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The “plant neurobiology” revolution

Peter V. Minorsky

Department of Natural Sciences, Mercy University, Dobbs Ferry, NY, USA

ABSTRACT
The 21st-century “plant neurobiology” movement is an amalgam of scholars interested in how “neural processes”, broadly defined, lead to changes in plant behavior. Integral to the movement (now called plant behavioral biology) is a triad of historically marginalized subdisciplines, namely plant ethology, whole plant electrophysiology and plant comparative psychology, that set plant neurobiology apart from the mainstream. A central tenet held by these “triad disciplines” is that plants are exquisitely sensitive to environmental perturbations and that destructive experimental manipulations rapidly and profoundly affect plant function. Since destructive measurements have been the norm in plant physiology, much of our “textbook knowledge” concerning plant physiology is unrelated to normal plant function. As such, scientists in the triad disciplines favor a more natural and holistic approach toward understanding plant function. By examining the history, philosophy, sociology and psychology of the triad disciplines, this paper refutes in eight ways the criticism that plant neurobiology presents nothing new, and that the topics of plant neurobiology fall squarely under the purview of mainstream plant physiology. It is argued that although the triad disciplines and mainstream plant physiology share the common goal of understanding plant function, they are distinct in having their own intellectual histories and epistemologies.

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1. Introduction

Are plants intelligent? Can they learn? Are they sentient? These are just some of the unorthodox questions considered by Proponents of the modern plant neurobiology movement. Plant neurobiology has roots dating back centuries, but its most recent incarnation is centered around The Society of Plant Signaling and Behavior (SPSB) founded in 2005.[1] In its early years, from 2005 to 2009, the Society’s name was The Society for Plant Neurobiology, but the term “plant neurobiology” proved so controversial that early members complained that their affiliations with the Society were, in some circles, negatively impacting their careers.[2]

One cannot delve too deeply into the topic of “plant neurobiology” without discussing the term itself. It is a name disliked by many mainstream biologists, and even by some Proponents. However, as Juliet rhetorically asks in Shakespeare’s *Romeo and Juliet* (Act II, Scene II), “*What’s in a name? That which we call a rose by any other name would smell as sweet*.” Similarly, the movement called “plant neurobiology”, referred to by any other name, would still be as revolutionary. Although the SPSB’s new name may be more generally palatable, both sides in the debate continue to use the term “plant neurobiologists” to describe Proponents. For this reason, and because the present contribution concerns in part the historical origins of the movement, this paper will use the term “plant neurobiology” despite its inadequacies.

With hindsight, perhaps a more fitting name for the Society would have been the “The Society for Plant Neuroethology”, although “plant neuroethology” still suffers from the problem of employing the controversial prefix “neuro-“. Neuroethology, however, is the science of how “neural” processes, broadly defined, lead to changes in behavior. Neuroethologists do not require that the objects under study possess neural systems *sensu strictu*. In a review of the subject, for example, Bullock noted that neuroethology includes studies on protozoans and humans and, implicitly, plants as well.[3]

The aim of the plant neurobiology movement is to create a paradigm shift in how plant biologists regard plants conceptually. As such, it is not surprising that the discipline of plant neurobiology has faced strong resistance from the mainstream. Indeed, immediately after the debut announcement of the Society,[1] a group of 36 powerful and influential plant biologists, including textbook authors, academy members, institutional directors, journal editors, and endowed professors, attempted, essentially by public petition, to strangle the monstrosity in its cradle[4]; since then, a smaller cadre of Opponents has been unrelenting in their efforts to quash the movement at every opportunity. [5–7] Opponents consider many, if not most, of the questions raised by plant neurobiologists to be dubious in the extreme. In their view, plants are aneural organisms: thus, the term “plant neurobiology” is an oxymoron, and the scientific discipline of “plant neurobiology” *a priori* cannot exist. Proponents, in contrast, based on their experiences studying the behavioral, electrical, and psychological responses of plants, argue *a posteriori* that many of the radical ideas discussed by plant neurobiology are intriguing re-interpretations of various plant behaviors.

CONTACT Peter V. Minorsky pminorsky@mercy.edu Department of Natural Sciences, Mercy University, 555 Broadway, Dobbs Ferry, NY 10522

Regrettably, the unilateral attacks against plant neurobiology have often fallen short of the norms of academic collegiality and decorum. A signatory of Alpi *et al.*,[4] for example, described the plant neurobiology controversy as the latest " . . . *confrontation between the scientific community and the nuthouse* . . . "[8] More vulgar expressions of derision could be cited. In general, however, the polemical tone of the most vigilant Opponents has been that of concerned senior scientists selflessly shepherding naïve students and the public away from a harmful pseudoscience.

A post-modern perspective, however, suggests a less heroic explanation for the orthodox attacks against plant neurobiology: these unilateral assaults may represent nothing more than establishment elites rallying to protect the Enlightenment traditions that define their creed. Indeed, Michel Foucault critiqued the tendency of the Enlightenment tradition to explain all matters according to a dominant master-narrative. Foucault emphasized that all disciplines are defined by elites who control the academy, and who determine, often based on self-interests, the standards of normality.[9] Once certain scientific philosophies have been selected over others, alternative epistemologies become deviant. Those who do not conform to the epistemology of the master-narrative, are shunned, treated as heretics, or accused of insanity (*i.e.*, of belonging in a "nuthouse").[9]

History shows that the splintering of maverick groups of thinkers from the orthodox mainstream often has a salubrious effect on the progress of science. For example, the flowering of plant physiology into a mature discipline with its own journals and scientific societies, arose from the frustrations that a handful of experimental plant physiologists had concerning the mostly descriptive botany that dominated plant biology in the early 20th century.[10,11] Since new journals and new scientific societies are often born of frustration, it is of interest to consider why scores of plant biologists felt compelled in 2005 to form a separate society.

Because the views of plant neurobiologists are far from monolithic, it is difficult to distill from the ferment of plant neurobiology, a list of tenets to which all plant neurobiologists universally ascribe. As such, it is presumptuous for one individual to speak for the entire movement: the following, therefore, is not a manifesto but rather one scientist's perspective concerning why plant neurobiology emerged as a new discipline in the early 21st century, how it differs from mainstream plant biology, and why it has suffered unrelenting attacks from the orthodoxy.

The specific aim of the present contribution is to refute an overarching criticism leveled by Opponents, that " . . . *plant neurobiology does not add to our understanding of plant physiology, plant cell biology or signaling* . . . "[4] (p135–136) It is argued that the unique and controversial aspects of plant neurobiology stem from its inclusion of a triad of historically marginalized disciplines (plant ethology, plant comparative psychology and whole plant electrophysiology) that have found safe harbor within the larger plant neurobiology movement. The following eight sections (Sections 2–9) explore different ways in which the "triad disciplines," and thus, plant neurobiology as a whole, differ from today's mainstream plant biology. Integrated into these eight sections are discussions relating to the history (Sections 2 & 4), philosophy (Section 4), sociology (Sections 6 and 8) and psychology (Section 9) of the triad disciplines. Based on these considerations, the thesis is presented that plant neurobiology, because of its inclusion of triad disciplines, has, in broad view, a separate historical and epistemological lineage from orthodox plant physiology. It is further proposed that the unpopularity of plant neurobiology amongst today's mainstream is attributable to the fact that the plant neurobiology movement challenges three philosophical pillars upon which mainstream biology is currently built: These include: 1.) *reductionism*, the idea that finer mechanist details are of greater fundamental importance and should be the main focus of scientific research (see Section 3) 2.) *genetic determinism*, the belief that all behaviors are directly controlled by an individual's genes, generally at the expense of the role of the environment (see Section 3), and 3.) *absolute positivism*, the idea that the only worthy contributions to science are those that are verified through experiments or mathematical proof (see Section 7).

