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Plants lack the functional neurotransmitters and signaling pathways required for sentience in animals

Commentary on [Segundo-Ortin & Calvo](#) on *Plant Sentience*

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Abstract: We cannot agree with Segundo-Ortin and Calvo that plants are sentient organisms. We have critically examined several aspects of their target article, and find their claims are not supported by the published evidence. We address these claims in sections on whether plants have a ‘neurobiology’ analogous to that of animal nervous systems, including neurotransmitters and synaptic receptors that respond to anesthetics; and whether plant signaling resembles neural transmission. For the latter, we especially consider the unique way plants signal their responses to wounding. Although the plant vascular system has been compared to the animal nervous system, animal blood vessels would be a better point of comparison.

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"The gravest danger to a speculative biologist is analogy. It is a pitfall to be avoided--the industry of the bee, the economics of the ant, the villainy of the snake, all in human terms have given us profound misconceptions of the animals."
Steinbeck & Ricketts (1941)

1. Introduction

Claims for plant sentience, or consciousness, have been made numerous times since the advent of the controversial field of Plant Neurobiology in 2006. In the target article, Segundo-Ortin & Calvo (2023) state: *"The goal of Plant Neurobiology (PN) is to understand how the information signaling mechanisms across the root and shoot systems that give rise to intelligent behavior are in plants integrated and fine-tuned"*. In its original formulation (Baluška et al., 2005; Brenner et al., 2006) plants were proposed to have functional equivalents to synapses, to transport auxin in synaptic-like vesicles and to perform neuron-like electrical signaling via the vascular system, especially the phloem. Subsequently, additional animal characteristics such as hearing, seeing, feeling pain, consciousness, and memory were introduced into the PN concept. We have challenged the validity of these claims on numerous occasions (Taiz et al. 2019, 2020; Mallatt et al., 2021a, b, c; Robinson & Draguhn, 2021), and have argued against PN's putative heuristic value for understanding plant behavior (Mallatt et al., 2021b). We continue to adhere to the standpoint that plants are neither cognitive nor sentient in the sense that these terms are commonly used in psychology, ethology, cognitive- and neurosciences. In this commentary, we comment on several neurobiological properties that the target article claims are shared by animals and plants and thus pointing to plant sentience. These erroneous equations demand clarification, if not refutation.

2. "Plant neurotransmitters" and anesthetics

As with other articles hypothesizing plant neurobiology, Segundo-Ortin & Calvo (2023) attribute to sentience the fact that (1) plants have some of the same molecules that act as neurotransmitters in animals and that (2) anesthetics reduce plant responsiveness. As defined by Wikipedia *"a neurotransmitter is a signaling molecule secreted by a neuron to affect another cell across a synapse. The cell receiving the signal, or target cell, may be another neuron, but could also be a gland or muscle cell"*. The most common neurotransmitters are glutamate, gamma-aminobutyric acid (GABA) and acetylcholine. The former two are found in the phloem of plants, and act as signaling molecules, but do not fit the definition of neurotransmitters because plants lack synapses (Robinson & Draguhn, 2021). In plants, glutamate signals are involved in growth, development, and defense responses (Toyota et al., 2018; Qiu et al., 2020; Liao et al., 2022) whereas GABA increases stress tolerance (e.g., upon wounding), activates antioxidant enzymes, facilitates photosynthesis, and signals development and growth (Li et al., 2021). It is to be noted that these roles are hormone-like and unrelated to what is expected for *neural* activities (Robinson & Draguhn, 2021).

Glutamate receptors exist in plants as 'glutamate receptor-like ion channels' and are structurally similar to their animal counterparts (Mousavi et al., 2013); however, as just mentioned, this glutamate-receptor system performs many plant-specific physiological functions that neurons do not perform (Wudick et al., 2018; Moroz et al., 2022). GABA receptors are also found in plants (Žárský, 2015), but have little sequence homology to their animal counterparts (Ramesh et al., 2017). Glutamate and GABA receptors are gated ion channels (Franks, 2015; Nguyen et al., 2018); they evolved earlier than nervous systems (Bouché et al., 2003; Varoqueaux & Fasshauer, 2017). Since glutamate and GABA in plants,

plus their receptors, differ from neurotransmitter systems in many ways, caution should be exercised in using these molecules as evidence for neurological similarities between plants and animals.

