THE PHILOSOPHY OF PLANT COGNITION: A NATURALISTIC AND COMPARATIVE APPROACH

Miguel Segundo Ortin

Abstract

This chapter challenges the widespread exclusion of plants from comparative cognitive science by critically examining three dominant arguments against plant cognition: that plant behavior is merely reflexive, that cognition requires internal representations, and that cognitive processes necessitate a brain or central nervous system. Drawing on recent empirical research, I contend that the assumptions underlying these arguments are overly restrictive and rooted in anthropocentric and neurocentric biases rather than in sound scientific reasoning. By reframing cognition as a set of functional, multiply realizable processes rather than traits tied to specific anatomical structures or representational mechanisms, we can better recognize the diversity of cognitive architectures across biological systems. Incorporating plants into cognitive science expands the field's explanatory scope and invites a reevaluation of long-standing theoretical commitments.

Keywords: Comparative Cognitive Science; Plant Behavior; Representationalism; Neurocentrism; Anthropocentrism.

1. *Introduction*

Comparative cognitive science investigates how cognitive traits vary and align across different species, while also examining the underlying processes that support these abilities. It is an inherently interdisciplinary field, drawing insights from diverse areas of research, including comparative psychology, cognitive ethology, or evolutionary biology, all united by the common goal of mapping the distribution of cognitive functions throughout the natural world.

As noted by Street and colleagues (2025, p. 1), comparative cognitive scientists have traditionally focused on studying "'charistmatic' vertebrate species […] particularly mammals and birds". One likely reason for this

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focus is the persistent anthropocentrism within the discipline. This bias leads researchers to disproportionately concentrate on species that resemble humans in behavior or anatomy, while maintaining a skeptical stance toward more distantly related species. The problem is even more pronounced in the case of non-animal species, which are virtually absent from most discussions of comparative cognition and receive no mention in key textbooks in the field (see, e.g., Olmstead & Kuhlmeier 2015; Shettleworth,2010, 2013; Wynne & Udell 2021).

This paper will focus on plants. Over the past two decades, a growing body of research has sparked debate over whether plants possess cognitive capacities akin to those found in humans and non-human animals (see, e.g., Trewavas 2003, 2014; Calvo 2016, 2018; Segundo-Ortin & Calvo 2022). Critics of plant cognition typically advance three main objections. The first is that plant behaviors are merely automatic responses to stimuli and thus too simple or rigid to qualify as cognitive. The second argues that cognition necessarily involves internal representations, which plants are presumed to lack. The third maintains that cognitive processes require a brain or nervous system, thereby excluding plants from the outset.

In this chapter, I argue that all three objections rely on overly restrictive assumptions about the nature and implementation of cognition. Moreover, they are increasingly at odds with empirical findings in contemporary plant science. My aim is not to place plants on an equal footing with animals, but to explore how cognitive science might better account for the diverse strategies organisms (including plants) use to navigate their environments adaptively.

2. *No, plants are not like garage doors*

As Huang et al. (2021) put it, "[o]ne reason many theorists resist applying cognitive vocabulary to simpler organisms, especially those without neurons, is that they behavior is thought to be just the product of reflexes" (p. 1057). For most people, plants fall into this category of "simple organisms." A common argument against plant cognition rests on the idea that plant behaviors – such as directional growth and nastic movements – are merely hardwired responses triggered by environmental stimuli. From this perspective, plant behavior appears too basic and inflexible to signal any genuine cognitive capacity.

This view is echoed by Patricia Churchland (1989), who famously stated: "If you root yourself in the ground, you can afford to be stupid. If you move, you must have mechanisms for moving, and mechanisms to ensure that the movement is not utterly arbitrary and independent of what is going on outside" (p. 13). Along similar lines, Fred Adams (2018) has likened plants to garage doors, suggesting that their behavior is purely reactive, triggered by relevant stimuli, and therefore not cognitive. Based on this analogy, he concludes: "the plant thinks not, cognizes not (the same as the garage door)" (p. 28; for more examples see Segundo-Ortin & Calvo, 2019).

However, an expanding body of empirical research challenges this inherited view (see Segundo-Ortin & Calvo, 2022, 2023). Much of this research is based on meticulous observation of plant behavior under controlled conditions. This presents a methodological challenge: while it is essential to tailor observational tools to the specific biology and ecological niche of the organism in question, it is equally important to ensure that our methods allow for meaningful cross-species comparisons (Ponkshe *et al.*, 2024).