2. Plant neurobiology provides harbor to three historically marginalized subdisciplines

A distinctive feature of the plant neurobiology movement is its inclusion and integration of scientists from a triad of historically underappreciated subdisciplines of biology: 1.) *Plant ethologists* who seek to apply the general principles of the traditionally zöocentric disciplines of behavioral ecology, ethology, and sociobiology, to plants; 2.) *Plant electrophysiologists* who seek to instill a modicum of balance to the heavily lopsided chemocentric view of plant physiology that has dominated the field for the last century, and 3.) *Plant comparative psychologists* who are exploring the possible occurrence of higher cognitive functions in plants, including goal-directed and anticipatory behaviors, learning, cognition, memory and sentience. Although the triad disciplines are the focus of the present contribution, plant neurobiology also encompasses other emerging sub-disciplines, including phytosemiotics[12,13] and ecological psychology.[14,15] Moreover, the triad disciplines also appreciate and collaborate with scientists from more conventional subdisciplines, including plant physiology, biochemistry and molecular biology, as well as with colleagues in the behavioral sciences, the humanities and the arts. Because of its embrace of the triad disciplines, plant neurobiology has a markedly different scholarly demographic from mainstream plant physiology.

In order to understand why the triad disciplines were historically marginalized, it is useful, before returning to the seven remaining differences between plant neurobiology and mainstream plant physiology, to take three long detours in the remainder of this section, to discuss the respective histories of plant ethology, plant electrophysiology and comparative plant psychology.

History of plant ethology

Throughout most of the 20th century, the term "ethology" was strictly limited to discussions of animal behavior. Toward the end of the 20th century, however, many ethological terms and concepts, such as foraging,[16,17] mate choice,[18] habitat choice,[19] and kin selection,[20] that had hitherto been limited to discussions concerning animals, were increasingly finding application in plant biology. These trends led to calls for the recognition of plant behavioral biology (plant ethology) as a new subdiscipline of biology.[21,22]

In the early years of the 21st century, the term "plant behavior" quietly transitioned from the taboo to the mainstream. Today, even the most fervent Opponents are not averse to the concept of plant behavior.[5] However, before armistice celebrations can commence, it is necessary to examine what precisely is meant by "behavior", a thorny question about which even behavioral biologists cannot agree.[23,24]

Ethology, as originally conceived, was limited to the study of animal behavior. Tinbergen, one of the founders of ethology, defined "behavior" as " … *the total movements made by the intact animal* … "[25] (p2) From a plant neurobiological perspective, Tinbergen's definition is deficient in three regards. First, behavior is not a property of animals alone. In the 21st century, the purview of behavioral biology has expanded to include many types of brainless organisms, including plants, fungi,[26,27] protists[28,29] and bacteria.[30] Second, Tinbergen's limitation of behavior to intact organisms is also problematic. Tinbergen presumably limited behavior to intact organisms because in the highly cephalized and locomotory animals studied by the early ethologists, amputated parts, once separated from the brain, do not demonstrate behavior. In simpler animals, however, amputated parts, can, in some cases, even though completely severed from the brain, still exhibit behaviors. Amputated, brain-free sections of the acoelomate worm *Symsagittifera roscoffensis*, for example, still contract and cease movement in response to the vibrations caused by tapping on their petri dishes.[31] In higher plants, isolated plant organs can also demonstrate behaviors: isolated pulvini, for example, exhibit nyctinastic behavior.[32] Third, most Proponents would reject Tinbergen's view that all behaviors involve movement. Rather, a more semiotic definition of "behavior" proposed by the eminent psychologist Jean Piaget is perhaps more in keeping with the views of many plant neurobiologists. Behavior, according to Piaget, is:

> … all action directed by organisms toward the outside world in order to change conditions therein or to change their own situation in relation to these surroundings … an animal's reflexes, or the ornithogalum flowers reactions to light, may legitimately be described as behavior because they are intended, no matter how locally or occasionally, to modify the relationship between organism and environment.[33] (pxiii-ix)

Although animal reflexes and plant phototropism, the two examples of organismal behavior specifically cited by Piaget, are movement-related behaviors, it may not have been his intention to limit behavior solely to cases involving changes in spatial orientation. Much depends on what Piaget meant by "situation." If, by "situation," Piaget meant "a state of affairs" or "a set of circumstances" rather than merely "a physical location," then organismal behavior may encompass other activities in addition to movement.

As an example of a behavior not involving movement, consider the ripening of a tomato fruit on a vine. The final stages of fruit ripening involves neither a multiplication of cells nor a change in physical location but it does represent a change in the plant's "state of affairs" with relation to the outside world; by ripening, the plant no longer protectively camouflages its fruits from fructivores but rather signals to them non-cognitively by means of bold colors and enticing aromas, to devour them. Interestingly, "ripening behavior" is a term widely used by field biologists,[34] while molecular biologists tend to place "ripening" strictly under the purview of developmental biology.[35]

In considering the proposal that the color change of a ripening fruit is a type of non-sentient behavior, it is of interest to ascertain whether animal ethologists regard color changes in animals as examples of behavior. In many animal taxa, the ability to change color over a range of timescales exists, and such color changes can occur in seconds, minutes, and hours, to longer term changes associated by many with phenotypic plasticity and development.[36] Animal behavioral biologists certainly consider rapid, chromatophore-based changes in animal color as a type of behavior.[37,38] More recently, Eacock et al. used the term "behavior" to describe the slow background-matching color changes occurring in peppered moth caterpillars (*Biston betularia*) over the course of hours to weeks.[39] Since the concepts of "slow" and "rapid" are relative and context-dependent, time specifications should not be included in definitions of behavior.

In addition to changes in spatial orientation and color, plants also alter their relationship with the environment by architectural changes. Plants, for example, decrease their exposure to harmful conditions by reducing their interface with negative environmental factors; a case in point is "self-pruning" wherein the collective protoplasm of an overly shaded plant limb is deconstructed and its molecular components partially salvaged for reallocation elsewhere in the plant. Therefore, the collective biomass of a plant, composed solely of living cells, is constantly reorienting itself in space, contracting from negative environmental cues, and extending toward positive rewards. In plants, growth that is unrelated to the unfolding body plan (*Bauplan*), is behavior, and environmentally altered morphogenesis (i.e., phenotypic plasticity) falls under the purview of behavior.[40] Self-pruning by plants, of course, is mechanistically unrelated to the physiological processes by which locomotory animals reorient themselves in space but phenomenologically they are similar in that both reorient the collective protoplasm of the organism toward more favorable environments and away from adversity.

History of plant electrophysiology

In 1873, Sir John Burdon-Sanderson [1828–1905] first demonstrated the occurrence of action potentials (APs) in a plant, namely Venus' flytrap (*Dionaea muscipula*).[41] Burdon-Sanderson's contributions to plant electrophysiology, which were limited to *Dionaea*, were dwarfed in the early decades of the 20th century by the prolific research of the Bengali polymath Sir Jagadis Chandra Bose [1858–1937]. Unlike Burdon-Sanderson, Bose made the conceptual leap that all plants, not just motile plants like *Dionaea*, are excitable.

Before becoming a plant physiologist, Bose was a pioneer in wireless communication and semi-conductors, and among the first to create and characterize microwaves in the laboratory. [Today, there is a permanent exhibit devoted to Bose's contributions to physics and electrical engineering at the National Electronics Museum in Washington DC.[42]] In the early years of the 20th century, however, Bose, then in his mid-forties, abruptly and completely shifted his research focus to the question of plant sensitivity, and for the remaining three decades of his career, the study of plant function consumed his scientific attention.[43]

Much of Bose's botanical research concerned the leaf movements of the sensitive plant (*Mimosa pudica*) and the telegraph plant (*Codariocalyx motorius*). More importantly, he extended the findings he had made using these two species to "ordinary" plants not showing rapid movements. In Bose's mind, the propagating leaflet closures of *Mimosa* were reminiscent of the APs that propagate along the nerves of animals. *Codariocalyx*, on the other hand, exhibits a spontaneous oscillatory leaf movement in which the two, diminutive lateral leaflets of the trifoliate leaf alternately rise and fall with a periodicity of a few minutes: these movements reminded Bose of the beating of the animal heart. In light of modern knowledge, it is likely that the electrical and mechanical pulsations Bose measured both in *Codariocalyx* and in ordinary plants were correlates of propagating Ca^{2+} waves. Regrettably, because of the Nordic supremacist views held by many Western scientists of the day, Bose's reputation was smeared by accusations of fraud, incompetence and mysticism, and his legacy went into a deep eclipse from which it has only recently begun to reemerge.[44]

