

Plant neurobiology: from sensory biology, via plant communication, to social plant behavior

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Abstract In plants, numerous parameters of both biotic and abiotic environments are continuously monitored. Specialized cells are evolutionary-optimized for effective translation of sensory input into developmental and motoric output. Importantly, diverse physical forces, influences, and insults induce immediate electric responses in plants. Recent advances in plant cell biology, molecular biology, and sensory ecology will be discussed in the framework of recently initiated new discipline of plant sciences, namely plant neurobiology.

Keywords Action potential · Plant behavior · Plant neurobiology · Sensory biology · Communication · Signaling

Sensory plant biology and plant electrophysiology were two lively disciplines up until the 1970s (Bünning 1959; Haupt and Feinleib 1979), but then, for somewhat obscure reasons, they showed no further development. In the last few years, however, there have been numerous advances in plant sciences, which necessitate not just a revival of plant sensory biology but also the introduction of plant neurobiology (Baluška et al. 2006a; Brenner et al. 2006a). First of all, and contrary to all ‘mechanistic’ predictions based on the high turgor pressure of plant cells, endocytosis has been found to be an essential process of plant cells, which

impinges upon almost all aspects of plant life (Šamaj et al. 2005, 2006). Moreover, recent advances in the plant molecular biology have identified, besides classical neurotransmitters, also several proteins typical of the animal neuronal systems, such as acetylcholine esterases, glutamate receptors, GABA receptors, and endocannabinoid signaling components, as well as indicating signaling roles for ATP, NO, and ROS (Baluška et al. 2006b). Importantly, plant action potentials have turned out to influence processes such as actin-based cytoplasmic streaming, plant organ movements, wound responses, respiration, and photosynthesis, as well as flowering (Wagner et al. 2006; Fromm and Lautner 2007). Last, but not least, there have been significant advances in ecological studies on plant–plant and plant–insect communications, in behavioral studies on memory and learning phenomena in plants (Trewavas 2005a, b; Galis and 2008; Ripoll et al. 2009), as well as the revelation that complex plant behavior (Karban 2008; Scott 2008) implicates signal perception, processing, and the integration of ambient signals (Brenner et al. 2006b).

Recent advances in plant cell biology, molecular biology, and ecology have accumulated a critical mass of data, which are not ‘digestible’ within the framework of these, now classical, disciplines of plant sciences (Baluška et al. 2006a, b; Brenner et al. 2006b; Bruzzone et al. 2007). New approaches are required, characterized by system-like analysis of information acquisition, storage, processing, and the making of decisions.

Plants retrieve from the abiotic environment information critical for their survival, especially relating to light and gravity, two physical factors pervading the universe. Plants actively experience environment and can both store and retrieve memories (Galis and 2008; Ripoll et al. 2009). Intriguingly, the translation of these physical forces into

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plant activities—typically differential growth responses—is based on the transcellular transport of auxin, which helps to bring about the final shape of the plant body (Friml 2003; Baluška et al. 2006b; Brenner et al. 2006b). Thus, this information-bearing molecule is central to our call for plant neurobiology.

Although the history of auxin can be traced back to the Darwin's early experiments with phototropism of coleoptiles (Baluška and Mancuso 2009), we still know almost nothing about its peculiar features. Let us examine the mystery of this unique molecule. Although auxin can be synthesized probably in each plant cell, it is tediously transported from cell to cell throughout the plant body (Friml 2003). Puzzling is the well-known phenomenon by which, although the auxin molecule is sufficiently small to pass easily through plasmodesmatal channels, plants cells somehow manage to prevent this direct cell-to-cell means of auxin transport. Rather, plants maintain an energetically costly system based on vesicle trafficking, closely resembling neuronal and immunological cell–cell communication, to drive transcellular auxin transport (Baluška et al. 2003, 2005; Friml and Wiśniewska 2005). The next peculiarity is that when extracellular auxin hits the outside leaflet of the plasma membrane, it induces electric responses based on the ABPI auxin-binding protein (Felle et al. 1991; Steffens et al. 2001; Baluška et al. 2004). All this suggests that auxin, besides hormone- and morphogen-like properties, also possesses neurotransmitter-like properties. Since the cell-to-cell transport of auxin is also involved in plant response to light and gravity, plant neurobiology approach is needed to explain this great mystery of plant nature (Baluška and Mancuso 2008).

DeWeese and Zador (2006) loosely defined neurobiology as having three basic characteristics: (1) all biological systems (organisms) are embedded within a physical environment that shapes their organization and behavior; (2) to survive, all biological systems need to effectively retrieve of information from their physical environment; (3) neuronal activity is essential to translate information sensed concerning the environment into electrical impulses, which are then capable of rapid transformation into biological signals that induce motoric responses. Importantly, sensing of the biotic environment is physically mediated through the senses: hearing, seeing, feeling, or smelling; all this is based on the laws of physics. In short, the neurobiological apparatus translates sensory information first into electrical impulses and only then into biological information inducing organismal actions. Human perception of the outside world relies on so-called 'neural code,' which links together sensory signals and neural responses.

