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Reflections on 'plant neurobiology'

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Abstract

Plant neurobiology, a new and developing area in the plant sciences, is a meeting place for scientists concerned with exploring how plants perceive signs within their environment and convert them into internal electro-chemical ('plant neurobiological') signals. These signals, in turn, permit rapid modifications of physiology and development that help plants adjust to changes in their environment. The use of the epithet 'neurobiology' in the context of plant life has, however, led to misunderstanding about the aims, content, and scope of this topic. This difficulty is possibly due to the terminology used, since this is often unfamiliar in the context of plants. In the present article, the scope of plant neurobiology is explored and some of analogical and metaphorical aspects of the subject are discussed. One approach to reconciling possible problems of using the term 'plant neurobiology' and, at the same time, of analysing information transfer in plants and the developmental processes which are regulated thereby, is through Living Systems Theory (LST). This theory specifically directs attention to the means by which information is gathered and processed, and then dispersed throughout the hierarchy of organisational levels of the plant body. Attempts to identify the plant 'neural' structures point to the involvement of the vascular tissue – xylem and phloem – in conveying electrical impulses generated in zones of special sensitivity to receptive locations throughout the plant in response to mild stress. Vascular tissue therefore corresponds, at the level of organismic organisation, with the informational 'channel and net' subsystem of LST.

Keywords: Biosemiotics; Electrical impulses; Environmental signs; Information; Living Systems Theory; Plant neurobiology

1. Introduction

Some writers have lamented the ignorance surrounding the ways in which the multiplicity of external and internal stimuli (or signs) are registered by plants and then transmitted often to distant locations where they elicit characteristic developmental and behavioural responses. For example, the eco-physiologist, Ariel Novoplansky, asks the following question: "in organisms lacking a nervous system, what are the mechanisms, functional implications and costs of integrating these stimuli?" (Novoplansky, 2002). Interestingly, a significant number of questions and statements concerning plant 'nervous systems' (statements that not only suggest their absence, but also argue for their presence) have appeared in the literature during recent years. In writing on the regulation of phloem solute translocation, M.V. Thompson and N.M. Holbrook state that: "plants lack a nervous system, and phloem translocation control must rely on locally available signals" (Thompson and Holbrook, 2004). The same authors nevertheless continue: "sieve tubes...behaving like 'neurons' transmit information from one part of the plant to another with little material transfer." A.G. Volkov is more assertive with regard to whether or not plants possess nerves. Recalling that Bose (1926) was the first to use the term 'plant nerve', Volkov confidently draws a parallel between plant phloem and animal axons: "phloem is an electrical conductor of bioelectrochemical impulses over long distances . . . structures of phloem and axon can be pictured as hollow tubes filled with electrolyte solutions" (Volkov, 2000). If they do not deny a plant nervous system, then comments such as those above hold out the possibility that there may be a common form of internal, and non-hormonal transmission of information by which both animals and plants, for their own benefit, deal with a shared set of environmental variables; but, in the case of plants, whether this involves the utilization of nervous transmission is still an open question. However, as M. Gersani and colleagues have remarked: "plants may be more sophisticated and share more in common with animals in their non-cognitive behaviours than previously thought" (Gersani et al., 2001). All this indicates that it would be in order to examine more closely whether there are hitherto unappreciated ways, such as by the use of nerve-like transmission, whereby plants can

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link the sensation of stimuli with the execution of appropriate responses.

Recently, the term 'plant neurobiology' has been introduced into the scientific literature (Baluška et al., 2006a; Stahlberg, 2006). One objective of this new science is to find answers to questions and comments such as those quoted above. It does so by focusing on the degree to which plants use a nerve-like system (or systems), similar to those of animals, in the course of signal–response relationships (Baluška et al., 2006b,c; Brenner et al., 2006). Unfortunately, problems arise at this point in the minds of many readers because terms such as 'neural system', 'intelligence' (Trewavas, 2003) or, *in extremis*, the word 'brain' (Darwin, 1880; Barlow, 2006), do not generally lie within the orbit of plant life. One of the issues, then, is whether the usage of such terms is legitimate in the light of observational and experimental evidence, or whether interpretation of the evidence has been stretched too far in an attempt to create what some might consider an illusory science (Alpi et al., 2007). Furthermore, whether 'plant-nerve' terms are being used as metaphors or analogies (Trewavas, 2007) which refer to invalid correspondences with animal nervous systems is also a question which has to be considered. In this respect, there should be enquiry into whether these putative correspondences between plant and animal neural attributes are indications of homoplasies (Brooks, 1996) and exaptations (Buss et al., 1998), brought into existence by evolution to provide an efficient internal communication system within plants, utilizing those components and processes which are already within the manufacturing capabilities of all members of the plant and animal kingdoms. This process, deployed at the cellular level, François Jacob (1983) has termed 'bricolage' or 'tinkering'. In other words, the advantage of an electrical, or 'nervous', communication system has been perceived by the evolutionary process as an item contributing to fitness; and attracted into the construction of this nervous system have been elements which could either be synthesised *de novo* or derived from other already existing systems. It seems worthwhile, therefore, to see whether some of the more negative responses raised by Alpi et al. (2007) with regard to the term 'plant neurobiology' can be clarified, and to enquire whether plants and animals have indeed elaborated similar processes and structures (within the framework of their respective cell types) to solve similar signal–response situations. If 'plant nerves' are invoked as a structural–functional feature of plants, then 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? And, importantly, from the point of view of the usage of the term 'plant nerve', where are these 'nerves' located within the plant, and what correspondences – physiological, structural – do they have with animal nerves?

Before moving to address some of these questions, let us briefly, in Section 2 below, consider some aspects of plant structure because, ultimately, it is this feature which has to be surmounted by any system whose job it is to facilitate the flow of information around the plant and initiate physiological responses, whether by the use of 'nerves' (Baluška et al., 2006b) or some other means. We shall also recall some of the early observations that served as a basis for modern ideas on 'plant neurobiology'.

2. Plant Construction and Information Transmission

The majority of plant organisms are constructed according to a modular plan whereby units of structure and function are repeatedly developed during growth (White, 1979; Barlow, 1994; Notov, 2005). An alternative, non-modular unitary plan is found in a few familiar algal species: e.g., the mononucleate green alga, *Acetabularia mediterranea*, and the multinucleate, coenocytic green alga, *Caulerpa prolifera* (note that other green algae of the genus *Chara* are modular). Modules are evident at all levels of plant organisation. For example, the 'cell body' module (Baluška et al., 1998) is a repeatedly produced constituent of the cellular level of organisation. Then, cells and cellular groups are the basic repeated modules of the organ level; organs comprise the whole body level, ramets the societal level, and so on. The modules are connected together: plasmodesmata and cross walls connect cell bodies and cells (Benitez et al., 2006), nodes and their vasculature connect the sympodial modules of vegetative shoot organs (Barlow and Palma, 1997), and stolons connect ramets (Van Kluenen et al., 2000).