It is no small matter to summarize Bose's numerous discoveries relating to plant electrophysiology, but among the most important were his demonstrations, each confirmed by subsequent research, that local graded potentials and propagating, all-or-none APs are elicited in plants by a variety of environmental stimuli, including rapid temperature change, electrical shocks, and mechanical stimuli. Bose also determined that the velocities of propagation of plant APs are several orders of magnitude slower than the APs of animals, and that direct stimulation as well as the passage of excitation are accompanied by a transient shrinkage of plant stems. Bose found that the rate of AP propagation was faster in one direction than the other, and that plant APs propagate long distances through plants via phloem cells that he called "plant nerves." Regrettably, the racist scientists who attacked Bose in the late 1920s won the day, and Bose's contributions to plant biology fell into near oblivion over the next half century.[44]

In the 1950s through the 1970s, there was a reemergence of interest in plant electrophysiology in Japan,[45] Australia[46,47] and several Soviet bloc nations,[48] and to a more limited degree, in China[49] and the West.[50,51] Regrettably, the important contributions made by non-Western scientists such as Bose,[52,53] Kôketsu,[54] Asida,[55] Okamoto,[45] Lou,[49] Sibaoka,[56] and Sinyuhkin,[48] have tended to be overlooked in recent Western historical accounts of plant electrophysiology.[57,58]

In the case of the United States, the modest burst of interest in plant electrophysiology in the early 1970s was soon derailed by the publication in 1974 of a pseudoscientific bestseller *The Secret Life of Plants*,[59] which placed a stigma on the entire field of plant electrophysiology. Ironically, some Opponents, in their attempts to discredit the plant neurobiology movement, have gone so far as to employ an association fallacy to form in their readers' minds a connection between plant neurobiology and the pseudoscience presented in *The Secret Life of Plants*, writing, "*Even more controversial have been Monica Gagliano's intriguing behavioral studies on habituation and associative learning, which have captured the public's imagination in a way not seen since the 1973 publication of* The Secret Life of Plants."[5](p679) One would, of course, be hard pressed to find a work more strongly disavowed by plant neurobiologists than *The Secret Life of Plants*.

In the early 1930s, when Bose's health was failing and his reputation and, by extension, the reputation of plant electrophysiology in general was unraveling, reductionist scientists made an important advance, the identification and characterization of indole-3-acetic acid (auxin).[60] The discovery of other endogenous plant growth regulators (i.e., "hormones") soon followed. Unlike the early studies of plant behavior, plant hormone research yielded practical results that improved crop production and wealth. In his 1943 address as the retiring President of the American Society of Plant Physiologists, Edwin C. Miller triumphally announced the eradication of plant behavioral biologists from the profession:

> Forty years ago the work in plant physiology was changing from the old to the new. Those who were interested in the subject were concerned chiefly with the nature of the response of Mimosa or similar plants to stimuli of various sorts. In the main, they were not interested at all in any practical or applicable results that might accrue from their investigations . . . The public, rightly or wrongly, may eventually reach the stage where the workers not only in plant physiology, but also in most other lines of scientific work, must show that the results of their labors will contribute to the happiness or advancement of mankind. . . This attitude of the public may be wrong, but right or wrong, it exists and anyone interested in research must reckon with it. The practical aspect now dominates investigational work in all regards and the so-called purist, especially in plant physiology, is now prominent only on account of his absence.[61] (p315)

During the mid-20th century, research into plant hormones blossomed, while whole plant electrophysiology and plant ethology languished in obscurity. Several generations of 20th-century plant physiologists were raised to think about the integration and regulation of plant function almost exclusively in terms of the interactions of endogenous chemical regulators.

The Opponents do not disagree with the view that APs occur in plants. Alpi *et al.*, for example, write, "*Plants cells do share features in common with all biological cells, including neurons. To name just a few, plant cells show action potentials, their membranes harbor voltage-gated ion channels, and there is evidence of neurotransmitter-like substances. Equally, in a broader sense, signal transduction and transmission over distance is a property of plants and animals.*"[4](p136) While it is gratifying that plant APs, more than a century after their discovery, are beginning to be accepted even amongst the Opponents, celebrations must be delayed until the nerve-like activities of plants are so integral to discussions of plant function that they are discussed in plant biology textbooks. Indeed, in animal physiology textbooks, there is usually an entire chapter devoted to bioelectrical signaling. Comparable chapters in plant physiology textbooks are universally lacking. If one examines, for example, the subject index of a leading English-language plant physiology textbook published in 2010, the 5th edition of Taiz and Zeiger's textbook,[62] one finds there is no mention of APs or, for that matter, receptor potentials,[63,64] reflex arcs,[65,66] variation potentials,[67] system potentials,[68] summation,[69,70] tetanus,[54] habituation,[71,72] or sensitization.[72]

Only in the 6th edition of Taiz and Zeiger's textbook, published in 2015 (with additional coauthors), do plant APs at last receive some scant mention.[73] Unfortunately, the authors in their brief treatment of this topic introduce naïve readers to some serious misconceptions. They write, for example, that, "*The most common type of electrical signaling in plants is the action potential, the transient depolarization of the plasma membrane of a cell generated by voltage-gated ion channels . . .* "[73](p430) This definition would be perfect, save for three exceptions. APs are not the most common type of electrical signaling in plants[74]; higher plant APs primarily employ not voltage-gated ion channels during depolarization but Ca^{2+}-activated anion (Cl^{-}) channels[75]; and not every "transient depolarization" is an AP.[76]

History of plant psychology

During the last 80 years, the discipline of comparative psychology has largely been limited to the scientific study of the behavior and mental processes of non-human animals, but this was not always the case: for example, a three-volume 1940 treatise entitled *Comparative Psychology*, included a 108-page chapter devoted to the psychology of the Metaphyta.[77] Half a century later, Crellin queried in a newsletter, "*Whatever happened to plant psychology*?"[78] Her query fell on deaf ears except for one reply by Parker who, apparently unaware of the plant neurobiology movement, responded, "*Like the criminal trials of animals, such things are wiped away by history because they become unthinkable when new epistemological and ontological boundaries are installed in a culture.*"[79](p48) The plant neurobiology movement has pushed the epistemological and ontological boundaries of current scientific culture and, for better or worse, the "unthinkable" has again become "thinkable." Indeed, there have recently been renewed calls to include studies of plants under the banner of comparative psychology.[80,81]

Early comparative psychologists had no hesitancy in embracing the study of plant behavior in their discipline: As pointed out by Yerkes in 1913, "comparative" refers to the method of a science rather than to its objects of study.[82] In discussing the meaning of "comparative psychology", Yerkes suggested that it is:

> . . . desirable, therefore, that we . . . employ the term to designate the study of consciousness, behavior, or the products of behavior – no matter what the type of organism concerned – by the method of comparison. . . In fact, comparative psychology studies alike . . . the psychology of man in the various stages of development and degrees of normality; of other animals; of plants . . . [82] (p580)

The field of plant psychology got off to a shaky start in the figure of Gustav Fechner [1801–1887], a brilliant German polymath who made important contributions to experimental psychology, philosophy, and physics. Unfortunately, Fechner's interest in plant psychology arose during a period in his life, from 1839 to 1843, when he descended into a debilitating madness that nearly killed him. As he was emerging from this near-death experience, he had a mystical experience as he walked through his garden: he noted that the flowers were all illuminated from within as if revealing their souls to him.[83] This experience led to his publication of *Nanna or Concerning the Spiritual Life of Plants*.[84] In this work, named in honor of Nanna, the Nordic goddess of flowers, Fechner argued that plants are conscious beings that have souls, and exhibit feelings and free will. Although his interest in this subject was inspired by this mystical experience, he insisted that his views concerning plant consciousness were wholly supported by science.

More recently, Monica Gagliano, whose plant neurobiological research has been especially controversial, has reached conclusions similar to Fechner's regarding the spiritual dimensions of the botanical world, but these views came to her because of her experiences, which she has openly discussed, ingesting the psychoactive brew *ayahuasca*.[85] Interestingly, near-death experiences and *ayahuasca*-induced experiences have been described as two unique pathways to a phenomenologically similar state of consciousness.[86] Such mystical thinking, of course, falls outside the realm of science, including plant neurobiology. In Gagliano's defense, however, it should be stressed that although she openly discusses her spiritual views in her popular writings,[85] she assiduously excludes them from her scientific contributions. Spiritually minded scientists, of course, have made great contributions to science throughout history and so long as they maintain their spiritual beliefs and their science in non-overlapping magisteria,[87] their contributions, assuming they are sound, should be welcomed by fellow scientists.