Since plant behaviors unfold over significantly slower timescales than those of animals, time-lapse photography is a crucial observation tool. Some critics worry that time-lapse photography may artificially make plant behavior look more animal-like, thereby biasing our interpretation of their cognitive capacities (Taiz *et al.* 2019). However, these concerns can be mitigated by combining time-lapse with additional techniques, such as computational methods for constructing 3D reconstructions of plant movement (see, e.g., Ruiz-Melero *et al.* 2024) and mathematical models adapted from studies of human and non-human animals (Figdor 2018). For instance, Raja *et al.* (2020) used tools from dynamical systems theory to study plant nutation, uncovering movement patterns that suggest internal regulation and goal-directedness. Notably, these examples show that models and techniques of observation originally devised for studying human and non-human animals can be meaningfully applied to the study of plant behavior.

One cognitive trait that is receiving considerable attention is decision-making. Broadly defined "an organism is said to make a decision whenever (i) it selects between alternative courses of action, and (ii) this selection is not random but is based on an evaluation of the alternatives in light of some collected information" (Lee *et al.*, 2023, p. 1). Following recent work on bacteria (Fulda 2017; Reid *et al.* 2016) and slime mould (*P.polycephalum*) (Latty & Beekman 2011; Smith-Ferguson & Beekman 2020), researchers have begun asking whether plants too can make flexible, adaptive choices.

For instance, the parasitic plant *Cuscuta pentagona* has been shown to preferentially grow toward tomato plants rather than wheat seedlings, a decision seemingly based on the chemical volatiles released by the hosts (Runyon 2006). Likewise, Trewavas (2014) reports that individuals of

Calamagrostis canadiensis, commonly known as 'bluejoint', selectively grows toward microhabitats offering better combinations of light, warmth, and competition. What is notable, however, is that plants do not respond to isolated factors; rather, they "discriminate these conditions in combination […] choosing light plus warm soil in preference to others" (p. 84).

Light competition offers a good opportunity for research too. Gruntman, Groß, Májeková, and Tielbörger (2017) conducted an experiment with the clonal plant *Potentilla reptans*. Clonal plants are known for adopting different phenotypic responses in contexts of light competition: shade avoidance (characterized by morphological changes that promote vertical growth, helping the plant reach better-lit areas), shade toleratence (through increased leaf area), and competition avoidance (characterized by lateral expansion).

The researchers created three experimental conditions. The first simulated neighbors of similar height and density – conditions that could be overcome by vertical growth but offered limited horizontal advantage. The second involved tall, densely packed neighbors, restricting both vertical and horizontal strategies. The third scenario presented tall but sparsely distributed competitors, which could not be outgrown vertically but allowed for increased lateral light access.

The results showed that *P. reptans* adjusted its growth strategy based on the surrounding conditions. In the first scenario, plants exhibited the greatest vertical growth, reflected in a high height-to-diameter ratio. In the second, they produced more leaf area, suggesting a shift toward shade tolerance. In the third, plants invested in longer stolons, increasing horizontal spread. These findings illustrate a form of adaptive decision-making, with phenotype adjustments tailored to maximize light acquisition under varying competitive pressures.

Similarly, in a study on *Abutilon theophrasti*, Cahill *et al.* (2010) examined how root growth patterns change in response to variations in both competition and resource distribution. Their findings revealed that when plants grew in isolation, they spread their roots broadly, showing no particular sensitivity to where nutrients were located. In contrast, when competition was introduced, *A. theophrasti* adjusted its foraging strategy, adopting avoidance or competitive foraging strategies, based on how resources were distributed – demonstrating context-dependent root allocation in competitive settings.

Dener *et al.* (2016) investigated how root growth in *Pisum sativum* (garden pea) is influenced by fluctuations in nutrient availability over time. They employed a split-root design, forcing the lateral roots to grow into two separate pots. One pot provided a constant level of nutrients, while the other delivered nutrients with variable but always increasing concentrations. Their findings revealed a clear pattern: when the nutrient levels in the constant pot were sufficient to meet the plant's metabolic demands, plants grew more roots in this pot. However, when those nutrient levels were insufficient, the plants shifted their investment, allocating more biomass to the pot with the variable nutrient regime. Notably, this happened even in cases where the variable pot did not provide enough resources either. For Dener and colleagues, this suggests that plants can make decisions based on anticipated scenarios, in this case, that the variable pot will eventually provide enough nutrients, and that they "respond strategically to patches varying in their average of nutrient availability" (p. 1765), switching between risk-prone and risk-averse behavior depending on the future availability of resources.