At whatever organisational level they are considered, the modules are only relatively independent. They have to be integrated with the function of similar modules at the same organisational level, and also with the modules of other levels. With this realisation, only then can there be a useful understanding of the true nature of plant construction. The information which integrates the structure of modules with their function at each level has to cross the structural boundaries between each module. Not only is such an integration needed to bring about balanced growth and development of a given level in the short term (Berleth and Sachs, 2001) but also in the longer term it helps perfect the next-higher organisational level; organs, for example, are 'perfected', or emerge from collections of elements at the cellular level. Similarly, the cell can be understood only in terms of the integration of its metabolic and structural components (Cornish-Bowden et al., 2004). Many of these examples of modular activity occur within the context of gradients of mobile growth regulators and morphogens, the auxin indole acetic acid arguably being the most important; the gradients themselves may also be regarded as physiological modules at the cellular level (Berleth et al., 2007).

Clusters of modular sympodia (metamers) constitute the stems of many dicot plant species (Dormer, 1972). Each developed stem module consists of node, internode, leaf and bud primordium, and sometimes a root primordium (Barlow and Palma, 1997). Nodes mark the meeting place of two modules and are of particular interest with regard to the passage of information. Most module junctions have complex vascular organisations in the xylem (and presumably within the phloem also) which lead to bottlenecks in the flow of solutes. Wherever there is local accumulation of auxin at a node (Jacobs and

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Morrow, 1957; Berleth et al., 2007) there is the potential for regulating the development of associated shoot-bud and root primordia (Leyser, 2006; Bennett et al., 2006). It is also possible that nodes affect solute flow in a differential manner. For example, experiments with maize seedlings suggested that the mesocotyl node is an impediment to the flow of fluoroscein but not to that of auxin (Epel et al., 1992).

If nodes interrupt the flow of aqueous solutes, might they not also affect electrical transmission, acting like resistors in an electrical circuit – here, a putative plant-nerve circuit? Resistance to current flow was found in some early electrophysiological experiments. Electrical stimulation of lupin (*Lupinus angustifolius*) stems elicited measurable action potentials which, although they travelled the length of the stem, could not traverse the node at the stem–root junction (Zawadski, 1980). In *Luffa cylindrica*, the nodes of the above-ground portion of stem also presented barriers to action potentials (Shiina and Tazawa, 1986), as indeed was also found to be the case in stems of the modular alga, *Chara braunii* (Sibaoka and Tabata, 1981). Since the time of these early experiments, there have been numerous other demonstrations of the passage of induced electrical impulses along stems, and notice has sometimes been taken of the effect of stem anatomy upon this passage (Dziubińska et al., 2001). More recently, movements of action potentials from leaf to leaf, and from root to leaf, have been shown for barley plants (Felle and Zimmermann, 2007). Such observations are important in clarifying the pathways of electrical signals, albeit at a relatively low, macroscopic level of resolution. Two recent books, “Communication in Plants” (Baluška et al., 2006c) and “Plant Electrophysiology” (Volkov, 2006), as well as the reviews by Davies (1987), Dziubińska (2003), and Fromm and Lautner (2007), provide references to many other relevant experimental observations concerning the initiation and passage of action potentials, and the propagation of other electrical impulses.

Another type of electrical impulse found in plants is the slow-wave potential (sometimes called variation potential) (Stahlberg et al., 2006). It is usually produced by more severe wounds and traumas than is the case for the induction of action potentials. Whereas action potentials could not pass barriers imposed on stems of *L. angustifolius*, this was not the case for slow-wave potentials (Paszewski and Zawadski, 1976). The reason for this seems to be the different routes taken by each impulse: phloem is used for the action potentials, and xylem for the slow-wave potentials.

The electrical impulses elicited within plant organs do not seem to be just some sort of default feature without consequence but, on the contrary, they are signals which move from their site of initiation and are translated into a growth response in some distant location – that is, they impart information concerning the circumstances of their initiation. Two examples from early work can be mentioned. The first concerns electrical action potentials due to mild traumatic shocks (wounding of leaves, heating and chilling) (Wildon et al., 1992; Herde et al., 1995). Ultimately, these shocks led, via the depolarisation of membranes, to alterations of solute balance (Fromm and Bauer, 1994), and thence to the stimulation of protease inhibitor gene expression in remote tissues. Other experiments involving trauma have also been shown to induce new patterns of gene activity and protein synthesis (Van Sambeek and Pickard, 1976; Stankovic and Davies, 1996; Vian et al., 1996; Tafforeau et al., 2006). The second example concerns the response of droughted maize plants to the rewetting of their soil. An action potential was then induced in the roots which, in a matter of minutes, passed via the phloem to the leaves where the rate of CO_2 assimilation was affected (Fromm and Fei, 1998). Recently, it was shown that, although alterations to internal hydraulic pressure and the attendant electrical impulse often travel together within stems, their effects on leaf physiology can be separated – the hydraulic signal from the electrical signal by pressure adjustments around the root, and the electrical signal from the hydraulic signal by cooling the leaf which was to receive that signal (Grams et al., 2007). In leaves of the mentioned droughted and re-watered maize plants the hydraulic signal was found to regulate stomatal aperture whereas the electrical action potential affected photosynthesis. Because the stimuli which bring about electrical signalling often impinge upon the metabolism and transport of hormones (Schlicht et al., 2006), the two systems – that is, the primary electrical system and the secondary chemical system – could together be dual regulators of physiological, behavioural and growth processes (Starck, 2006).

A further highly interesting result that reveals more of this relationship between the endogenous electrical and the hormonal features of organs was obtained by Kudoyarova and her colleagues using maize plants (Kudoyarova et al., 1990, 2001). Roots were exposed to a salt stress (1 M KCl) for 5 min. A spike of electrical potential was recorded immediately at an observation point located at the root shoot junction. It was then followed by an increase in free auxin content within the shoot, the amount doubling in the 10 min following the stress. Simultaneously, the amount of the bound (conjugated) form of auxin decreased. It seems that the stress-induced electrical signal immediately passed from the root to the shoot and there brought about a change in hormone metabolism; the electrically induced elevation of auxin level then repressed shoot growth. Chisnell and Bandurski (1988) also examined the alteration in the amounts of free auxin from its conjugated form within germinating maize shoots in response to external auxin application to endosperm. Both the time-course and the quantities of endogenous auxin involved suggested that a rapid signal passing from the shoot tip was responsible for this modulation of auxin metabolism. The authors proposed that “a poised electrical potential” within the shoot tissue might be responsible for this. However, no direct evidence was presented. Kudoyarova et al. (2001) reviewed many other instances where hormone metabolism (of cytokinin, via cytokinin oxidase, and of abscisic acid) was rapidly affected in organs distant from the site of application of a stress and where concomitant alterations to growth and/or physiology were recorded. Similar work on hormonal metabolism was also presented by Polevoi et al. (1997) who concluded that a hydraulic signal and a resultant electrical impulse emanating from roots chilled for only 4 s led to rapid (within 10 min) local changes in both auxin and abscisic acid conjugates in shoots that were 9–10 cm away from the stressed region. A light pulse given to shoots of maize could also very rapidly alter the free/conjugated ratio of auxin in roots (Kudoyarova et al., 1990). Again, an electrical signal was suggested.