Following Fechner, a number of noteworthy 19th-century contributions concerning plant psychology were published in venues outside mainstream plant biology. [88–91] I wish to draw especial attention, however, to the largely forgotten work of the Austro-Hungarian polymath Raoul Heinrich Francé [1874–1943]. Thanks to René Romain Roth, a Canadian biologist who spent his retirement years writing a biography of Francé, we now have a more complete picture of Francé and why he deserves to be remembered.[92] [Regrettably, Roth's biography of Francé, which was self-published by his family after his death, has also languished undeservedly in obscurity; it deserves to be read more widely.] Roth opines with justification that Francé's name being " . . . *unfamiliar to the present generation is deplorable. Francé was virtually the first biologist to recognize the importance of ecology for the well-being of mankind and to warn against the mismanagement of the environment.*"[92](p4) Francé also published an important work in 1909 entitled *Plant Psychology as a Working Hypothesis of Plant Physiology*, in which he listed 21 psychological and neuroethological similarities between plants and animals.[93] Unlike most of the 19th century plant psychologists, Francé presented his views concerning plant psychology without subtexts of vitalism or natural theology, and he rejected the ideas that plants have souls or feel pain. In Francé's opinion, plants demonstrate agency but only in the most primal matters of nutrient acquisition and reproduction. Francé also discussed some of these ideas in his earlier popular work *Germs of Minds in Plants*.[94]

Why has Francé's legacy largely been forgotten? Francé was a victim of politics. Perhaps it was his gallicized name [he was born Rudolf Heinrich Franz, but as a pre-teen, was re-christened Raoul Heinrich Francé by his Francophile father], or his hasty relocation to Dubrovnik, Yugoslavia following the German annexation of Austria, or the fact that the English translation of *Germs of Minds in Plants* was issued by a Communist publishing house in Chicago, but, for whatever reason, the Third Reich was suspicious of Francé. Perhaps feeling the pressure, in late 1935, Francé joined the Yugoslavian Nazi party. The German authorities were unimpressed: the National Literary Chamber deemed that, "*A dissemination of the works of Francé and of his wife in the territory of the German Reich is not wanted*."[92] (p145) The selling and publication of their books were subsequently banned, thereby depriving the couple of any income from royalties. Moreover, the Gestapo, suspecting his wife of having Jewish heritage, also began demanding genealogical information about her. In Roth's view, the Francés were " … *politically naive people who had only two aims: to survive and to be able to continue their scientific and literary work undisturbed … the Francés were no Nazis but they also were no heroes and even less martyrs. They tried to be as inconspicuous as possible.*" [92] (p149) Francé died of leukemia in 1943 while still a member of the Nazi party. It is likely that the stigma of his association with the Nazi Party contributed to the withering of his legacy after the War.

Tragically, the legacies of Sir Jagadis Chandra Bose and Raoul Henri Francé, two of the greatest plant neurobiologists of the early 20th century, were destroyed by cultural trends and geopolitical events beyond their control.

3. Plant neurobiology is more holistic

Plants are exquisitely sensitive to environmental perturbations. If one considers that simply measuring a maize (*Zea mays*) leaf with a ruler inhibits its elongation,[95] or that illumination equivalent to a few seconds of moonlight affects the growth rate of oat (*Avena sativa*) coleoptiles,[96] or that a rapid drop of temperature of 1 to 2°C elicits leaf closure in *Mimosa pudica*,[97] or that the parasitic plant *Striga* detects *picomolar* concentrations of strigolactones,[98] it is inarguable that plants are exquisitely sensitive to their environments. The idea that plants are highly sensitive organisms is not disputed by the Opponents. However, while the mainstream simply acknowledges this fact, plant neurobiologists embrace this point as a foundational principle.

Despite plants' impressive sensory abilities, plant physiology has since its earliest days been dominated by destructive measurement techniques. Generations of plant biologists have blithely ablated, abraded, burned, centrifuged, chilled, chopped, clamped, clipped, coated, compressed, diced, dissected, drilled, excised, handled, immersed, impaled, infiltrated, injected, irradiated, mashed, peeled, protoplasted, sectioned, stained, stirred, tagged, tied, transplanted, transported, tweezed, uprooted, and washed plants. Often experimental organisms are subjected to a combination of such assaults, but even if one considers just one of these acts, the physiological ramifications are staggering to contemplate. Consider, for example, the massive physiological upheavals wrought by the felling of a seedling. Among the chemical changes that might be expected to arise are profound changes in damage-associated molecular patterns (DAMPs), including extracellular ATP (eATP), extracellular DNA (eDNA), and oligogalacturonides, which together affect the transcription of many hundreds, if not thousands, of genes. [99–103] Many of the genes upregulated by wounding encode protein kinases, the activation of which undoubtedly brings forth a tsunami of phosphoproteomic changes and resultant modifications in a host of structural, metabolic, transport and signal transduction proteins.

The local effects of wounding are also broadcast to distal parts of the plant by a variety of mechanisms,[104,105] including propagating waves of Ca^{2+} and reactive oxygen species in the inner cortex,[106] propagating APs in the phloem,[107] slow-wave (or variation) potentials[67,108,109] and system potentials[68] in the apoplast, and rapid hydraulic signals in the xylem that can affect plants systemically either via their effects on the hydrostatic pressure or by effecting the rapid transport of chemical agents to distal areas [107–109] Among the distal changes recorded in response to wounding are the upregulation of defense gene expression and the enhanced production of jasmonic acid.[110,111] Through crosstalk, jasmonic acid works in concert with other phytohormones, such as abscisic acid, auxin, cytokinin, ethylene, gibberellic acid and salicylic acid, to regulate growth- and defense-related processes.[112]

Due to the tsunami of biochemical and physiological changes wrought by typical experimental manipulations, many in the triad disciplines favor the study of plant functions by continuous, nondestructive (CnD) measurements. Fortunately, we live in an exciting time in history when numerous new and innovative CnD measurement technologies are emerging, including novel microscopical techniques,[113] optogenetics,[114] a wide range of optical, electrochemical and gas sensors,[115,116] biomagnetometers,[117] various types of spectroscopies, including Raman,[118,119] Near-Infrared,[120] and Terahertz,[121,122] light detection and ranging (LiDAR),[123] and many others. These noninvasive techniques promise to usher in a renaissance in holistic plant biology.

CnD measurements reveal a profound botanical truth not discussed in today's textbooks: plants are literally pulsating. Ultradian rhythms occur in growth, [52,123–127] membrane potential,[128,129] cytosolic calcium $[Ca^{2+}]_{cyt}$,[130] Ca^{2+} and H^+ fluxes,[131] nutrient uptake[132] water uptake,[133] transpiration,[134] auxin transport,[135] respiration,[136] photosynthesis,[137] isoprene emission[138,139] and nitric oxide levels.[140] Why have plant pulsations been ignored by mainstream plant physiology? First, their existence is obscured by the common practice of averaging data generated from discontinuous measurements.[141] Second, some types of ultradian rhythms are of small amplitude and, therefore, conceptually relegated to "background noise".

Ultradian rhythms deserve to be a major research focus in plant biology. Information can be communicated not just by amplitude but by frequency as well.[141] Frequency-dependent signaling by oscillations in signal concentrations, for example, have been demonstrated to occur in non-plant systems. In the slime mold *Dictyostelium discoideum*, for instance, certain cells act as aggregation centers and secrete pulses of cyclic AMP with a period of several minutes; other cells respond chemotactically to these pulses and aggregate. The function of these clarion cells can be mimicked by the experimental application of cyclic AMP pulses with a periodicity of a few minutes. Importantly, however, the continuous application of cyclic AMP fails to promote aggregation.[142] Frequency-dependent signaling and communication occur in diverse plant processes.[143–145] The flowers of *Oenothera drummondi*, for example, sweeten their nectar within minutes when stimulated by the sound frequency of a flying bee pollinator but not by the sound frequency emitted by a non-pollinating fly.[143] Stomatal closure occurs optimally at a certain frequency of $[Ca^{2+}]_{cyt}$ oscillations.[144] When an *Arabidopsis* pollen tube approaches synergid cells, the synergid cells alter the frequency of their $[Ca^{2+}]_{cyt}$ oscillations to match those of the pollen tube.[145]

Many ultradian rhythms demonstrate non-linear dynamics,[146–152] which can lead to unpredictable, or chaotic behavior. Such unpredictability is anathema to the linear models of plant processes generally favored by reductionists.[153]

Further complications in interpreting plant physiological measurements stem from the ability of plants to respond to lunisolar tidal[154] and geomagnetic[155] variations, both of which are difficult to eliminate or control experimentally. If plants do sense lunisolar tides and the geomagnetic field and given the fact that both tides and the geomagnetic field vary in space and time, then experimental results may not necessarily be 100% repeatable at every time and every place on Earth. These viewpoints are unpopular with genetic determinists because they challenge a mythology widely embraced by many mainstream plant physiologists that they are performing their experiments under "controlled conditions."

