are maintained, as is the field structure, despite continued growth and development of the cells in the tissue (Mancuso & Shabala, 2015). Measurement of the internal electrical potential in tall trees indicates the same pattern of oscillation, or pulsations as Bose (1923) describes them. These are located in the endodermis, a group of cells that surrounds the excitable phloem. Later work demonstrated that the endodermis in shoot stems contains the statoliths that detect gravitational signals (Morita et al., 2002; Psaras, 2004).

Early research used the cereal coleoptile grown in darkness. The tissue was easy to grow, and growth after a certain stage of development was only by cell extension. Instructive properties of the bioelectric field were indicated in three different experimental categories.

1. Mechanical stimulation, either to root or shoot, led to immediate change in the bioelectric field. The stimulated region became electronegative compared to the unstimulated tissue and recovered to the unstimulated field in about 20 min, implying negative feedback (Marsh, 1930; Schrank, 1944, 1945a). Phototropic stimulation led to the exposed side becoming electronegative compared to the shaded region (Schrank, 1946). The bioelectric changes here are slow but precede any curvature by some 20 min. Placing a vertical tissue on its side, thus initiating a gravitropic stimulus, led to an immediate increase in electronegativity of the upper side (Schrank, 1944, 1945b). Curvature again commenced some 20–30 min later. More recent research has described the involvement of membrane voltages, surface potential, apoplasmic flows, and ion fluxes in gravitropic signalling (Monshausen, Miller, Murphy, & Gilroy, 2011; Weisenseel & Meyer, 1997).
2. Brief application of a transversely applied and tiny electrical gradient initiates curvature (Schrank, 1948), with curvature again towards the negative side of the bioelectric field. Application of an applied current from tip to base inhibited growth and responses to light and gravity. When applied from base to apex, it had no effect (Lund, 1947).
3. Shunting, (Schrank, 1950). Immersing tissues in an electrolytic solution was known to short circuit the bioelectrical polarity. Immersion strongly inhibits gravitational, unilateral light responses and the influence of an applied electrical field. The effect of the solution was shown to be nonosmotic.

The signals provide the tissue with new information about its environment that can come from any direction or in variable size and in a large number of different environments. The learning process involves changes in the established electrical polarity that then acts a new memory redirecting growth and phenotype change to (hopefully) return the electrical polarity to its former condition.

9.3 | Investigations of plasma membrane voltage as a surrogate for the bioelectric signal

Recent technical advances have reawakened interest in the plasma membrane potential or voltage as a surrogate for the bioelectric field (Konrad & Hedrich, 2008). Radical technical advances have been published that use probes introduced by transformation and image membrane voltage through fluorescence. These new probes introduced by transformation have the capability to detail “potential-omics” (Matzke & Matzke, 2013). Other reported probes can assess absolute voltage, (Hou, Venkatachalam, & Cohen, 2014). Fast changes in membrane potential, as in action potentials, can also be imaged (Miller et al., 2011; Zhou et al., 2015).

9.4 | The importance of bioelectric investigations and necessary decoding of the bioelectric signal

Much research on bioelectric potentials is concerned with the control and specification of particular aspects of animal embryo development (Levin, 2014). Although equivalent embryological processes might be thought to be limited to seed production, plant growth and development beyond germination are recognizably embryological through its production of new tissues and cells. Bioelectric fields have thus greater relevance for plants through their life cycle. The growing plant experiences different environmental situations from the tip of the shoot to that of the root. To profit from that highly variable situation surely requires an ability of each branch, shoot, tendril, or root, to learn how best to exploit its individual environment. The bioelectric field of each tissue might enable both learning and memory of that developing tissue to be tailored to individual circumstances and connected through to action potentials and hormones to others. Examples of such individual tissue behaviour have been recorded (Trewavas, 2014, 2017). The relationship between the bioelectric potential and action potential remains to be uncovered.

10 | PRIORITIZING WHICH SIGNAL TO RESPOND TO

Earlier, it was indicated that mental states in animals are thought to be able to prioritize the importance of different signals. Is this the case here using the phytoneurological circuitry? Some of the signals perceived by plants can, when used singly, elicit effective contradictory responses when occurring in combination with some others. Some form of prioritization of any tissue or organ as to which to respond to first would then seem essential. From what has been described above, some suggestions are now possible.