Electrical signals may also underlie certain light-induced morphogenic events in germinating bean (*Phaseolus vulgaris*) shoots (Caubergs and De Greef, 1975; De Greef et al., 1976). Although the light receptor, phytochrome, was involved in the morphogenic signal–response chain, it did not operate in the expected way. An internal signal, triggered by a pulse of red light, was found to leave the first leaf within 1 min and not be impeded in its effect on the hypocotyl by the usual inhibitory response due to a subsequent pulse of far-red light, a response also mediated by phytochrome (Caubergs and De Greef, 1975). Further experiments by De Greef et al. (1976) confirmed the rapid release of a signal from the leaf to a site in the cell layers of the outer stele of the hypocotyl where changes in ATP content were recorded. Also detected was a rapid (100–120 s) change in electric potential around the embryonic axis consistent with it being a phytochrome-mediated electrical response due to light falling on the leaves at the shoot tip. As the authors state: “By means of a transmission system (primitive nervous system) phytochrome directs the flow of perceived light signals throughout the whole plant body” (De Greef et al., 1976, p. 305).

On the basis of their work with action potentials in plants, Thain and Wildon (1992) proposed that impulses of this type spread through plant tissues in much the same way as they do in tissues of animals, using plasmodesmata (special cell–cell contacts analogous to gap junctions of animals) as their channel. Now, however, the indications are that wound-induced action potentials travel in the phloem (Rhodes et al., 1996), perhaps making use of plasmodesmata (Fromm and Lautner, 2007), and that slow-wave potentials may possibly also move via plasmodesmata in the living xylem parenchyma surrounding xylem vessels through which passes the hydraulic surge that initiates this type of electrical impulse. Interestingly, the metaxylem elements of maize roots are contacted by cells enriched with H^+-ATPases, an enzyme that helps maintain electrical gradients (Jahn et al., 1998). In this connection, one might propose that the thickened cells of the endodermis which surrounds the stele might help maintain the electrical pathway by virtue of its rigidity: that is, the membranes cannot escape the effect of the hydraulic pressure waves within the bundles of xylem elements and surrounding files of parenchyma cells. Endodermis may also prevent radial leakage of the electrical signal and thus act like the electrical insulation conferred upon mammalian axons by the myelin sheath. The much-reduced vascular cylinder of ericaceous ‘hair roots’ may reveal the structure of the root’s nervous tissue only (Barlow and Lück, 2007).

Other evidence suggests that there is a third way in which cell–cell propagation of impulses takes place in plants. These impulses make use of, or are the result of, structures akin to synapses (Baluška et al., 2005, 2006b), thus indicating a further similarity with impulse transmission in animal neurons. Plant ‘synapses’ share certain characteristics with animal synapses (Baluška et al., 2003, 2005), in particular the presence of a calcium-sensitive vesicle trafficking apparatus. The finding that auxin molecules are associated with membranous endosomes which participate in vesicular cycling at certain ‘synaptic’ cellular end-walls leads to three important propositions. The first is that auxin can be actively secreted from cell to cell (Baluška et al., 2003; Schlicht et al., 2006; Mancuso et al., 2007) as though it were a component of a chemical synapse (a characteristic of animal nervous tissue). Moreover, ‘synaptic strength’, as estimated by the amount of auxin transport per unit of time, is directly related to actin abundance at the synapse-like cross wall (Schlicht et al., 2006; Mancuso et al., 2007). The second is that alterations to the direction of vesicle-recycling at the cell membrane with respect to the orientation of the cell elicits a response which rapidly leads to new patterns of behaviour, such as differential growth movements (tropisms) (Baluška et al., 2007). And thirdly, that membrane recycling activities at the synapse lead to transmissible electrical impulses.

Electrical fluxes around the root apex have highly significant consequences for root growth and behaviour. They result from the inherent polarity of cells in accordance with the movement of auxin driven by PIN proteins (Tanaka et al., 2006); the fluxes are, in effect, a by-product of the synaptic structures mentioned above (Mancuso et al., 2007). It may be that these electrical fluxes, as they circulate through the tissue, reinforce the polarity of cells, and hence the polarity and on-going development of the organ of which the cells are part, by an influence on the orientation of cortical microtubules (see Hush and Overall, 1991). The proteins, AUX1 and PIN1, together with the actomyosin associated with the end-wall synaptic structures of the ‘nerve’-like cells, propel acropetally (towards the root apex) auxin which has been either synthesised in the root during the course of its growth (Ljung et al., 2005) or supplied from the shoot (Bhalerao et al., 2002). After reaching the apex, auxin is then directed into the root cap and a fraction of it is also redistributed basipetally, via the root epidermis and cortex, by means of other species of PIN proteins (Tanaka et al., 2006). In this configuration, auxin is then available to initiate root movements by differential growth due to differential PIN distribution – providing an appropriate stimulus is received, as in gravitropism, for example (Baluška et al., 2007).

The end-to-end arrangement of cells within root-apical tissue, the presence of ordered actin filaments, and the plasmodesmatal connections between cells, help orientate the currents produced by each single cell (Waller et al., 2002; Nick, 2006) and thereby set up of an electrical ‘field’ around the whole root organ, and thence around the whole organism (Nuccitelli, 1984). This field gives rise to a phenomenon referred to as ‘bioelectricity’ (Meylan, 1971; Weisenseel and Meyer, 1997). Bioelectric fields are a general feature of living organisms. Moreover, the fields around roots and root systems (Toko et al., 1989; Watanabe et al., 1995; Weisenseel and Meyer, 1997) extend into the wider environment of the rhizosphere. Here, the bioelectric field presents a sign to organisms in the vicinity. One significant example of this is that it is by means of a root-generated bioelectrical sign that oomycetous fungi within the soil initiate their pathogenic invasions of plants (Van West et al., 2002).

Light microscope images of the putative synaptic structures within root apices suggest, as already indicated above, that they colocate with cellular cross walls to which are attached actin bundles together with myosin (Baluška et al., 2005). Prominent actin bundling is seen within differentiating cells of the stele (young xylem vessels, parenchyma and pericycle) (Baluška et al., 1997), especially in the so-called ‘transition zone’ (Verbelen et al., 2006) located just proximal to the root meristem. The cells bearing these actin-enriched ‘synapses’ might be considered ‘nerve’-like. If so, then the actin material at the cross wall might be analogous to the cytoplasmic structure termed ‘postsynaptic density’ found in animal neurons (Ziff, 1997). Collectively, the synapses confer on the root apex the property of a ‘brain’, as first suggested for roots by Charles Darwin (Darwin, 1880; Barlow, 2006). This root ‘brain’ is a site where incoming sensory signals are processed to elicit a response. In the shoot of bean, the hypocotylar hook has also been suggested by De Greef et al. (1976) as being a similar ‘coordination centre’ for light-induced, electrical signals. If so, then such ‘plant brains’ might be self-organising structures, as suggested by Szentágothai and Érdi (1989), perhaps drawn into these particular cyto-physiological states by feedbacks operating between the electrical field generated by the plant synapses and the intracellular actin bundles (Waller et al., 2002; Nick, 2006). The synapse-bearing root-apical cells may also extend basipetally within the pericycle (unpublished observations) and there make contact, at the stele–cortex boundary, with the site of metabolism of the neurotransmitter, acetylcholine (Momonoki, 1992). Although acetylcholine is known as a chemical constituent of plants (Tretyn and Kendrick, 1991), its precise function is not known, though interesting data suggest it is connected with stomatal guard-cell physiology (Meng et al., 2001; Wang et al., 2003) – the guard cells being another location of ‘plant synapses’ (F. Baluška, personal communication).