Schmid *et al.* (2016) applied Risk Sensitivity Theory (RST) to data generated by Denner *et al.* (2016). RST provides a mathematical formalism for understanding when it is advantageous (or 'rational') for an organism to shift between cautious and risk-taking strategies, based on internal conditions and environmental cues. Similarly to Raja *et al.* (2020), the analysis of Schmid *et al.* (2016) demonstrated that "theories of decision-making and optimal behavior developed for animals and humans can be applied to plants" (p. R677).

Another increasingly studied cognitive capacity of plants is communication. One key aspect of both intra- and inter-plant communication is the emission of airborne volatile organic compounds (VOCs). These compounds are released through various plant structures such as leaves, flowers, fruits, and stems (Baldwin, 2010; Meents *et al.* 2019), and some function as adaptive signaling vehicles, facilitating interactions between plants and a wide range of organisms (He *et al.* 2019; Novoplansky 2019). For instance, we know that plants often emit VOCs in response to herbivore attacks, triggering defensive behaviors in neighboring plants (Caruso & Parachnowitsch 2016; Dicke & Baldwin 2010; Heil & Karban 2010; Ninkovic *et al.* 2016).

Nonetheless, some researchers are skeptical that we can call this "communication" in a non-metaphorical way. For instance, Correia-Caeiro and Liebal (2023) have argued that "[t]he definition of animal communication, particularly in primates, often requires the concept of "intentionality", in which the signal indicates the goal of the sender to the receiver" (p. 1), implying that empirical reports of communication in plants do not meet the criteria for intentionality. As they argue, "VOC-release during stress does not have a directed goal" and it "is picked up incidentally by neighbouring plants, which in turn react to it" (p. 2). According to them, to infer the presence of communication in plants we must be able to demonstrate that plants release VOCs with "the intention to influence or modify the receiver's behavior" (p. 2).

Mimicry, a phenomenon well-documented in the animal kingdom, has also been studied in plants. For instance, Gianoli and Carrasco-Urra (2014) report that *Boquila trifoliolata* mimic the leaves of its supporting host, including size, color, shape, and the length of the petiole. Interestingly, they also report that the same individual can mimic two different host in a series.

Two hypotheses are usually posited to explain this ability: VOC communication and horizontal gene transfer. However, given that physical contact between *Boquila* and its host is not required for mimicry, a more radical explanation has been suggested: a plant-specific form of proto-vision, potentially analogous to the ocelloid-based photoreception observed in some dinoflagellates and cyanobacteria (Gianoli 2017). This admittedly contentious hypothesis finds preliminary support in a recent study by White and Yamashita (2022). In their experiment, *Boquila* specimens growing toward plastic vines developed leaves with markedly different traits – such as shape, area, perimeter, length, and width – compared to control plants, indicating that visual-like cues may influence leaf morphology. Researchers interpreted the results as indicating that *Boquila* are mimicking the plastic vines.

Now, consider numerosity, the ability to estimate and process discrete magnitudes. According to Böhm *et al.* (2016), *Dionaea muscipula* (aka 'Venus flytrap') can keep track of the amount of times the hairs located in the inner side of the snap trap are stimulated. When an insect contacts the sensory hairs inside the trap, it triggers the firing of action potentials (APs) that initiate the closing mechanism. However, for the trap to actually close, a second stimulus must occur within 20 to 30 seconds of the first; otherwise, the system resets and no movement is initiated. Once an insect is caught, its movements continue to activate the trap's hairs, prompting *Dionaea* to begin digestion. Notably, however, the secretion of digestive enzymes does not occur immediately but initiates after five distinct touches.

As noted by Rapp *et al.* (2020), insects are also capable of using APs to keep track of basic numerical quantities in a non-symbolic way, indicating that basic numerical competence may be a widespread phenomenon in nature. Elaborating on this parallelism, Nieder (2020), hypothesizes that plant sensitivity to numerical quantity, even if rudimentary, may contribute to adaptive decision-making across a range of ecologically relevant situations.