Most of the signals experienced by plants that initiate action potentials can be loosely grouped as potentially threatening: predation, physical and mechanical damage, rapid tissue flexure, rapid temperature changes (either cold or hot), or even rapid loss of water. The threat is the loss of fitness. Some, if not all, of these threats induce cytosolic Ca^{2+} transients (Knight, Smith, & Trewavas, 1992; Knight et al., 1991).

However, in humans, damaging or wounding circumstances and excessive temperature treatments are those that deliver pain through nociceptors. By so doing, they indicate a priority in both attention and response. The action potentials that are generated in plants to damaging circumstance could, we suggest, provide a priority to the response against other potential signals. How these are assessed and priority determined is another goal for future research.

Networks, particularly ones as clearly complex as these, should have some potential for signal assessment, and if not in the phytoneurones themselves, then in the cells that surround them and that also experience the specific electrical changes. The light or dark transition does induce a form of action potential and that may have critical functions in the assessment of shade. The threat here is loss of light unless behaviour is induced to counterbalance. Shade avoidance is a defined syndrome. In young plants, shoot growth rates are increased with reduced branching and at the expense of root growth. Its function surely is to overgrow the competition and places reproductive organs where they can be pollinated. A daily assessment at the light or dark transition may be the means of making that assessment although in large woody angiosperms, it is likely complex.

Signals that do not induce action potentials seem at present to be most notably those of gravity. In green stems, the statoliths detecting gravitropic responses are located in the endodermis, a group of cells surrounding the excitable phloem (Morita et al., 2002; Psaras, 2004). But if green plants grown in pots are inverted over a light source, the expected gravity response is overridden. Phytochrome A, a light sensitive pigment, is found at highest concentrations in these endodermal cells too (Hisada et al., 2000). In that case, the prioritization might simply be brute force in the responsive cells with stronger promoters for light reactions against those for gravitropism responses. The root cap contains cells with statoliths. Placement of other signals at right angles to a gravitational signal leads to loss of the statoliths (Eapen, Barroso, Ponce, Campos, & Cassab, 2005; Massa & Gilroy, 2003). This is one alternative method of prioritization.

If a plant is subject to shade situations and to a mild deprivation of water, which response would be prioritized? Would the stem increase or decrease its growth? Would the stem grow faster to avoid shade, or resources instead be given to enhance root exploration for water? Could the phytoneurological network indicated above resolve such situations and thus provide a way in which the individual plant can assess the overall environmental situation and make decisions as to which physiological group of responses is preeminent? These questions need better resolution if understanding of the behaviour of wild plants and trees is to be gained.

11 | CONCLUSION

We have used some very old and modern literature to indicate unanswered questions about electrical signaling. The reticulated excitable phloem system described above offers a potential for assessment of signals and perhaps their prioritization. The bioelectric field in seedlings and in polar tissues may also act as a primary source of learning and memory. But we suspect that with time and experience, the developing phloem becomes increasingly cross-linked and memory could then reside in the electrical capabilities determined by numbers and characteristics of the cross linking. Local phenotypic changes to accommodate local environmental situations are characteristic of the behaviour of the self-organizing plant, and maybe, the bioelectric field coordinates with the electrical system to provide for the characteristics of self-organization. Both local and long distance changes are characteristics of higher plants. The vascular network is a complex interactive system, and once stimulated, it has the potential for assessment through possible feedbacks and alterations of connection strength. Animal–plant similarities being reported in the last decade point toward an electrochemical equivalency at the level of the nervous system elements (Baluška, 2010), integrated by spatiotemporal dynamics (Masi et al., 2009). Whether it should be regarded as a functional equivalent to a fairly primitive, brain cannot be determined until its properties are more clearly defined by research.

This article commenced by pointing out that lack of obvious movement in plants has led to incorrect suppositions about a nervous control. With recognition that this highly branched excitable plant nervous system might act holistically, some issues that have dogged this area of research might be better understood.

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