It is discoveries and conjectures such as those briefly mentioned above which have sensitised some plant scientists to the possibility of a ‘neural’ system being present in plants. This system resides within elements such as phloem and companion cells which traverse long distances (cms) and which carry fast-moving action potentials. The second system of synapse-bearing cell complexes are expressed most strongly in the root ‘transition zone’, but also extend in more attenuated form both acropetally and basipetally. They deal with medium-distance (mm range) electrical transmission. The third electrical system, initiated by severe trauma, follows the course of the xylem and is also a long-distance conduit. It results from hydraulic pressure waves which induce, as they pass, slower-moving depolarisations in the surrounding parenchyma cells. It will have been noted that the pathways of the slow-wave potentials and the action potentials colocate (probably) to cell-types – pertaining to the xylem and the phloem tissues – whose functions are better known in the context of supporting solute flow.

Impulses of each of the three types in one way or another enable internal communication (carried out at the level of the whole plant), though the synaptic pathway may also facilitate the inter-communication between the plant (especially the roots) and its environment, regulating not only root tropisms but perhaps also stimulating, via the bioelectric fields, the release of chemical signs which can be perceived by, and influence the behaviour of, neighbouring plants (Walker et al., 2003; Falik et al., 2005; Bais et al., 2006). The entire ‘plant neural system’ with its complex of structures and responses therefore provides plant organisms with a means to extract information from, and perhaps exchange information with, the environment. Such an exchange may not only bring about adjustments to plant physiology and behaviour but also establish a higher, social level of plant life within the rhizosphere and phyllosphere.

3. Modern Beginnings of Plant Neurobiology

Certain, now classical, experiments with trees and shrubs (Champagnat, 1965), as well as more recent analyses of the differential growth of their metamers (e.g., Draye, 2002; Novoplansky, 2003; Renton et al., 2006), have led to the idea that plant form is the product of morpho-physiological ‘correlations’ (Champagnat, 1974) which operate throughout the whole organism and are responsive to environmental factors. The main perceived effect of such correlations is the cooordination of the growth of buds and the extension of branches. They are thus an expression of ‘positional information’ (Barlow and Carr, 1984) which itself is fed by, and is embedded within, the correlative system. Auxin produced by shoot apices is generally believed to play an important role in correlative pathways of development (Naylor, 1984), either supressing or activating cell division in apical meristems according to the prevailing conditions within the developing plant.

In the 1980s, studies of wound-induced growth of cotyledonary buds of *Bidens pilosa* (Thellier et al., 1981; Frachisse et al., 1985) led to the hypothesis that endogenous electrical impulses, or signals, might also form part of a correlative system. In relation to these experiments, it was concluded that “while plants have no actual nerves, they seem to possess at least some of the basic cellular mechanisms whose evolution has led to the development of the nervous system in animals” (Thellier et al., 1982). Subsequent studies on electrical impulses (mentioned in the previous section) have gradually shaped the view that there is indeed some type of ‘neural’ pathway in plants (Baluška et al., 2006b,d, 2007; Brenner et al., 2006) and that it participates in the integration of the modules of plant construction by facilitating either negative or positive correlative growth responses. The rapid reactions of certain sensitive zones such as *Mimosa* petioles and the insect traps of *Dionaea* (Simons, 1981) also feature as near-iconic manifestations of particular specialisations of this neural system. It may even be hazarded that a phytoneural pathway could be so extensive as to reach the stem-cell compartments of root and shoot meristems and thereby designate (or re-designate) cell fates in these domains.

The belief that there could be a match between animal and plant information-processing systems, and that both involve similar types of neural signalling, furthers the idea of a commonality of living forms. This concept of ‘inclusivity’, as we may call it, was proposed over a century ago by Wilhelm Pfeffer (Bünning, 1977), amongst others, and has been borne out in many aspects of the plant and animal sciences, notably in the field of hormones (Leopold, 1987). However, molecular analyses aimed at tracing the origins of the most primitive forms

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of animals and plants have not entirely favoured the inclusivity concept (Meyerowitz, 2002), though the unfavourable aspects of this view were not defined in detail. Nevertheless, despite the early divergence of the animal and plant phylogenies from a common predecessor about 1.2×10^9 years ago, Meyerowitz noted that “there are some surprising similarities in the overall logic of development in the two lineages” and that “there are clear demonstrations of parallel processes having evolved in each kingdom” (Meyerowitz, 2002). This accords with the concept of convergent evolution, or homoplasy (Brooks, 1996). In other words, the physiological and structural attributes that characterise a nervous system could have arisen independently at least twice, without necessarily being inherited from a common ancestor. Sets of these attributes within pre-existing cells, perhaps within the vascular system, were thus able to support the newly evolving lines of the future plants and animals. By the time that some of the more advanced coelenterates were evolving, some 0.5×10^9 years ago, nervous synapses were already present in these organisms (Westfall, 1996); and at about the same time, phloem-like structures (presumed ‘plant nerves’) were already present in early plants (bryophytes, lycopsida) (Esau, 1969).

A contrasting scenario to that implied by Meyerowitz (2002) is one in which there is no need to call upon the concept of homoplasy to explain the similarities of development in the two lineages: rudiments of nervous tissue might have already been present in the common ancestor of plants and animals. Elongated cells with surface membranes of great area and capable of propagating electrical potentials could have been one such ancestral neuronal rudiment (Volkov, 2000). Then, within the constraints of their contrasting anatomies, the hypothetical excitable cells in animals came to be what we now call ‘nerves’, whereas in plants these excitable cells came to correspond with the fibrous, dual-purpose phloem strands, especially their sieve tube–companion cell complexes (Volkov, 2000; Eschrich et al., 1988) which had been already developed as channels for photosynthates. One such extremely long cell type in plants which extends from root tips to shoot tips, and which ramifies into their branches, is the coenocytic non-articulated laticifer (Mahlberg, 1993). However excellent as these cells might have been for long-distance signal transmission, they cannot do so now due to their content of insulating latex.

The evolution of plant ‘nervous’ activity (Goldsworthy, 1983) probably proceeded from the small electrical discharges associated with sites of spontaneous cell membrane repair [which can be recorded in organisms such as *Acetabularia* (Novák and Bentrup, 1972) with a unitary body-plan, as well as in higher plants (Zawadski et al., 1995)] and culminated in the more intense electrical phenomena – which are perhaps also due to membrane repair – that travel from module to module as action potentials within the phloem (Eschrich et al., 1988; Fromm and Eschrich, 1993; Dziubińska et al., 2001). The controlled membrane exchanges at specialised cell junctions – the ‘plant synapses’ (Baluška et al., 2005) – may be a further development and has led, as a consequence, to the establishment of bioelectric fields. The most highly developed plant synapses occur in the transition zone of the root apex which thereby constitutes a putative ‘command centre’ or ‘root brain’ (Baluška et al., 2006d). Slow-wave potentials resulting from hydraulic stimuli may have allowed the xylem tissue also to be incorporated into the electrical information (‘plant nervous’) system.