Learning constitutes another important area of research. To begin with, consider habituation. Habituation occurs when there is a decrease in the response to a meaningless stimulus after repeated exposure and this decrease is not caused by fatigue or sensory adaptation. Habituation is common in the animal kingdom, and, along with sensitization, is considered to be the most basic form of learning (Shettleworth, 2010). Habituation allows organisms to ignore meaningless stimuli and maximize efficiency and energy consumption.

In plants, reports of habituation date back to the 19th century (Abramson & Chicas-Mosier 2016), but it became a topic of debate after the publication of a study by Gagliano *et al*. (2014). Gagliano *et al*. subjected exemplars of *Mimosa pudica* to repeated 15cm falls, a harmless stimulus capable of eliciting a leaf-folding reflex. The goal was to see whether *Mimosa* plants would eventually stop folding the leaves. In addition, they manipulated the light conditions to see whether leaf-folding habituation was context-sensitive. Gagliano *et al*. reported two striking facts. First, leaf-folding behavior exhibits habituation, and this habituation lasted up to 28 days in some plants. Second, leaf-folding habituation occurred before and lasted longer in plants growing in energetically costly environments (e.g., conditions where light is scarce).

More sophisticated forms of learning, such as associative learning, have also been reported in plants. One example is classical conditioning. Classical conditioning occurs when a Conditioned Stimulus (CS), e.g., a bell, incapable of eliciting a response in the organism by itself, is repeatedly presented alongside an unconditioned stimulus (US), e.g., food, that naturally triggers a reflexive response, e.g., salivation. After repeated CS-US pairings, the CS alone starts evoking the same response originally produced by the US.

Gagliano *et al*. (2016) have reported that exemplars of *P. sativum* can associate the presence of a fan (CS) with the onset of light (US). This finding was interpreted as evidence of a more advanced form of learning in plants. However, the study has been met with controversy, particularly due to difficulties in replicating the results (Markel 2020).

Given the mixed findings reported so far, the Minimal Intelligence Lab[1] at Universidad de Murcia (Spain) is currently undertaking an independent replication of Gagliano *et al*. (2016). In addition, they have identified eleven critical methodological shortcomings – ranging from seedling germination and transplantation protocols to the experimental design and apparatus setup – that may influence outcomes and have proposed several improvements on the original experiment. They include the use of non-invasive time-lapse photography for more precise control over stimulus delivery, continuous monitoring of plant growth, enhanced statistical power to ensure robust

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[1] https://www.um.es/mintlab/

analysis, and the use of transparent, instead of opaque, Y-mazes (Ponkshe *et al.*, 2024). Given those methodological shortcomings, shared by Gagliano *et al*. (2016) and Markel (2020), at the moment we are not in a position to confirm or refute the existence of associative learning in plants.

We began this section by echoing a common argument according to which the behavior of plants is too simple and hardwired to be considered cognitive. This view, however, contrasts with a growing amount of behavioral evidence indicating the presence of different cognitive abilities in plants. Needless to say, crucial experiments are difficult (if not impossible) to find in comparative cognitive science, as hypotheses are highly underdetermined by the evidence (see Dacey 2025), and plants are no exception to this. Future work, including the independent replication of published empirical studies and more philosophical discussions, is needed, but there is no substantive reason to keep turning a blind eye to plants in comparative cognitive science.

3. *No representation, no cognition?*

A second major argument challenges the attribution of cognition to plants based on the supposed absence of internal representations. This line of reasoning is defended by proponents of what Ramsey (2017) calls the "Representation Demarcation Thesis". According to this view, cognition is fundamentally defined by the manipulation of internal representations. The argument can be outlined as follows: for a behavior to count as cognitive, it must be driven by a cognitive process; only processes that involve representations qualify as cognitive; therefore, only behaviors caused by representational processes are genuinely cognitive. Since plant behaviors are assumed to be non-representational, they are excluded from the cognitive domain.

Ken Aizawa articulates this position clearly:

> Plants might display adaptive behaviors, such as phototropism, without deploying representations to do this. Such cases would be the cases in which plants produce behaviors that are not cognitive behaviors. They are not behaviors that are produced, in part, through cognitive processes. (2014, p. 36).