Does the way volatile anesthetics affect plants indicate plant sentience? In animal neurons, the principal targets of anesthetics are ion channels; e.g., ligand-gated receptors for glutamate and GABA, and voltage-gated K⁺ channels (Kelz & Mashour, 2019; Hao et al., 2020; Luo & Balle, 2022). Since glutamate and GABA receptors are present in plants it would appear to be a sensible strategy to investigate the effects of these drugs on plants. Indeed, a number of studies have documented that volatile anesthetics block sensory reception, inhibit diverse plant-organ movements, disrupt vesicle trafficking and paralyze Venus flytrap movements (Yokawa et al. 2018). Although a direct effect on plant glutamate and GABA receptors remains to be demonstrated, it is known that anesthetics do interfere with long-distance transmission of electrical signals in plants (Jakšová et al., 2021), and with transport across plasma membranes, particularly to suppress the entry of Ca²⁺ (Pavlovič et al., 2022). Anesthetics also lead to a strong reprogramming of gene expression akin to heat shock stress (Pavlovič et al., 2022).

On the other hand, anesthetics have so many specific, nonspecific, and phylogenetically universal effects that it is difficult to tell whether the plant-animal similarities are homologous. For example, anesthetics are likely to target glutamate receptors in both plants and animals (the similarity), but in plants their only known effect on these receptors is on an electrical wound-signal called a slow wave potential (see below), which animals do not produce (a big difference) (Jakšová et al., 2021). Another example of the difficulty is that although anesthetics affect vesicle-mediated transport in both the plant *Arabidopsis* (Yokawa et al., 2018; Pavlovič et al., 2022) and in animal synapses, it seems too big a leap to equate these vesicle effects because anesthetics have so many additional effects on synapses (Kelz & Mashour, 2019) and because plants lack synapses. It is safer to conclude that the differences are more important than the similarities, for the major reason that plants do not show the disrupted neural networks that dominate animals' responses to anesthetics. Thus, the similarities are too sparse to support the hypothesis, repeatedly proposed by plant neurobiologists (Baluška et al., 2016; Trewavas et al., 2020), that plants are sentient organisms merely because they lose responsiveness under anesthesia.

3. Is signaling in plants similar to neural transmission?

3.1 Action Potentials. The fact that both plants and animals have action potentials (APs) was a basis for the Plant Neurobiology concept (Brenner et al. 2006) and remains so up to the present time (Baluška & Mancuso, 2021; Lee & Calvo, 2022; Segundo-Ortin & Calvo, 2023). The resulting propensity to look for neuron-like characteristics in plants seems to have become an *idée fixe* among plant neurobiologists, despite the fact that the electrochemical origin of APs in nerves is completely different from that in plants, involving a Ca²⁺ influx rather than a Na⁺ influx (Canales et al., 2018; Klejchova et al., 2021; Mallatt et al., 2021a). Moreover, the propagation of plant APs is 100 to 1000 times slower and, unlike neuronal APs, is associated with a wave of elevated cytosolic Ca²⁺. Whereas neuronal APs are osmotically neutral, plant APs serve for osmotic regulation in aquatic plants such as *Chara* (Bielby, 2007; Kisnieriene et al., 2022), drive stomatal closure through osmotic-turgor pressure in land plants (Minguet-Parramona et al., 2016), and are responsible for the rapid closure of the Venus

flytrap (Scherzer et al., 2022). As emphasized by Kjelchova et al. (2021) “*such electrical characteristics do not imply higher sensory function*”. Thus, and in contrast to the suggestion of plant neurobiologists (e.g., Calvo et al., 2017; Calvo & Trewavas, 2020), there is no “electrochemical equivalency” between plants and animals.

3.2 Slow wave potentials and wounding. Plant neurobiologists’ overemphasis on APs as the major factor in electrical signaling in plants unfortunately diverts interest away from other types of electrical signaling which are unique to plants. The best-studied of these signals is the slow wave potential (SWP, or variation potential). Whereas APs, conducted along the phloem, are often responses to nondamaging stimuli such as touch, SWPs signal a plant’s defense responses to destructive wounding (Zimmermann et al., 2009; Farmer et al., 2020). However, it should be noted that the most severe wounding triggers both phloem APs and additional long-duration SWP signaling (pers. communication, E. E. Farmer). In addition, wound-induced SWPs have been shown to mediate direct plant-to-plant transmission (via physical touching) of systemic physiological changes in plants and systemic acquired acclimation (Szechynska-Hebda et al., 2022).

Enormous advances have been made in the past decade in understanding the transmission of leaf-to-leaf wound responses, although the exact roles of some of the participating factors remain to be clarified (Gao & Farmer, 2023; Gao et al., 2023). It is now clear that unlike electrical transmission in neurons, wound signaling in plants involves at least two different types of elicitors (all leading to the synthesis of the defense hormone jasmonate: Wang et al., 2019). One is glutamate, principally found in the phloem, and the other is carried in the xylem; these are the so-called Ricca’s factors, which are β -thioglucoside glucohydrolases. Both elicitors trigger the production of SWPs followed by a wave of Ca^{2+} moving through the phloem and surrounding tissues leaf to leaf. Nguyen et al. (2018, Fig. 5D) have demonstrated the SWP-to- Ca^{2+} sequence by showing that in a leaf distal to a wounded leaf, cytosolic Ca^{2+} levels peak approximately 40 seconds after the maximal membrane depolarization.