4. Living Systems Theory in Relation to Plant Neurobiology and Plant Structure

It should be possible to aim for a holistic view of nervous systems in relation not only to plants but also to animals and, indeed, to the generality of ‘living systems’ and thereby amplify and develop W. Pfeffer’s concept of inclusivity.

Whereas General Systems Theory (GST) was conceived as a means of understanding the immense complexity of animate and inanimate Nature (von Bertalanffy, 1968), Living Systems Theory (LST), as originally proposed by Miller (1955, 1978), seems a more accessible concept for consideration by biologists since it deals only, as its name implies, with ‘living systems’. The appeal of LST is that, together with the emerging field of biosemiotics (Kull, 1999; Witzany, 2007), it can serve not only to organise the ideas and concepts concerning information processing in plants (Barlow, 1999) but also harmonise the neural homoplasies of plants and animals. These two aims based on LST seem to correspond, in part, to the ‘two-component signal transduction system’ (TCST) proposed by Van Duijn et al. (2006). The TCST is proposed to support a simple neural system comprised of a flow of information unrelated to immediate metabolic requirements. The components of TCST are receptors, a transmitter, and a response regulator, and might correspond to the respective LST subsystems: 11 – input transducer, 15 – decoder, and 20 – output transducer (see Table 1). But is such a small number of subsystems sufficient for a minimal nervous system?

According to LST, each level of biological organisation is supported by a set of 20 critical subsystems (Miller and Miller, 1990). The same subsystems are repeated at every level, thus building a self-similar organisational hierarchy. According to HA Simon, “nature is organised in levels because hierarchic structures ... provide the most viable form for any system of even moderate complexity” (Simon, 1973). The subsystems and the information stored within them may be said to construct a level of (n) biological organisation. At each level (n, $n+1$, $n+2$, etc.), the tasks of the subsystems are of the same type, but the elements from which a given level is constructed, and by means of which subsystem tasks are accomplished, are different; and they become more complex the ‘higher’ the organisational level.

Listed in Table 1 are 10 of the 20 canonical subsystems which are dedicated to the processing of information (Miller and Miller, 1990, 1995), the remaining systems process matter and energy (Miller, 1978; Miller and Miller, 1990). The information-processing subsystems bring about the organism’s interpretation of its environment. Out of the various sign–organism interactions emerge informational material which can be relayed to receptive and reactive sites within the plant. At least some of this information, as we have seen above, is relayed by electrical impulses.

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Table 1
According to J.G. Miller's Living System Theory (Miller, 1978) there are 10 subsystems out of a total of 20 subsystems which process information

Subsystem	Subsystem properties		Representatives of the subsystem structures and processes at the three named levels of biological organisation		
			(1) Cellular level	(2) Organ level	(3) Organism level
11. Input transducer	The sensory subsystem which brings markers bearing information into the system, changing them into other matter-energy forms suitable for transmission within the system. (Exteroception)	**P**	Touch receptors	Sensitive cells	Sensitive hairs and leaves
		A	*Hormone receptors sites on plasma membrane*	*Receptor cells of sense organs*	*Sense organs*
12. Internal transducer	The sensory subsystem which receives, from subsystems or components within the system, markers bearing information about significant alterations in those subsystems or components, changing them to other matter-energy forms of a sort which can be transmitted within it. (Interoception)	**P**	Internal stretch receptors	Altered cell dimensions. Central root cap cells (statocytes)	Buds and branches
		A	*Cyclic-AMP, cyclic-GMP*	*Specialized cells of sinoatrial node of heart*	*Sensory cells in organs*
13. Channel and net	The subsystem composed of a single route in physical space, or multiple connected routes, over which markers bearing information are transmitted to all parts of the system.	**P**	Microtubules. Endomembranes, plant synapse, plasmodesmata	Symplasm and plasma membranes. Mechanosensing system of cell walls and membranes (→)	Phytoneuronal system of sieve elements and companion cells. Xylem tissue
		A	*Openings through receptors on membranes*	*Nerve net of organ*	*Nervous system of neurons and glial cells*
14. Timer	The subsystem which transmits to the decider (18) information about time-related states of the environment or of components of the system.	**P**	Chronon, Biochemical oscillators, Periodosomes	Sensitive cells of leaf pulvinus	Organs of nastic and nutational movement (leaves, tendrils)
		A	*Biochemical oscillators*	*Heart pacemaker*	*Suprachiasmatic nuclei of hypothalamus*
15. Decoder	The subsystem which alters the code of information input to it through the input transducer (11) or internal transducer (12) into a 'private' code that can be used internally by the system.	**P**	Release of auxin	(←)	Unknown
		A	*Molecular binding site*	*Second echelon cell of sense organ*	*Sensory nuclei*
16. Associator	The subsystem which carries out the first stage of the learning process, forming enduring associations among items of information in the system.	**P**	Electrical impulses and ions (?)	Unknown	Unknown
		A	*Calcium ions(?)*	*None found; upwardly dispersed to organism*	*Unknown neural components*

Table 1 (*Continued*)

	Subsystem properties		Representatives of the subsystem structures and processes at the three named levels of biological organisation		
			(1) Cellular level	(2) Organ level	(3) Organism level
17. Memory	The subsystem which carries out the second stage of the learning process, storing information in the system for different periods of time, and then retrieving it.	**P**	Inducible protein molecules, synaptic structures, epigenetic structures	(←)	(←)
		A	*Synapses*	*None found; upwardly dispersed to organism*	*Unknown neural components*
18. Decider	The executive subsystem which receives input information inputs from all other subsystems and transmits to them information outputs for guidance, coordination, and control of the system.	**P**	Homeobox genes, regulator genes	Hormone-producing tissues	Hormone network
		A	*Binding sites for information transmission*	*Sympathetic fibres of sinoatrial node of heart*	*Neural components at several echelons*
19. Encoder	The subsystem which alters the code of information input to it from other information processing subsystems, from a 'private' code used internally by the system into a 'public' code which can be interpreted by other systems in its environment.	**P**	Genes that specify allelochemicals	Allelochemical-producing tissues	Allelochemical-producing organs
		A	*Genes that specify hormones*	*Synthetic components of output neurons*	*Temporo-parietal area of dominant hemisphere of human cortex*
20. Output transducer	The subsystem which puts out markers bearing information from the system, changing markers within the system into other matter-energy forms which can be transmitted over channels in the system's environment.	**P**	Ionic changes. Presynaptic vesicles in plant neural channels	Glands	Leaf and flower colours. Flower shape
		A	*Presynaptic vesicles in neurons*	*Presynaptic region of output neuron*	*Larynx*

The ten information-processing subsystems numbered 11–20 are listed at left together with a brief description of their properties (from Miller and Miller, 1995). Some of the representatives of these subsystems are proposed for three levels of organisation of increasing complexity, cell, organ, and organism in plants (**P** and Roman script) and animals (**A** and italic script) (Barlow, 1999; Miller and Miller, 1995). Arrows (← and →) indicate that the process is delegated, respectively, to either a lower or higher organisational level.