A similar view is expressed by Fred Adams (2018), who argues against attributing cognitive abilities, such as learning or anticipation, to plants and bacteria. According to him: "since [plants and bacteria] lack beliefs and concepts – the higher-level, discriminating representations associated with genuine knowledge – what they do isn't really cognition" (p. 23). He concludes that researchers who attribute cognition to plants are using the term in a different, more metaphorical sense, than standard cognitive scientists.

This argument faces important limitations. To begin with, some authors have argued against the necessity of a "mark of the cognitive". For instance, Allen (2017) contends that "cognitive scientists need neither an abstract definition of 'cognition' nor a theoretically pure conception of 'cognitive system'" (p. 4237). Likewise, Clark (2008, fn. 3, p. 239) compares cognitive science with other scientific disciplines and wonders whether we need a mark of the cognitive while we don't have, for example, a mark of the physical or a mark of the living. Instead, they defend that we use "cognition" as an umbrella term to refer to a series loosely characterized traits, including behaviors.

Second, we might ask what justifies us in taking the Representation Demarcation Thesis. One possible answer is that representationalism is the default position in the discipline and, thus, that adopting a representational demarcation of the cognitive is in line with the mainstream. This is true, but still unsatisfactory. Whether or not representation is *necessary* for cognition is a contingent matter that needs to be discovered by looking at the world, not something to be established from the armchair. Most likely, this can be done only by examining the explanatory merits of representational theories of cognition against their non-representational contenders in different domains and for different cognitive abilities. Even if we grant that *some* cognitive abilities may require representations, there is no reason to assume that *all* do. Likewise, we should not block *a priori* the possibility that similar cognitive abilities may be instantiated by different cognitive mechanisms and processes in different species. Ramsey (2017) aptly warns against the uncritical assumption of representationalism:

> If the history of science has taught anything it is that our theorizing often goes in directions that are unexpected. […] Consequently, we have learned that it is unwise to restrict our theorizing by placing artificial boundaries on what an appropriate account is supposed to look like. […] We should not prejudice theory development in favor of so-called received wisdom, nor should we rule out novel and unconventional perspectives that strike us as radical (p. 4202).

Indeed, theorists that invoke mental representations as for the mark of the cognitive often assign a dual role to mental representation: "it functions as an explanatory posit in various information-processing accounts of cognition. But it also functions as part of the *explanandum* – as a defining element of the very phenomenon we want to understand" (p. 4204). Doing so may lead these theorists to conflate *explanandum* and *explanans*. One major consequence of this conflation is that representationalism becomes an unfalsifiable hypothesis.

To see this more clearly, imagine that we are interested in the study of episodic memory. Consider a hypothetical scenario in which, after conducting several empirical studies, we find no convincing reasons as to why the processes involved in episodic memory are best characterized as involving representations. It appears that we have three options if we accept the Representation Demarcation Thesis.

First, we can simply dismiss our reasoning. For instance, we can hold that episodic memory is a cognitive phenomenon, deducing that since all cognitive phenomena must involve representations, episodic memory cannot be non-representational. No matter what the evidence might say, our conclusion must be wrong. A second option, slightly more nuanced than the previous one, is to state that our account is incomplete. If episodic memory is cognitive, and if cognition necessarily entails representation, then it follows that our non-representational account is providing only part of the explanation. A full explanation of episodic memory will necessarily include representations that, in combination with other physical or biological processes, bring about episodic memory. Alternatively, we can accept that our account is correct and complete but then conclude that episodic memory is not cognitive. If representation is necessary for cognition, it follows that if it turns out that episodic memory does not involve mental representations then it is not a form of cognitive activity. This is exactly the maneuver Aizawa adopts in his treatment of plant behavior: rather than accepting the possibility of non-representational cognitive processes, he classifies phototropism as non-cognitive.

The problem is thus clear. Invoking mental representations as part of the demarcation criteria of the cognitive undermines the scientific, explanatory status of representationalism, rendering the representational hypothesis empirically vacuous. Those who advance representationalism as empirical theory of cognition should avoid accepting the Representation Demarcation Thesis.