4. Plant neurobiology has different philosophical origins

Taiz *et al.* state that "*Plant neurobiologists are hardly the first biologists to ascribe consciousness, feelings, and intentionality to plants. Parallel claims were made by the Romantic biologists of the 18th and 19th centuries*".[5] (p684) Although modern-day plant neurobiologists typically do not ascribe "emotions" to plants, if that is what Taiz *et al.* mean by "feelings," the preceding statement by Taiz *et al.* is otherwise correct. Students of the triad disciplines are, indeed, the 21st century intellectual descendants of the Romantic (*Naturphilosophe*) tradition that reached its zenith in the early 19th century. In drawing this comparison, however, Taiz *et al.* are not simply stating a neutral fact: they are using "Romantic biologist" as a smear, linking plant neurobiology to what in their view is an extinct, discredited and dangerous "wrong turn" in Western intellectual history. Regrettably, in doing so, they present a highly distorted history of the Romantic Era of Science and ignore entirely reappraisals by modern scholars of the historical importance and value of Romantic Science.[156–158]

The Romantic movement of the early 19th century arose from a growing dislike by many intellectuals for the tenets promoted by the Enlightenment that had created an approach to science that attempted to control, rather than to peacefully co-exist, with nature. Romantic biologists emphasized man's connection to nature and held that knowledge of nature should not be obtained by force. Diderot, for example, criticized mechanists for subscribing to a number of "*absurdities*", and opined that " . . . *whenever* [the mechanist] *omits the sensibility, the irritability, the life, the spontaneity, he knows not what he is doing*."[159] (p20–21) From the perspective of Romantic biology, function has priority over structure, and the whole has priority over its parts.

But how did Science fare during the Romantic Age when holistic, nondestructive plant biology reigned supreme? In thinking about the plant scientists of the Romantic Era, two intellectual giants, Johann Wolfgang von Goethe [1749–1832] and Alexander von Humboldt [1769–1859], come to mind.

Goethe was a poet, a playwright, a novelist, a theater director, a lawyer, a government advisor, a physicist and a botanist. Goethe's fresh perspectives helped plant the seeds of the greatest of all revolutions in biological thinking, the theory of evolution. Unlike his contemporaries who assumed, based on the infallibility of the Creator, the fixity of species, Goethe clearly recognized the existence of natural evolution. Moreover, his contributions to plant comparative morphology suggested mechanisms to explain how slight developmental changes might give rise to new adaptations; thus, he can be considered to be the founder of "pre-molecular evo-devo".[160,161]

Alexander von Humboldt was a German polymath, geologist, geophysicist, geographer, explorer, naturalist, and proponent of Romantic philosophy and science. Humboldt viewed nature holistically and tried to explain natural phenomena without appeal to religious dogma. Humboldt's approach to science was highly quantitative. "*In preparation for his expedition to the tropics, Humboldt engaged the most prominent instrument-makers in Vienna and Paris and collected the whole array of instruments made precise by applying the divided scales and micrometric verniers proper to mathematical instruments to physical measures . . .* "[162](p477) Based on his detailed measurements and observations, von Humboldt created biogeographic maps that showed the distribution of characteristic forms of vegetation combined with observations and measurements of the local climate and topography.[163]

In considering the great geniuses of 19th century biology, the question naturally arises as to the extent to which Charles Darwin's thinking was influenced by Romanticism. A battle, refreshingly a collegial one, rages amongst Darwinian scholars as to how large an influence Romanticism was in Darwin's thinking.[164–167] Those who wish to consider both sides of the debate should consult *Debating Darwin*.[163] Here, evidence is presented that Darwin was markedly influenced by *Naturphilosophie*, and that Darwin belongs in the Pantheon of plant neurobiologists.

Darwin, as a young scientist, certainly exhibited an interest in the cognitive processes of aneural organisms. According to Beer, "*In his 1837–38 Notebooks, Darwin explores ideas of consciousness, the senses, variability, dream, descent, and animal behaviour. He ransacks his reading and explores even seemingly absurd possibilities in the adventure of mental exploration: does an oyster have free will? Do plants have an* *idea of cause and effect? Do wasps have reason?*"[165] '(p8) Darwin's interest in "minimal cognition" as a young man continued into his later years. In his *Power of Movements in Plants*, Darwin presented the results of much painstaking data collection, portrayed in the form of hundreds of kinematic ethograms of plant movements.[168] Moreover, Darwin compares root tips and the brains of lower organisms, writing, ' ... *it is hardly an exaggeration to say that the tip of the radicle (and the stem) thus endowed, and having the power of directing the movement of the adjoining parts, acts like the brain of one of the lower animals, the brain being seated with the anterior end of the body, receiving impressions from the sense organs and directing the several movements.*'[168] (p573)

Darwin's root-brain hypothesis has been revisited by a handful of modern plant neurobiologists,[169,170] but the term "plant brain" has not been widely embraced even within the plant neurobiology community. Comparisons of the root tip to the brain simply refers to the high density of sensory input that is processed in these "terminal assessment-of-information zones." As Arthur and MacDougal pointed out, ' ... *if an examination of the mechanism of irritability of the root is made, it will be found that an extremely small portion of the organ may receive a stimulus from gravity, light, temperature, moisture, running water, chemicals, electricity, contact or injury. This sensory zone consists of a mass of cells in the shape of a cylinder beginning immediately back of the growing point and not more than one millimeter in length.*'[171] (p28–29)

So, if Romantic biology was so wonderful, why did it fall into disfavor in the late-19th century? For one, the technologies of reductionists developed at a faster clip. In 1869, for example, Friedrich Miescher first used a crude centrifuge to isolate nuclei, ushering in the era of destructive subcellular biology.[172] Secondly, the Agricultural Revolution of the 17th to 19th centuries was making nations and individuals wealthy. In contrast, the combined biological contributions of the *Naturphilosophen* created nary a *pfennig* for any person or entity. It is no wonder that the brilliant, but very pragmatic and entrepreneurial 19th-century organic chemist Justus von Liebig described *Naturphilosophie* as " ... *the pestilence, the Black Death, of the nineteenth century.*"[173] (p7–8)

5. Plant neurobiology is more grounded in ecology and natural studies

In recognition of the fact that plants typically function in the natural world, the triad disciplines believe that plant physiology needs to be more grounded in ecology and natural studies. Unfortunately, most plant physiological experiments are performed upon plants grown under controlled conditions designed to optimize growth (and also to reduce variation between trials). Although specimens reared under these pampered artificial conditions may look the picture of health and vitality, it does not necessarily follow that their molecular apparatus for converting environmental information into physiological response, are in peak condition. Is it possible that the sensory physiologies of plants might be altered substantively by their cultivation under such "sensory-deprived" conditions? When plants are grown in low-stimulus environments such as greenhouses or test tubes, where they are neither buffeted by wind and rain nor sampled by herbivores nor aided by mutualists, does their overall level of excitability, their tonus, remain the same? Bose made an interesting observation in this regard:

> ... a plant carefully protected under glass from the stimulating buffets of the elements looks sleek and flourishing, yet as a perfect organism proves defective. Its conducting power is found to be in abeyance, though the motile organ exhibits its normal power of contraction. Anatomically the conducting elements are present, but from want of use they remain functionally inactive. Now in this condition it is very interesting to watch the growth of conducting power under the influence of stimulating blows. There is at first no transmission; after a time, excitatory impulse begins to be initiated. Continued stimulation enhances the conducting power to a maximum.[174] (p1106)

Indeed, it is not uncommon for normally excitable plant cells to lose their excitable properties, although the underlying reasons for such occurrences are unclear. Fromm and Spanswick, for example, in studying APs in willow (*Salix viminalis*) clones, noted, "*Although the plants were similar in shape, size and age and were grown under identical conditions, their excitability was quite different. Some plants were highly excitable, some were moderately excitable, and others were not excitable.*"[175] (p1121) Williamson and Ashley found, in their studies of *Nitella* cells, that one batch of specimens did not respond to electrical stimulation in the typical all-or-none manner, but that electrical stimuli of increasing magnitude evoked increasingly large photoluminescent signals from cells loaded with aequorin (a Ca^{2+}-dependent photoprotein) and resulted in correspondingly graded inhibitions of protoplasmic streaming.[176] Earlier workers also reported cases of stimulated characean cells disobeying the all-or-none law.[177] It should also be noted that many sensory processes in plants are under circadian regulation,[178–184] although times of day are rarely mentioned in the methodology sections of plant physiology papers. Understanding the physiology underlying changes in tonus should be a major research focus of plant biology.