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For an understanding of plant neurobiological phenomena it clearly is important to identify the relevant LST subsystems (Barlow, 1999, 2006). Amongst these are the 'input transducer' and 'internal transducer' (numbered 11 and 12, respectively, in Table 1) (Miller, 1978; Miller and Miller, 1995). The former (subsystem 11) is a subsystem of exteroception (Tortora and Grabowski, 1996) which engages with signs within the external environment. The latter (subsystem 12) relates to the interoception (Tortora and Grabowski, 1996) of signs arising from an internal state. An example of interoception would be the perception of stress (Aon et al., 1999) such as might be elicited by water deficit and temperature shocks, their interoception being due to osmotic- and turgor-generated signs within the cytoplasm. As we have seen, stresses such as these lead to the generation of long-range action potentials and slow-wave potentials. Sensing of a gravitational stimulus is also interoceptive because the internal states of gravi-receptive cells are directly affected by the sedimentation of statoliths: it is an internal 'touch' sensation. However, in this case, information is transmitted over a relatively short range (mm) by the plant synapses. Other subsystems of relevance are the 'decoder' (number 15), the 'associator' (number 16) and, importantly – for this is the conduit of information flow – the 'channel and net' (number 13) (Miller, 1978; Miller and Miller, 1995).

Another crucial subsystem (number 17) is memory (Miller and Miller, 1990). Memory has not yet been mentioned in relation to plant neurobiology, but would evidently have a place there. Ordinarily, memory is best known at the level of the organism, at least in animals where it is dispersed throughout the nervous system. However, a simple, and in many ways a paradigmatic, memory system operates in the insect-trapping organs of *Dionaea muscipula* (Simons, 1981). Hairs of the trap require two separate stimuli for its closure and for the capture of an animalcule. The second stimulus has to occur less than 40 s after the first. Both stimuli evoke action potentials. The first stimulus clearly creates a primitive memory with a decay time of 40 s. This memory is utilised by the second stimulus in order to complete the trap-organ response. The memory system is deployed to ensure that trap closure due to a single accidental stimulus is avoided.

The organismal 'memory' which operates in plants is probably relatively simple, as in *Dionaea*. Unfortunately, the site of the memory proteins, such as those induced by microwaves, physical damage and calcium depletion, and which have been found to evoke adventitious meristem formation in both flax and *Arabidopsis*, have not yet been uncovered at the tissue level (Verdus et al., 1997; Tafforeau et al., 2006). Memory units (engrams) are linked together at the organismal level by means of the 'associator' subsystem (subsystem 16). It is possible that calcium plays the part of an 'associator' subsystem and regulates organismal memory recall (Verdus et al., 1997). In animals, the neuronal synapses have been proposed to contribute to memory (Fedulov et al., 2007). It has been suggested that memory also exists at the cellular level where it plays a part in cellular differentiation and histogenesis (Chandebois and Faber, 1987); reversible epigenetic modification of DNA may, at this level, here represent the phenomenon of cellular memory (Bond and Finnegan, 2007).

After the intriguing question of where memory is located, another vital question concerns the cells and tissues which correspond to a neurological 'channel and net'. Xylem and phloem strands have already been mentioned in this respect. Phloem tissue is consistently present as an unbroken network throughout the whole plant, and its conductance of electrical action potentials has been reliably documented (Eschrich et al., 1988; Fromm and Lautner, 2007). Phloem therefore conforms to the criteria of a 'channel and net' subsystem with respect to its conveyance of electric, plant-nervous signals. Given these observations, the significance of other aspects of phloem physiology (Thompson and Zwieniecki, 2005) comes into question in the light of a putative phloem-based plant neurobiological context. Potassium ions, for example, play a part in sucrose transport in the phloem, as physiologists have long supposed. But could these ions also participate in the electrical signalling within this tissue? Interestingly, potassium, as well as calcium, was found to facilitate the putative 'plant-neural' signalling of a wound stimulus in petioles of *Bidens* (Frachisse et al., 1985; Julien et al., 1991). Potassium is required for auxin transport in roots (Vicente-Agullo et al., 2004), perhaps being utilised by the synaptic structures mentioned earlier. Potassium also drives electric currents through the parenchyma of secondary xylem in the wood of trees (Arend et al., 2005). Thus, in plants, potassium takes the place of sodium which, in animal nervous tissue, is required for electrical impulse propagation.

The correspondences between subsystems and familiar structures and their functions make for a 'concrete' system of LST. Naturally, this helps to facilitate communication between biologists and LS theorists (Miller, 1986). An alternative is an 'abstracted' system (Miller, 1986), where subsystems are the only items referred to at a given organisational level; there is no requirement to seek out anatomical or physiological correspondences. The dual nature of LST, either as an abstracted system or as a concrete system, means that disputes might abate over what is or what is not a plant 'neurobiological system' (Alpi et al., 2007; Brenner et al., 2007). Whatever structure or process is being studied could be regarded simply as belonging to one of the abstracted subsystems. This is an idealistic proposition, however. Enough information is now coming from anatomical and physiological studies (see Table 1) to show that structural correspondences with information-processing subsystems can be found at each of the various levels of organisation (Barlow, 1999, 2006). There are some elusive subsystems, nevertheless: for example, the 'associator' (subsystem 16). Even J.G. Miller, after 40 years of publishing updates on LST, was unclear about its concrete identity (Miller and Miller, 1990). At the organismal level in the animal sphere, associations between units of memory help form adaptive behavioural strategies via cognition, but whether a similar possibility holds for plants is an open question.

The correspondences between subsystems and actual structures are sometimes difficult to discern (see Table 1 where the plant items are marked 'P'), partly, no doubt, because the totality of the information processing subsystem has not yet been sufficiently revealed (Barlow, 1999, 2006). Similarly, because of the different anatomies of animals and plants, searches for cross-correspondences between their subsystem components at each level (the animal items being marked ‘A’ in Table 1), are not particularly fruitful, except, perhaps, at the molecular level (Baluška et al., 2006b). Notable, however, is the similarity of structure of the ‘channel and net’ at the organism level: each type of organism – plant and animal – has, respectively, its own elongated ‘super cells’ (neurons and phloem strands) together with ‘helper’ cells (glial cells, companion cells) and their boundaries (myelin sheaths, endodermis). The role of the ‘helper’ cells in electrophysiology is not well known in either plants or animals. In plants, besides providing metabolic support to the enucleate phloem elements, the companion cells may possibly assist in the conveyance of information within these elements.