Finally, it is worth remarking that neither Adams nor Aizawa offers a substantive argument for why plants categorically lack representations. One possible reason, discussed in the next section, is that plants do not have brain, but it is far from obvious that all forms of representations and representational processes require brains to be instantiated. In line with this perspective, Davis *et al.* (2024) propose that plant behavior can be understood as the result of distributed, decentralized computation whereby "a unified [behavioral] output […] is achieved through aggregation using an algorithm" (p. 746).

Of course, we can doubt that plants have higher-level, conceptual representations such as the ones Adam demands, but there are even less reasons to suppose, as he does, that all cognitive processes involve representations of this kind. Even though representationalism is the default position in the field, most representational theories are of a much lower level than that. Moreover, Adam's criterion seems overly demanding and anthropocentric (if not straightforwardly anthropofabulatory)[2], for even if we granted that adult human beings are capable of conceptual competence, we can rationally wonder whether this capacity spans to non-adult humans and nonhuman animals. As Segundo-Ortin and Calvo puts it:

> by positing conceptual representations as the *hallmark* of cognition […] we run the risk of advancing important (and undue) limitations to our cognitive science, leaving out of consideration all forms of sophisticated behavior that we find in the animal and plant kingdoms, and restricting the domain of the cognitive to human beings exclusively (2019, p. 69).

In sum, while the Representation Demarcation Thesis has deep roots in the tradition of cognitive science, its application to plant behavior appears increasingly untenable. Insisting that cognition must involve representations not only risks circularity but also suppresses alternative explanations before they've had a chance to be tested. Theoretical commitments should follow from evidence, not precede it. As research on plant behavior reveals increasingly sophisticated and flexible responses to environmental conditions, it becomes clear that a rigid commitment to representationalism may obscure more than it explains. If we wish to develop a truly comparative cognitive science, we must remain open to the idea that cognition might be realized through diverse cognitive architectures.

4. *No brain, no gain?*

If representationalism is one pillar of contemporary cognitive science, the other is neurocentrism – the view that cognitive processes are tied to the brain or central nervous system. From this perspective, cognition cannot exist without a brain.

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[2] Anthropofabulation arises when a given cognitive ability is defined using an overly idealized model of human performance, and this inflated standard is then applied to assess cognition in other species. Buckner (2013) highlights this issue in the context of social cognition research, where it is often assumed that the ability to interpret and predict others' behavior necessarily involves mindreading. This assumption exemplifies anthropofabulation, as it takes mindreading to be an essential requirement for social cognition without considering that simpler, yet functionally comparable, mechanisms may underlie similar abilities in both humans and non-human animals.

Echoing this view, Mallatt *et al*. (2023) write that "[c]ognition is generally defined with respect to thinking and knowing, and as involving a brain" (p. 4; see also Mallatt *et al*., 2020). Similarly, Taiz *et al*. (2019) argue that "[n]o single plant organ or tissue functions as 'the plant brain,' integrating all of the signals affecting plant growth and development" (p. 679). And Firn (2004) takes it even further, claiming that applying cognitive terms to plants is misguided, for they require a level of centrality and individuality that plants lack: "the concept of the individual, to which intelligence and behavior are intimately linked, cannot usefully be applied to plants" (p. 345). Implicit in Firn's argument is the assumption that such centralization necessarily depends on the presence of a brain.

I find this position problematic. Like the representation-based objection, neurocentrism seems grounded more in inherited assumptions than in compelling arguments. It is, of course, true that plants lack brains and neurons. And it is historically accurate that cognitive science has typically located cognition within the brain. But it does not follow that cognition is *impossible* without a brain. That conclusion is a *non sequitur*. Whether brains are required for all forms of cognition is an empirical question, not something to be stablished before the investigation.

On the contrary, the principle of multiple realizability suggests that cognitive traits may be instantiated in a variety of biological substrates. While animals may rely on neural mechanisms, plants could potentially realize similar functions through entirely different means. This does not imply that plant cognition is equal in complexity or sophistication to animal cognition. There may well be limits to what brainless organisms can do – perhaps plants are capable of habituation but not trace conditioning. But none of this justifies the *a priori* dismissal of all cognitive capacities in plants solely because they lack a nervous system.