Excitation causes profound changes in a multitude of plant physiological processes, including respiration, photosynthesis, transpiration, gas exchange, growth, turgor, phloem unloading, water absorption, and systemic plant defenses.[185] In addition to their rapidity, the magnitude of the physiological changes evoked by an AP can be astounding. In the thalli of the liverwort *Conocephalum conicum*, for example, the induction of an AP causes a 30- to 70-fold increase in the respiration rate within 6 seconds.[186] Thus, plant APs are energetically very expensive. As such, it is possible that some higher mental functions in plants may not be constitutively expressed. Plants may only be fully "intelligent" or "sensitized" when conditions require that they be. It is also possible that the sensory and/or integrative capabilities of domesticated crops may be reduced compared to their wild relatives,[187] mirroring the decrease in intelligence that accompanied animal domestication.[188]

6. Plant neurobiology is more transdisciplinary

If one browses the pages of *Plant Signaling & Behavior*, one can read contributions made not just by plant physiologists and molecular biologists, but by historians,[44,189] comparative psychologists,[190,191] neurologists,[192] philosophers,[193,194] and bioethicists.[195] As a transdisciplinary field, plant neurobiology fits poorly into traditional academic frameworks, which are generally organized into schools and departments that reflect what are generally viewed to be sharply demarcated intellectual disciplines separated from each other by broad intellectual chasms: such views, in their most extreme form, are promoted by a particular mind-set that the sociologist Eviatar Zerubavel has termed "mental rigidity".[196] Zerubavel writes:

> To the 'rigid mind', the world is basically made up of discrete, insular entities separated from one another by wide mental gulfs. Distinctively characterized by its unyielding commitment to the mutual exclusivity of those 'islands of meaning' ... , the rigid mind allows no 'contact' whatsoever between them and eschews any effort to build 'bridges' across those divides. As one would expect, it cherishes sharp, clear-cut distinctions between mental entities and leads a vigorous campaign against the vague, the in-between, and the ambiguous in a deliberate effort to create a 'world without twilight' ... Mixtures, composites, and other mental mongrels, of course, inevitably threaten the cognitive tranquility of anyone committed to such a rigidly compartmentalized view of the world. (p1095)

Certainly, the efforts of the Opponents could be summed up as a vigorous campaign against the "mental mongrel" that is plant neurobiology. Zerubavel also argues that a rigid-minded vision of academic scholarship promotes a parochial outlook, a "*tribal intellectual provincialism*" that inhibits creativity: "*After all, transgressing boundaries is a hallmark of being creative, which almost by definition presupposes not accepting any rigid structure as a given.*"[196] (p1097–1098) No one would argue that plant neurobiologists lack creativity: the questions are whether they are too creative, and whether their hypotheses or "*serial speculations*" exceed known facts to too large an extent.[6] Hypotheses in themselves, however, are harmless: as Darwin famously wrote in Volume II of his *Descent of Man*, "*False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness.*"[197] (p385)

7. Plant neurobiology is more synthetic

Along with mechano-reductionism and genetic determinism, the third pillar of mainstream biological philosophy is positivism, the idea that every defensible rational assertion in the experimental sciences must be scientifically verified. Absolute positivists frown upon any speculation in science. Opponents, for example, have objected to the "*serial speculations*" of Proponents that violate " ... *science's ironclad rule of empirical testing without theorizing beyond the evidence.*" [198](p1090) Identical sentiments were expressed in 1840 by von Liebig who summarized *Naturphilosophie* as " ... *so full of words and ideas, so poor in real knowledge and thorough studies* ... "[199] (p177) Plant neurobiologists, however, encourage creative thinking (subjective imagination) and recognize that hypotheses function as theoretical scaffoldings that can expedite the building of the temple of scientific knowledge.

In *Flora Unveiled*, Lincoln Taiz, a leading Opponent, and his wife Lee, write that the *Naturphilosophen* " ... *granted equal weight to reason and the senses on the one hand, and to the subjective imagination on the other. Goethe believed that if scientists could only learn to use their imaginations as poets do, they could leapfrog over much of dreary data-collecting and accelerate the process of scientific discovery.*"[200] (p430) But is it true that the *Naturphilosophen* granted 50% of their mental capacity to reason and observation and 50% to subjective imagination? Taiz and Taiz present this 50:50 ratio as if it were an empirically derived fact rather than a conjured statistic.[199] And what nonsense to assert that the Romantic biologists were allergic to dreary data collection! Holdrege notes that, "*Goethe was no dabbler. He delved into each area by studying current literature in the field, reading about its history, interacting with and learning from experts, and by carrying out his own observations and experiments.*"[201] (p10) Humboldt made intensive use of state-of-the-art instruments to measure a wide range of physical parameters,[202] and Darwin famously spent 8 years studying barnacles.[203]

In bolstering the argument that Darwin's thinking was influenced by Romanticism, Richards points out that Darwin believed that speculative hypotheses or "*castles in the air*" as he referred to them, were "' ... *highly advantageous, before real training of inventive thoughts are brought into play.' The complimentary joining of analytical faculties with imaginative capacities was exactly what Darwin found in the works of Humboldt and what he would employ in fashioning the language of the Origin.*"[204] (p170)

Absolute positivism, such as that advocated by the Opponents, is counterproductive to the efficient progress of Science. One wonders, for example, what would have been the fate of Darwin's *The Origin of Species* had it landed on the desk of an absolute positivist for review? I imagine it might have read, "*Darwin presents a lot of information consistent with his speculations relating to the possibility of evolution by natural selection, but without direct experimental evidence, we cannot recommend publication at this time.*"

8. Plant neurobiology is more pluralistic

Plant neurobiology is more pluralistic than mainstream plant physiology in three ways: plant neurobiologists, 1.) appreciate that scientists from underrepresented demographic groups have valuable contributions to make to science, 2.) recognize that both top-down and bottom-up approaches toward understanding plant behavior are useful and complementary to the advancement of knowledge, and 3.) practice epistemic humility.

Tandon has noted the peculiar demographic composition of the Opposition[205]: all 36 signatories of the Alpi *et al.*[4] were or are, without exception, Westerners. This is quite extraordinary. What is the percentage of plant biologists who were raised in Western cultures? Perhaps half? If so, then the chances that a petition or Canon would be signed exclusively by 36 Western scientists are astronomical. In raising this demographic peculiarity, I sincerely and emphatically am not accusing the Opponents of being racist. What I am suggesting is that the apprehension – the "phytoneurophobia" – the Opponents feel regarding plant neurobiology is deeply rooted in the natural, intellectual, and political histories of the Western cultures in which they have been steeped.

In regard to natural history, the temperate West is blessed neither by a superabundance of plant species that exhibit rapid movements nor by a tropical climate that enhances these movements. This is not to say that the Western world is completely devoid of examples of rapid plant movements (*e.g.*, *Utricularia*, *Aldrovanda*, *Drosera*, *Dionaea*, *etc*.), but the species that show these movements are generally ephemeral, inconspicuous, rare, or found in inhospitable places where only the most dedicated field botanists dare tread. People from the tropics and sub-tropics, from early childhood, are surrounded by plants exhibiting movements. Naïve Westerners, on the other hand, are awestruck upon witnessing the leaf movements of *Mimosa* for the first time. Indeed, the first specimens of *Mimosa* delivered to the Western world were so alien and paradigm-shattering to Europeans that the thigmonasty of *Mimosa* was the subject of some of the earliest state-sponsored botanical research in European history. An officer of the Royal Society recorded on July 17, 1661, that " … *the King had, within four days past, desired to have a reason assigned, why the sensitive plants stir and contract themselves upon being touched* … "[206] (p23) For Westerners of a parochial bent, rapid plant movements are not part of their daily experience and, therefore, not important to them.