5. Analogies and Metaphors in Relation to Plant Neurobiology

Familiarity with one particular lifeform tends to create stereotypes which can be obstructions in a consideration of features of other lifeforms. In fact, one problem with the term ‘plant neurobiology’ lies with the stereotypic image of ‘nerves’ as anatomical attributes peculiar to the organs of sensate, motile animals – from mammals to hydra (e.g., Koizumi, 2007). Thus, it might seem fanciful to believe that similar structures should exist within the customarily perceived stereotype of insensate and immobile plants! But, as we have seen, the existence of some plant analogue of an animal nerve and nervous system might be anticipated. Research generated in the light of the concept of plant neurobiology would, if approached with an open mind, strengthen (or weaken) this possibility. Moreover, the abstract form of Living Systems Theory provides a way of dispelling stereotypes and permits nerves and nervous transmission to be viewed in the light of a universal ‘channel and net’ subsystem.

The language of science constantly employs analogies, metaphors and other linguistic devices (Garfield, 1986; Trewavas, 2007). By these means ‘new’ and imperfectly understood items can be described and partially comprehended in terms of ‘old’ and established facts. The term ‘neurobiology’ as applied to plants, is an analogical reference to the ‘known’ structures of animals, the only other type of ‘higher’ living system having a neurobiology which can presently be considered. It is easy, therefore, to miss the point (Alpi et al., 2007) of what a ‘nerve’, or a ‘neurobiological’ system, or indeed a ‘brain’, might really be in the context of a plant. And nerves, whether animal or plant, would originate in similar ways from simple electrochemical conducting channels such as the cellular membranes within particular cell types. Moreover, like ‘consciousness’, a ‘brain’ becomes manifest when nervous material of sufficient complexity and capacity for self-organisation has been developed (Szentágothai and Érdi, 1989).

Analogies imply a reciprocity of meaning, however: not only can a plant ‘nerve’ be an analogue of the animal nerve, but an animal ‘nerve’ can, in turn, be an analogue of the plant nerve. Animal anatomists might therefore have to give up their guardianship of the nerve; henceforth, ‘nerve’ could simply be the term which corresponds to and entity in the subsystem ‘channel and net’ (in the abstracted version of LST – see above), irrespective of whether the organism in which it is found is an ‘animal’ or a ‘plant’. A definition of a nerve could probably be devised that would cover the cell types of both plants and animals along which travel electrical impulses involving transient changes in membrane potentials. A suitable definition, together with the abandonment of the metaphorical or analogical status of ‘plant nerves’, would render superfluous the single quotation marks used to denote this ‘as if’ status.

Analogies apply across different levels of organisation. The meaning of a term at one level can be transferred to another level. Already, Albrecht-Buehler (2006) has referred to microtubules as the ‘nerves’ of the cell. Because of their properties, the microtubular ‘nerves’ do indeed correspond, by analogy, to the information-bearing ‘channel and net’ subsystem at the cellular level (Table 1). At this level, the usage and implications of the term ‘nerve’ is no different to its usage in the context of organs and organisms.

Although Charles Darwin mentioned the ‘root-brain’ of plants (Darwin, 1880), he probably used the term metaphorically. However, roots do show an extraordinary capacity for sign interpretation and adaptive movements (Baluška et al., 2006b,d, 2007), as do animals with their own relatively more complex, cognitive brains. The zone of the root which appears to integrate and process the mentioned features, and which is also replete with plant synapses, has been termed a ‘command centre’ (Baluška et al., 2006d). Like an animal brain, it provides a mechanism for coordinating responses of the root to sensory stimuli. According to the point of view of Givnish (2002), the energy cost of maintaining a neural system is so high – it has been estimated that each bit of information transfered at a chemical synaptic vesicle costs 10^4 ATP molecules (Laughlin et al., 1998) – that plants would gain little advantage by using rapid neural processes when their rates of response, in terms of growth, are so slow. But this is to ignore the need for swift communication to physiological processes in response to sudden stresses. Furthermore, according to Givnish (2002), only with a much higher flux of solar energy, as on the surface of Venus, would evolution of a plant brain be possible. Even so, root systems consist of thousands of apices. They thus constitute a massive collective ‘brain’ (Barlow, 2006) capable of capturing huge amounts of information on behalf of the whole organism. There is no need for one centralised brain, especially when a root system has to make so many local assessments and responses during its exploration of a heterogeneous soil environment.

One other vivid metaphor to emerge from plant neurobiology is the term ‘plant intelligence’ (Trewavas, 2003). However, ‘intelligence’ is a concept difficult to define, even in the sphere of animals, in an objective and non-anthropomorphic sense. There is even more difficulty when we are faced with the almost unknowable characteristics of ‘intelligence’ in plants. Probably, the ordinary, or innate, intelligence of an organism involves a degree of self-awareness and an ability to adapt to the circumstances of the moment. These two traits can be highly developed so that intelligence can eventually refer to the ability of an organism to possess cognition as well to fashion and use a tool made from elements in the external environment and by so doing achieve a more efficient mode of existence (Gould and Gould, 2007). While many animals are intelligent according to this definition, as far is known there are no plant species which make tools. Certainly, some plants (myrmecophytes) appear to fashion specialised shelters and food-bodies for ants and other insects, but these structures are inherent to the plant; they are incidental resources thrown up by natural course of plant development (Huxley, 1987) and only rarely are they induced by the presence of ants (Risch and Rickson, 1981). Thus, there is little or no cognitive foresight on the part of myrmecophytes in their provision for ants.

Following from plant 'intelligence', reflection upon 'consciousness' cannot be avoided. Here it is worth recalling the title of an article by Lynn Margulis, 'The conscious cell' (Margulis, 2001). Although not explicitly discussed by this author, the consciousness of a cell would certainly have qualities distinct to the self-consciousness experienced by an organism. The consciousness of the latter is a recently emerged property arising from the organs of brain and soma, whereas the consciousness of the cell (if 'consciousness' is the right word for what is, at this level, an unknowable property) is gained from the merger of much older material derived from symbiotic associations of organelles. It may be that, at this cellular level of organisation, 'consciousness' resembles the 'minimum cogniser' proposed by Van Duijn et al. (2006), and which confers upon an organism (protozoon or bacterium, for example) the ability to exploit an environment independently of its immediate metabolic requirements. This problem of how lower levels of organisation perceive higher levels, and vice versa, was tackled years ago by the philosophers such as Ouspensky (1970).

6. Plants and Decision Making

When confronted simultaneously with all the subtle and varied signs within an environment, often at the threshold of perception (Volkmann and Tewinkel, 1996; Barlow and Powers, 2005), is it possible that, at some level of plant organisation, there might be a 'decision-making' process which is concerned with mounting the appropriate response to one or other of these signs (Berleth and Sachs, 2001; Polevoi, 2001)? In other words, can plants prioritise one type of response above others which could potentially be operative if conditions were slightly different?