Contemporary research is beginning to uncover some interesting facts that can contribute to the debate. A compelling example is the ability of plants to generate and sustain action potentials (APs) in response to various stimuli (Favre & Agosti 2007; A. Volkov 2012; Zimmermann *et al.* 2009). These APs exhibit the characteristic three phases (depolarization, repolarization and hyperpolarization) and, despite differences in their molecular composition, resting potentials, and propagation speed, Lee and Calvo (2022) argue they "closely resemble those action potentials in animals" (p. 11).

APs play a critical role in several functions of plants, including photosynthesis and the movement of organs. This is illustrated, for example, in the already mentioned case of *Dionaea muscipula* (Venus flytrap), where APs are involved in the plant's ability to count the episodes of mechanical hair stimulation, allowing the plant to avoid wasting energy on unsuitable prey.

Beyond APs, plants are also capable of generating other types of electrical signals. These include short-range signals known as local electrical potentials (LEPs), as well as long-distance signals like variation potentials (VPs) and system potentials (SPs) (Debono, 2020; Debono & Souza, 2019; Vodeneev *et al.*, 2016). These electrical signals travel along the membranes of plant cells and are conveyed throughout the whole plant via a complex vascular network composed of phloem, xylem, and cambium tissues (Baluska & Mancuso 2009; Brenner *et al.* 2006; Huber & Bauerle 2016).

Moreover, a variety of neurotransmitters typically associated with neural activity, such as acetylcholine, glutamate, dopamine, histamine, noradrenaline, serotonin, and GABA, have also been identified in plants (Volkov 2012, 2017). This overlap is unsurprising, given that many of the underlying molecular mechanisms, including ion channels, predate the evolution of nervous systems in animals (Baluška & Levin 2016).

This growing body of evidence has prompted Miguel-Tomé and Llinás (2021) to advocate for an expanded scientific understanding of what counts as a "nervous system". They suggest that nervous systems should be defined functionally (by the roles they perform) rather than anatomically (by the types of tissues involved), and add that "a definition [of nervous system] broader than the current one, which is based only on a phylogenetic viewpoint, would be helpful in obtaining a deeper understanding of how evolution has driven the features of signal generation, transmission and processing in multicellular beings" (p. 1).

Although plant signaling is still not fully understood, current hypotheses suggest that electrical excitability and propagation at the cellular level may underlie plants' ability to act as globally coordinated systems, rather than mere aggregates of reflexive responses. The central goal of plant neurobiology is to model and explain this integrated, intelligent behavior (Calco 2016).

Importantly, this research can be fruitfully integrated with embodied approaches to cognition, such as ecological psychology. This framework challenges the idea that cognition resides solely within the brain or (phyto-) nervous system of the organism and instead emphasizes the role of the organism's body and environment in shaping and enabling cognitive processes (Carello et al. 2012; Wilson & Golonka 2013; Segundo-Ortin & Raja 2024; Segundo-Ortin et al. forthcoming; Segundo-Ortin, M., Calvo, P., & Barrett, L. forthcoming). These perspectives help make sense of how diverse organisms, equipped with different bodies and neural resources, can solve cognitive tasks in distinctive ways.

5. *Conclusion*

Throughout the chapter, I have addressed three major objections to plant cognition: the claim that plant behaviors are merely reflexive and hardwired; the insistence that cognition necessarily involves internal representations; and the neurocentric assumption that a nervous system is required for any genuine cognitive process. These positions, I have argued, rest on outdated or overly narrow assumptions about what cognition is and how it must be implemented and are in conflict with a growing body of empirical research in plant behavior and plant neurobiology.

My aim has been philosophical as much as scientific. By reviewing recent research on plant behavior and signaling, I hope to help reframe how we think about cognition more broadly. Plants interact with their environments in flexible and adaptive ways, showing behavioral patterns that indicate decision-making, risk-sensitive foraging, learning, anticipation, and even forms of intra- and inter-organismic communication. These findings challenge deeply entrenched views about the minimal requirements for cognition, prompting a series of fundamental questions: What should count as cognition? Are nervous systems and internal representations necessary components, or merely one kind of biological solution among others?

Expanding the scope of comparative cognition to include plants is not merely about being more inclusive. It is about refining our criteria, questioning our assumptions, and opening new avenues for understanding the diversity of cognitive strategies in nature. In this light, plants do not just add to our data, they expand our conceptual imagination: They encourage us to think differently about what cognition is, and what forms it might take.

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