Glutamate is likely a gating ligand for the glutamate receptor-like ion channels (GLRs, Alfieri et al., 2020); and extracellular glutamate levels increase after wounding (Toyota et al., 2018). When applied at millimolar levels onto a cotyledon leaf, glutamate was found to cause large cytosolic influxes of Ca^{2+} (as calcium waves: Bellandi et al., 2022) and to generate SWP-like signals (Shao et al., 2020). However, unlike their counterparts in neurons, the highest levels of the GLR proteins are located either on the endoplasmic reticulum (Nguyen et al., 2018) or the tonoplast (Gao & Farmer, 2023), rather than on the plasma membrane.

The β -thioglucoside glucohydrolases (TGGs) were recently discovered to be important mediators of wound signaling in plants (Gao et al. 2023) and are completely absent from neurons. After herbivore wounding TGGs are released from myrosin cells in the phloem parenchyma, and glucosinolates (GSLs) are released from other damaged vascular idioblasts. The TGGs hydrolyze the GSLs, producing aglycones that elicit the SWP membrane depolarization. TGGs are transported in the upward-moving xylem sap and continue to hydrolyze GSLs when they are encountered. Mutants with defective *TGG* genes show reduced Ca^{2+} increases and diminished SWP propagation in response to wounding. Conversely, recombinant TGG introduced into the xylem of both wild-type plants and *tgg* mutants elicits membrane depolarization and Ca^{2+} increases (Gao et al., 2023). These effects of TGG are different from those of glutamate, however, based on experiments performed on *glr* mutants.

Interestingly, double and triple mutants of *TGG* and *GLR* showed strong attenuations in amplitude and duration of SWPs, indicating that both phloem and xylem participate in SWP propagation.

Wound-induced signaling in plants is therefore a complex form of electrical communication unique to plants. This is in no way comparable to the transmission of electrical signals in neurons. Moreover, and most important, especially in terms of sentience/consciousness, is the fact that plants lack any form of reciprocal communication. That is, while there are forward signals (travelling from the site of the stimulus to the site of action), there are no feedback signals. This contrasts sharply with the heavy reciprocal electrical signaling seen among neurons in the brains of conscious mammals (Lamme, 2006; Mashour et al., 2020).

4. Is the analogy of the plant vascular system to the animal nervous system valid?

Comparisons are often made between the vascular systems of plants and the nervous systems of animals (e.g., Segundo-Ortin & Calvo, 2023), even though plant vasculature lacks cells with synapses, which contrasts with animal neurons, many of which have thousands of synaptic connections to other neurons---and, of course, the plant vascular system has no brain (Mallatt et al., 2021a; Robinson & Draguhn, 2021).

Instead, plant vasculature is better compared to the blood-carrying vascular system of animals. Both these systems function to transport water, nutrients, mineral ions, and hormones throughout the body, and both conduct electrical signals over distances. More specifically, phloem conducts APs and SWPs (the latter with the help of xylem cells) for long-distance signaling (Canales et al., 2018), and independently, animal vasculature evolved voltage transients in its endothelium and musculature to modulate resistance to blood flow by regulating vessel diameter (Tran et al., 2012; Hall & Hall, 2020; Jackson, 2022). Both plant and animal vascular systems use electrical signaling to regulate the hydrostatic pressure. Thus, xylem and phloem cells are arguably more analogous to the endothelial cells of animal arteries, which also lack synapses, than to the neuronal cells of the nervous system. Similarly, the relatively simple networks of vascular tissue present in plant shoots are more comparable to branching animal vascular networks than they are to complex neuronal networks (Mallatt et al., 2021a). Importantly, vascular networks, unlike neuronal networks, are not directly involved in the mental functions of animals. Plants and animals both have vascular networks, but only animals have neuronal networks.

5. Concluding Remarks

Based on the foregoing, we are of the opinion that the relentless search for analogies in terms of electrical signaling between plants and animals is a futile intellectual exercise with limited practical value. The differences between plants and animals in this regard are so significant that attempts to draw conclusions about sentience in plants are simply not justified, nor pedagogically helpful. Thus, the humanization of plant life, or, more correctly, the application to plants of terms from mammalian sensory physiology (seeing, hearing, feeling, consciousness, intentionality), has no solid scientific basis. It perpetuates an anthropomorphic bias and misleads the uninformed reader.

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