The intellectual history of the West offers a second reason why the Opponents find plant neurobiology such an abomination. Western culture was shaped in large part by ancient Greek philosophers, particularly Aristotle. The most fundamental innovation of the plant neurobiology movement is no less than the tearing down of a 2300-year-old philosophical construct; Aristotle's division of non-human life into *anima vegetativa* (plants: organisms that can feed and grow) and *anima sensitiva* (animals: organisms that can feed and grow and sense).[207] Aristotle's views continued throughout the Medieval Era in the form of the *Scala Naturae* that proposed that Man was above all the animals and just below the angels in the scale of Nature. Aristotle's paradigm and the *Scala Naturae* concept live on today in popular culture: in English, for example, physically inactive people are referred to as "couch potatoes" and comatose individuals or those in a "vegetative" state are impolitely referred to as "vegetables." This prejudice, too, is even observed in modern science. Geneticists, for example, have isolated *Drosophila* learning and memory mutants and given them "desultory" names such as *rutabaga, turnip, cabbage, radish* and *zucchini*.[208] Western scientists come from cultures perfused with Judaeo-Christian traditions that teach that Man has a special place in the Universe because Man alone was made in the image of God. Is it possible that the speculations and hypotheses of plant neurobiology somehow threaten subconsciously the grandeur some biologists feel concerning their relatively exalted positions on the *Scala Naturae*?

Another wall that the plant neurobiology movement is tearing down relates not to science *per se* but to geopolitical divisions. Indeed, a most striking feature of the plant neurobiology movement is its delightful admixture of scientists from all sides of the former Iron and Bamboo Curtains. This admixture reflects the curious course of plant neurobiological history. For reasons more racist than scientific, the seminal insights provided by Jagadis Chandra Bose were extinguished in the West.[44] But Bose was a hero not just in his native Bengal but throughout all of Asia (and Eurasia). Bose's ideas inspired scientists in Japan,[56] China[49] and the Soviet Union.[209] Unfortunately, due to the occurrence of political upheavals in these countries that derailed their respective national science programs for decades, as well as language barriers and the low availability of these countries' journals in the West, the corpus of this work had little impact on the thinking of mainstream Western plant physiology. It would be wonderful to read more syntheses by scholars of different nationalities concerning the history of plant neurobiology in their respective countries.

9. Plant neurobiology is more convergent in thinking and in subject matter

One possible explanation for the antagonism of mainstream biologists toward the triad disciplines, may be that Proponents tend to be "lumpers" while Opponents tend to be "splitters".[210] Lumpers prefer broad categories that include items that share important features despite some differences; splitters prefer narrow categories, emphasizing variations rather than features held in common. Little is known about the psychology of lumping v. splitting but there is evidence that one's way of viewing Nature is shaped during childhood. One study found that raising a goldfish as a 5-year-old child, profoundly impacted the child's approach to biological inquiry. Compared to their peers, " … *goldfish-raising children could use their knowledge about goldfish as the source in making* ***analogies*** [emphasis mine] *about an unfamiliar 'aquatic' animal (i.e., a frog), and tended to produce reasonable predictions with some explanations for its reactions to novel situations.*"[211] (p119) Another study found that children who explore nature informally are more likely to make ecological inferences about Nature. According to Coley, " … *informal exploration played more of a role in predicting* ***ecological reasoning*** [emphasis mine] *than more formally structured experiences like zoos or aquariums…*" [212] (p1002) It would be interesting to gather data concerning whether early childhood experiences make one more or less predisposed to embracing a plant neurobiological viewpoint.

Not only is it possible that plant neurobiologists have a psychological proclivity for convergent thinking, but much of what they study, and many of the processes they compare phenomenologically to outwardly similar processes in animals, have arisen, albeit not exclusively, by convergent evolution.

With the advent of molecular sequencing technologies, mainstream biology has focused ever more myopically on the admittedly powerful force of divergent evolution (phylogeny), almost to the exclusion of convergent evolution. Convergent evolution is a topic especially germane to discussions of minimal cognition because many of the processes of most interest to this area of research, arose by convergence.

Gap junctions provide an example of the power of convergent evolution. The structural components of vertebrate gap junctions are connexins, while the structural components of pre-chordate gap junctions are innexins. Despite a lack of similarity in gene sequence, connexins and innexins have the same membrane topology and form intercellular channels. Both protein types oligomerize to form large aqueous channels that allow the passage of ions and small metabolites and are regulated by factors such as pH, calcium, and voltage."[213] What's even more extraordinary is that plant plasmodesmata, structures that are phylogenetically unrelated to either type of gap junction, also allow the passage of ions and small metabolites between cells, and are regulated by pH, calcium, and voltage.[214]

Convergence also underlies plant and animal excitability. For example, the APs of plants and animals both fulfill the three *sine qua non* that define APs: 1.) they are all-or-none, 2.) they self-propagate away from the site of stimulation, and 3.) in their wake, there occurs a refractory period.[215] The ion channels involved in the depolarizing phase of APs in animal neurons, however, are largely different from those that serve the same function in plant cells.[216] Plant and animal APs evolved convergently.

Habituation provides another example of the importance of convergent evolution. Habituation, in a behavioral sense, refers to a decrease in the frequency or probability of a response immediately following exposure to temporally close stimuli of the same type that is not due to motor fatigue [This is an older, more phenomenological definition of "habituation" than that used by the Opponents[5] who make a mechanistic distinction between "genuine habituation" and sensory adaptation.] Habituation, often considered to be the simplest form of learning, has long been known in plants. In the 18th century a student of the French botanist Desfontaines observed that the potted *Mimosa* specimens he was transporting in his carriage initially responded to the vibrations of travel by collapsing their leaves, but during the journey the leaves recovered, and the shaking and rattling of the carriage elicited no further response. However, after restarting the journey, following a 15-minute respite, the *Mimosa* plants responded anew to the carriage's vibrations.[217,218] Similar results were obtained by Pfeffer[71] and by Bose[72] in regard to the responses of *Mimosa* to iterative electric and mechanical stimuli. Diminished responsiveness following temporally close stimuli can also be seen in the graded electrical responses and graded $[Ca^{2+}]_{cyt}$ transients that follow rapid cooling stimulation in non-motile plants.[219, 220]

In addition to plants, habituation is found in a range of aneural organisms, including slime molds,[221,222] ciliates,[223] and possibly bacteria.[224] The ubiquity of habituation across such widely varying branches of life suggests that it is a fundamental property of all eukaryotic life, and perhaps even bacteria. According to van Duijn, "*The available molecular evidence suggests that habituation . . . evolved independently in phylogenetically distant species, such as protists, plants and neuralia, which appear to have converged towards the same adaptive solution, because of the important adaptive benefits conferred by flexible within-generation behaviours*."[225] (p7)

Thus, the gap junctions of animal cells and the plasmodesmata of plant cells arose convergently; the APs of plants and animals arose convergently; the habituation of plant and animal cells arose convergently; and virtually everything relating to multicellularity in plants and animals arose convergently.[226] Thus, if higher cognitive functions, such as memory, associative learning, mental mapping, and decision making exist in plants, then they must have arisen in one of two ways. The first possibility is that these higher cognitive functions existed in the common ancestral progenitorthat gave rise to the fungi, the plants, and the animals. Thus, some plant neurobiologists embrace the concept of biopsychism, the idea that plants, like all living organisms, including unicells, are sentient.[227] The second possibility is that the mental attributes traditionally associated with higher cognitive functions in animals, if they do exist in plants, arose by convergence.