Charles and Francis Darwin were the first to examine decision-making in plants (Darwin, 1880). They concluded that root tips were able to 'decide' between two alternative growth responses (in their study, these responses were either thigmotropism or gravitropism) in the course of experiencing simultaneously the relevant stimuli of physical trauma and reorientation relative to the gravity vector. It has become evident more recently that roots are also able to 'choose', or 'decide', between hydrotropism and gravitropism, and bend towards the preferred stimulus (Takahashi et al., 2003). In this instance, the outcome is related to the presence of a particular pattern of protein synthesis. When the sensory cells of the central root cap are caused to express a protein, MIZ1, in response to a moisture gradient then hydrotropism ensues. MIZ1 is also involved in the root phototropic response but is not necessary for root gravitropism (Kobayashi et al., 2007). With the possibility, therefore, that the root cap could sense at least four tropic stimuli simultaneously (touch, gravity, humidity and light), 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 another. The critical condition for one response or another may depend on differential thresholds for each type of stimulus. A 'decision' would therefore be based on whichever of the various susception and response thresholds was the first to be crossed.

A clear example of a plant decision, and one which can easily be related to decisions in human life, is shown by the parasitic dodder plant (*Cuscuta pentagona*) (Runyon et al., 2006). The seedlings of dodder have a well developed olfactory sense which allows them to recognise volatile substances characteristic of one of its laboratory hosts, the tomato, *Lycopersicon esculentum*. A young dodder plantlet will perform a chemotropism towards its potential tomato host in preference to a wheat seedling, say, which does not emit the same suite of volatiles as tomato, and which may even produce chemicals repellant to dodder. Another 'decision'-type of response, though in this case one based on optical sensing, is found in seedlings of the tropical epiphyte, *Monstera gigantea*. The young plants can distinguish between light and dark patches at a distance of many centimetres and preferentially grow towards dark areas (skototropism). In nature, these dark areas are the trunks of host trees up which the young plants will scramble and thereby become lodged within the canopy of the hosts (Strong and Ray, 1975).

Certain decisions in plants may depend on the ability to construct a 'memory' (Thellier et al., 2004). By means of memory the traces of past experiences are recalled and activated (see the example of *Dionaea* mentioned earlier). In addition, it is possible that molecules synthesised in response to previous stressful encounters with unfavourable soil conditions or wounding (as examples) are mobilised and thereby determine present and future patterns of behaviour.

7. The Scope of Plant Neurobiology

Plants synthesise, and presumably utilise, a wide range of chemicals which have known neuronal attributes in animals (Roshchina, 2001). These include the synaptic neurotransmitters acetylcholine, glutamate and γ-aminobutyric acid (GABA) (Baluška et al., 2006b), as well as other lesser-known neuroregulators (Murch, 2006). Recently, nitric oxide (NO), a regulator of animal nervous transmission, has been discovered to play various roles in plant development (Lamattina et al., 2003; Neill et al., 2003). Also effective in plants (Powell et al., 1973) are molecules which are anaesthetics in animal systems as a result of their suppression of neural activity (Campagna et al., 2003). Ethylene, for example, is a gaseous molecule which is effective both as an animal anaesthetic (Campagna et al., 2003) and as a powerful plant hormone (Abeles et al., 1992) able to regulate meristem activity (Růžička et al., 2007). Interestingly, ethylene is described as a plant 'wound hormone', its synthesis being elicited by physical damage to plant tissue (Abeles et al., 1992). Could ethylene, therefore, be a natural plant anaesthetic, summoned when required to relieve the analogue of animal 'pain' and initiate tissue repair responses?

Lastly, mention is made of the plant hormone abscisic acid (ABA). This bioregulator has been discovered within mammalian brains (Le Page-Degivry et al., 1986) and in granulocytes (Bruzzone et al., 2007). In the latter cells, its suggested role is that of a regulator of signalling cascades, and there are also speculations that it is involved in neuromodulation (Bruzzone et al., 2007). In plants, stress-induced ABA is a transmissible signal, passing from roots to shoots (Wilkinson and Davies, 2002). However, one report claims that there can be no immediate transmission of stress-induced ABA because an apparently typical ABA effect is recorded in remote receiver tissue within seconds – far faster than is possible by the expected transpiration-dependent mechanism of ABA transport (Fromm and Eschrich, 1993). Perhaps in some circumstances ABA is not the transmissible signal but, instead, remains at its site of synthesis where it regulates the transmission of electrical, nervous impulses which then modulate ABA metabolism at a distant site (Kudoyarova et al., 2001; Polevoi et al., 1997). Clearly, stressful circumstances are cases where rapid, long-distance electrical communication would be highly advantageous, especially if information could be conveyed about how to deal with unexpected stimuli such as toxins and acid rain applied to root systems (Shvestova et al., 2001, 2002). It is here that natural putative neuroregulators such as GABA (Kinnersley and Turano, 2000) might play hitherto unexpected neurobiological roles. However, little research appears to have been done on how the passage of say, an action potential in the phloem, is transduced into a physiological response.

8. Conclusions

Evidence is growing that, in plants, there is a simple type of 'neural' communication pathway involving electrical impulses which convey information both within and between modules (Dziubińska, 2003; Baluška et al., 2006b; Brenner et al., 2006; Stahlberg et al., 2006; Fromm and Lautner, 2007). Because different types of stimuli evoke different kinds of electrical impulses which include long-distance action potentials and slow-wave potentials (Baluška et al., 2006c; Stahlberg et al., 2006), it follows that their frequencies, amplitudes, velocities, and associated ionic fluxes could constitute a neurobiological 'language' which is interpreted in characteristic ways by receptive cells (Lautner et al., 2005; Fromm and Lautner, 2007). The presence of plant 'synapses' at the end walls of certain cells where vesicle turnover is active and which involve the plant hormone auxin (indole acetic acid) as a neurotransmitter, also conforms with the hypothesis that there is some kind of neurological system in plants.

The roles of many constitutive plant biochemicals, often known only from analyses of animal neural systems, remain obscure at present, but the possibility of their importance as neuroregulators in plants cannot be ignored. If the concept of a plant neural system is vindicated, it is then important to know the system's anatomical correlates. And given the evidence that plants sense a wide variety of stimuli, as well as emit signals into their environment, it is therefore crucial to know more about both these features in relation not only to a putative plant nervous system but also to the more familiar signal–hormone response routes of communication.

There is now an opportunity to reappraise the role of auxin in plant growth. If established as a neurotransmitter and generator of electrical impulses, auxin may then be seen to have a dual role – as a component of both a neural pathway and a chemico-regulatory pathway. Thus, not only could auxin and other hormones serve as the classical agents for integrating spatially separated developmental processes that characterise the life cycle of the whole plant but they could also effect rapid behavioural responses via nerve-like signalling, especially in circumstances of stress.

The vindication of a neural system in plants would fill a gap hitherto present in the application of J.G. Miller's Living Systems Theory (LST) to plants (Barlow, 1999, 2006) and hence would indicate the universality of LST with respect to all higher lifeforms. Together, LST and plant neurobiology might forge a strong theoretical basis for intra- and inter-plant communication processes, particularly since in other situations LST has been found to provide a useful bridge between apparently disparate concepts (Bailey, 2001).

Although it may be a small but perhaps difficult step to take advantage of the correspondences between the neurobiological attributes of animals and plants, such a step may nevertheless lead to substantial advances in knowledge of plants and increase respect for this irreplaceable green portion of our biosphere.

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