Similarly, in plants, numerous parameters of the physical environment are monitored. Specialized cells (e.g., root

cap statocytes and root transition zone cells) are evolutionarily optimized to translate sensory information obtained from the environment into motoric responses (e.g., gravibending of root apices). Moreover, physical forces, influences, and insults, all induce immediate electrical responses in plants. Obviously, one task is to make a connection between all these events with the molecules and cellular processes, which are known, from neurobiology, and for which there is firm or emerging evidence from plants. We need to understand how those processes transform physical information (e.g., light, gravity, temperature, mechanical and osmotic forces, etc.) into biological information. Particularly, we need to know if it is possible to convert physical information directly into biological information without inducing any bioelectrical responses, or if physical sensory information needs to be first transformed into bioelectrical information before it can be translated into purely biological information. For this, we need a merging of classical electrophysiology with cell biology and molecular biology. Obviously, plant neurobiology as a new branch of plant sciences is not only justified but also competent to solve the new and urgent questions of contemporary plant biology.

The plant neurobiological perspective reveals several surprises when the classical plant hormones like auxin, abscisic acid, ethylene, and salicylic acid are considered from this angle. Auxin and abscisic acid elicit immediate electric responses if applied to plant cells from outside (Pickard 1984; Felle et al. 1991; Roelfsema et al. 2004; Pei and Kuchitsu 2005), suggesting that their regulated release within plant tissues may be a part of neurotransmitter-like cell-to-cell communication (for auxin, see Baluška et al. 2003, 2005; Friml and Wiśniewska 2005; Schlicht et al. 2006). Abscisic acid signaling pathway is conserved between plants and animals, and this signaling molecule both stimulates and is endogenously produced in human granulocytes in a way suggesting that it acts as endogenous proinflammatory cytokine (Bruzzone et al. 2007). Importantly, biologically active abscisic acid was isolated also from brains of vertebrates (Le Page-Degivry et al. 1986) indicating possible roles of abscisic acid in the central nervous system. Salicylic acid activates similar subset of MAPKs as voltage pulses (Link et al. 2002). Ethylene, a classical plant hormone, is an anesthetic (Campagna et al. 2003), a fact that plant physiologists have ignored until now. Interestingly, anesthetics used on animals including man induce anesthetizing effects on roots similar to those of ethylene (Powell et al. 1973). Ethylene is released in mechanically stressed plant tissues, and structurally diverse anesthetics activate mechanosensitive channels (Patel and Honoré 2001; Patel et al. 2001). As ethylene is released after wounding, it might act to relieve 'pain' in plants. There are numerous other plant-derived

substances, which manipulate the pain receptors in animals, such as capsaicin, menthol, and camphor. Interestingly, the monoterpene volatiles, menthol, and camphor induce oxidative stress and inhibit root growth in maize (Zunino and Zygadlo 2004), indicating that they too act as plant signaling molecules. Finally, plants express inhibitors that are specific to the neuronal nitric oxide synthases (Lowe et al. 2007; Osawa et al. 2007). Another example of neuronal-like behavior of plants is the report that prevention of nyctinastic movements of leguminous leaves causes their death while leaves allowed to ‘sleep’ stayed healthy (Ueda and Nakamura 2006). This resembles the situation in animals (Cirelli et al. 2005). Although melatonin was discovered in plants more than 10 years ago (Kolár and Macháková 2005; Arnao and Hernandez-Ruiz 2006, 2007; Pandi-Perumal et al. 2006), we know almost nothing about the roles of melatonin in plants despite the fact that it is biochemically closely related to auxin. Interestingly, in this respect, melatonin mimics auxin in the induction of lateral root primordia from pericycle cells (Arnao and Hernandez-Ruiz 2007).

The Arabidopsis genome encodes ten NADPH oxidases (RbohA–J) of which six are expressed only in root apices (A, B, C, E, G, I) and two (D, F) are expressed in whole seedlings including the root apices (Sagi and Fluhr 2006). Expression of eight of these molecules in root apices makes this one of the most complex signal-mediated ROS-generating organs. It is currently unknown for what developmental and signaling purposes so many different NADPH oxidases in roots are needed. A similar perplexing complexity, unique also for root apices, concerns polar auxin transport. Five types of PIN molecule (PIN1,2,3,4,7) are expressed in root apices (Blilou et al. 2005), whereas only one PIN (PIN1) is sufficient for the morphologically more complex shoot apices (Reinhardt et al. 2003; Reinhardt 2006). What, then, is so special about root apices? This is a tough question, but answers seem to be emerging in the multitude of recent data, not easily interpretable by the classical plant physiological approach, but comprehensible from the approach of plant neurobiology (Baluška et al. 2005; Brenner et al. 2006a). One of them involves the idea that the transition zone of root apices acts as some kind of ‘command center’ (Baluška et al. 2004). In accord with the original proposal of Darwin (1875), this root apex zone resemble brains of animals, as its cells are very active in the sensory integration, via synaptic vesicle-recycling (Baluška et al. 2003, 2004, 2005), and do not have any other obvious biological duties.