A point of controversy between Proponents and Opponents is whether plants can learn by association. Computer models suggest that the evolution of associative learning may not be that complex and may have arisen convergently in many systems.[228,229] There is a growing body of evidence that modern unicells, such as *Paramecium caudatum*, [230,231,232] amoebas[233] and *Physarum polycephalum*,[234] and even macrophages in culture,[235] are capable of associative learning. These considerations, in toto, suggest that the concept of associative learning in plants is in the realm of the possible, although a recent study in support of associative learning occrring in pea plants[236] needs to be revisited in light of subsequent criticisms and reports of non-repeatability.[237],[238], Nevertheless, if and when plants are definitively shown to be capable of associative learning (either Pavlovian or operant conditioning), it will be interesting but not that surprising.

Learning requires a memory where the results of experience are accumulated. Plants do apparently have the ability to remember.[239] Plants, for example, possess memory of previous light incidents, called cellular light memory, which is used for optimization of future light acclimatory and immune defense responses.[240] Finally, interpretation requires a comparison of incoming signals with an internal reference (a mental map), and this can take place only in organisms that build internal representations of the world. Is it possible that plants possess this ability too?

The Opponents assert " . . . *that any organisms that demonstrably encode maps of the surrounding environment and of their bodies – from multiple senses such as vision, smell, touch, and hearing – will experience these mapped simulations consciously*..."[6] In their view, plants lack the ability to make a mental map of their environment. Recently, however, there has been a ground-shifting discovery relating to the South American vine *Boquila trifoliolata*, a woody vine that rambles through the canopy of temperate rainforests in southern Chile.[241] What makes *Boquila* so fascinating is its astounding feats of leaf mimicry. *B. trifoliolata* leaves mimic the shapes, colors, leaf orientations, petiole lengths, and vein conspicuousness of host plants over which they grow. An individual *Boquila* vine that over the course of its rambling growth traversed the canopies of three hosts, mimicked each of them in their respective areas of proximity.[242] This finding led the original discoverers to speculate that volatile signals or horizontal gene transfer may underlie the mechanism by which the mimicry is achieved. These two hypotheses, however, were dashed by the discovery that *B. trifoliolata* leaves also mimic the "leaves" of artificial plastic plants, albeit not as well as they do the living forms of plants.[241] Since neither volatile signals nor horizontal gene transfer are involved in *B. trifoliata*'s remarkable feats of mimicry, it is necessary to reconsider much more seriously Haberlandt's radical idea, resurrected by Baluška and Mancuso,[243] that certain leaf cells act like ocelli to produce vision in plants. Another possibility is that *Boquila* may have extraocular vision analogous to that which occurs in several phyla of brainless invertebrates.[244] Is it possible that extraocular visual capabilities may contribute to the plant's formation of an internal representation of the world?

No suggestion has evoked so much controversy as the proposal by some Proponents that plants are sentient, the simplest type of consciousness.[245,246] A recent review by some Opponents, for example, is provocatively entitled "Debunking a Myth: Plant Consciousness."[6] Opponents adhere to the Neural Correlates of Consciousness (NCC) school of consciousness. NCC refers to the minimum set of neuronal mechanisms necessary for conscious experience to occur. The view of the NCC school is that consciousness requires specialized neural structures that in more complex animals, are found in the central nervous system. In their view, vertebrates, arthropods, and cephalopods are the only conscious organisms. Some animal neurobiologists have even pinpointed the site of animal consciousness to a specific neuronal type in the animal brain; according to this group, cortical layer 5 pyramidal (L5p) neurons determine both the state (*e.g.*, dreaming, anaesthetized, deep sleep, *etc.*) and the contents (or qualia) of consciousness[247]: they conclude that "*cortical processing that does not include L5p neurons will be unconscious*,"[247] (p1) and that " … *the architecture and biophysical properties of the L5p cells enable flexible integration of segregated data streams*."[248] (p822) Are there "segregated data streams" in plants? Yes. Plant APs propagate through the phloem, whereas Ca^{2+} waves propagate through the inner cortex. It is certainly conceivable that there are cells between the phloem and inner cortex that are analogous to L5p cells in that they serve as "flexible integrators" of these two data streams.

The arguments of the NCC school, however, as its name denotes, are strictly correlative. Correlative arguments, of course, do not prove causality and, aside from anecdotal evidence, are generally regarded as the weakest form of scientific dialectic. To illustrate the inherent frailty of correlative arguments, one only need to consider the exemplum of *Moropus*. In the late 18th century, Georges Cuvier put forth his doctrine of the 'correlation of parts', which proposed that each anatomical facet, when examined separately, infers all the other. As an example, he pointed out that horns and hooves distinguished only herbivores. Claws, on the other hand, belong to carnivores, while no extant carnivore has horns or hooves.[249] Eight decades later, however, an analysis of the fossil remains of a *Moropus*, an extinct chalicothere outwardly resembling an oversize draft horse, showed unequivocally that *Moropus*, based on its dentition, browsed on vegetation, yet the creature had powerful claws on its front feet rather than hooves.[250] These claws were probably used for defense or digging but the point is that Cuvier's beautiful correlative argument was felled by a single example of evolutionary convergence. Is it possible that convergent evolution will prove to be the undoing of the NCC school?

The common ancestor of plants and animals was a unicellular eukaryote. About 500 million years ago, the predecessors of modern plants and modern animals began to diverge. Increases in the size of plants and animals required multicellularity and organ specialization. There is universal agreement that the respective developmental programs of multicellular plants and animals are very different processes, not only at the level of the whole organism but at the molecular level as well[226]: thus, seeking homologies between those attributes of higher plants and animals that are related specifically to multicellularity (and increased size) are likely to be less fruitful. As argued earlier, plant and animal APs are convergent bioelectrical processes, and plant "nerves" and animal neurons are convergent structures. In contemplating the question of whether plants are conscious or not, it stands to reason that if plants are conscious, and if consciousness requires multicellularity and nervous tissue *sensu strictu*, as posited by Taiz et al.,[5] then plant consciousness, if it exists, should be phylogenetically distinct from animal consciousness. Thus, consulting the NCC school to understand plant consciousness mechanistically is as useful as turning to *The Care and Feeding of Parakeets* for clues as to why one's potted geranium is bending toward the window: the NCC thesis concerning animal consciousness is simply immaterial to the question at hand.

Conclusion

Plant neurobiology and mainstream plant physiology share a common mission: to understand how plants function. The triad disciplines, however, have a different epistemic philosophy from mainstream plant physiology, as well as their own histories, and their own Pantheons of scientific heroes and heroines.

There is nothing wrong in being critical of plant neurobiology, just as there is nothing wrong in being critical of mainstream plant biology. Science grows stronger when fellow scientists point out, as the Opponents have, what they perceive to deficiencies in published papers. . Given the long, distinguished history of plant neurobiology, however, it is wrong to refer to plant neurobiology as a "pseudoscience;"[251] it is reprehensible to caricaturize and lampoon the movement ,[252]; it is beyond the pale to refuse to talk to plant neurobiologists[253]; and it is obnoxious in the extreme to publish anti-plant neurobiology petitions that essentially boil down to "appeals to authority" aimed at impressing Wikipedia authors, internet bloggers and the intellectually lazy.[4] Petitions of this sort do little to further scientific discourse. In fact, their goal is not to foster scientific discourse but to shut it down by mob intimidation (*i.e.*, bullying).

Only the future can judge whether today's Opponents deserve praise for safeguarding plant biology from the "serial speculations" of plant neurobiologists or whether they shall join the pantheon of "tittering savants" of the past whose primary legacies are having ridiculed maverick scientists who dared to ponder the "impossible" (confer, *e.g.*, the discoveries of the endosymbiotic origins of organelles, continental drift, transposons, nanobacteria, quasi-crystals, and prions). Of course, the truth may turn out to lie somewhere between the polarized views of the two camps.

I began this essay asking, "*Are plants intelligent? Can plants learn? Are they sentient*?" No one knows for certain how these processes work mechanistically, even in organisms that are clearly sentient. As such, there is a need for epistemic humility in all matters relating to higher cognitive functions. Certainly, there is burgeoning evidence that plants have greater neuroethological abilities than currently discussed in plant physiology textbooks.

Thus, in the spirit of epistemic humility, let us be collegial. Let us be free to imagine. Let us be free to investigate. Let us share. Let us debate. Let us, together, use our diverse talents and perspectives, to determine how plants function.

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ORCID

Peter V. Minorsky http://orcid.org/0000-0002-4909-1498

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