Despite a relatively simple body organization, plants need sophisticated sets of coordinative processes. Besides their root–shoot coordination, there is also need for coordination amongst radial tissues, especially within and between the cortex and stele. Action potentials run

preferentially in an axial direction and they link root and shoot apices. Despite the modular and apparently decentralized organization of the plant body, there are several critical situations requiring ‘centralized’ decisions, such as, for instance, the onset of flowering as well as the onset and breakage of dormancy. Although these decisions are based on information retrieved via numerous distant organs, they imply some central ‘processor,’ which would reliably control the whole plant body. Importantly, any wrong decision would have detrimental consequences for the whole plant. The transition zone of root apices is the only zone in the plant body showing oscillatory patterns of cellular activities responding also to leaf wounding (Shabala et al. 2006). Moreover, cells of this specific zone are the only ones to express up to five different PIN efflux carriers (Verbelen et al. 2006; Bandyopadhyay et al. 2006). Across the F-actin and myosin VIII-enriched plant synapses (Baluška et al. 2005), PINs drive complex transcellular patterns of polar auxin transport. These complex networks of auxin transport pathways are driven via synaptic processes at the plant synapses and translate diverse sensory perceptions into tropistic root growth responses, which allow roots to navigate their growth according to gravity, light, humidity, touch, and other environmental stimuli (Baluška and Mancuso 2009). Polar auxin transport is driven via vesicular secretion (Schlicht et al. 2006; Mancuso et al. 2007), and auxin elicits electrical responses in adjacent cells (Felle et al. 1991) as well as synchronizes cell activities within a cell file (Nick 2006; Maisch and Nick 2007). So auxin fulfils the minimum criterion for being a neurotransmitter-like signaling molecule in plants. We expect that plant synapses will be, similarly like synapses in animal and human brains, integrating sensory inputs to allow experience-based behavior and cognition. In fact, plant cognition is another just emerging topic of plant sciences (Calvo Garzón 2007; Calvo Garzón and Keijzer 2009).

Plants perform neuronal-like computation not just for rapid and effective adaptation to an ever-changing physical environment but also for the sharing of information with other plants of the same species. In fact, plants emerge as social organisms. Plants societies increase their immunity to damage after receiving warnings from attacked neighbors (Engelberth et al. 2004; Ton et al. 2007; Karban 2008). Strategies involve, among others, the release of volatiles, which then attract the enemies of the attacking herbivores (D’Alessandro et al. 2006). Moreover, there are examples of ‘war-like’ phenomena whereby invading plants kill other plants via the release of toxic allelochemicals from their root apices (Bais et al. 2006). That root apices of other plants can cause this hostility is a new discovery. However, roots are also well known for their ability to avoid dangerous places by actively growing away

from hostile soil patches. Also in ‘war-like’ mode, the root apices of parasitic plants actively recognize the roots of their prey, grow toward them, and then, to gain control over them, send out root-hair-like processes that later develop into parasitic haustoria (Tomilov et al. 2005). Thus, by using a vast diversity of volatiles, plants are able to attract or repel diverse insects and animals, and thereby are able to shape their biotic niche. The number of volatile compounds released and received by plants for communication is immense, requiring complex signal-release machinery, as well as an unprecedented ‘neuronal’ decoding apparatus for correct interpretation of received signals. These aspects of plant activity have not yet been studied yet.

Concluding remarks

Human perception of the outside world relies on a so-called ‘neural code,’ which links sensory signals and neuronal responses (DeWeese and Zador 2006). Similarly, in plants, numerous parameters of the physical environment, especially, light, temperature, and gravity, are continuously monitored. Polar auxin transport translates perceived and processed sensory information into adaptive physiological, developmental, and motoric responses. Structural and developmental plasticity of plants (Friml 2003; Baluška et al. 2006a, b; Baluška and Mancuso 2009) resembles experience-based plasticity of neurons and neuronal networks in brains (Trachtenberg et al. 2002; DeBello 2008). New concepts are needed, and new questions must be asked, for advancing our rudimentary understanding of the communicative nature of sensory plants.

Close similarities in sensory and neurobiological aspects seem to be at odd with the currently dominating evolutionary ideas about plants and animals (e.g., Baldauf and Palmer 1993). However, plants and animal share several very complex and conserved features that are missing from fungi and unicellular organisms, suggesting that they are phylogenetically much more closely related (Stiller 2007; Veerappen et al. 2008). Earlier phylogenetic analyses of gene sequences were obviously obscured from several phylogenetic tree-building artifacts (Stiller 2007). Removing the old Aristotelian schism between plants and animals will unify all multicellular organisms under one conceptual ‘umbrella.’

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