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Consciousness and cognition in plants

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Abstract

Unlike animal behavior, behavior in plants is traditionally assumed to be completely determined either genetically or environmentally. Under this assumption, plants are usually considered to be noncognitive organisms. This view nonetheless clashes with a growing body of empirical research that shows that many sophisticated cognitive capabilities traditionally assumed to be exclusive to animals are exhibited by plants too. Yet, if plants can be considered cognitive, even in a minimal sense, can they also be considered conscious? Some authors defend that the quest for plant consciousness is worth pursuing, under the premise that sentience can play a role in facilitating plant's sophisticated behavior. The goal of this article is not to provide a positive argument for plant cognition and consciousness, but to invite a constructive, empirically informed debate about it. After reviewing the empirical literature concerning plant cognition, we introduce the reader to the emerging field of plant neurobiology. Research on plant electrical and chemical signaling can help shed light into the biological bases for plant sentience. To conclude, we shall present a series of approaches to scientifically investigate plant consciousness. In sum, we invite the reader to consider the idea that if consciousness boils down to some form of biological adaptation, we should not exclude a priori the possibility that plants have evolved their own phenomenal experience of the world.

Cognitive Biology > Evolutionary Roots of Cognition
Philosophy > Consciousness
Neuroscience > Cognition

KEYWORDS

adaptive behavior, cognitive science, plant cognition, plant consciousness, plant neurobiology

1 | INTRODUCTION

Neither cognition nor consciousness appears to have evolved de novo in humans (or in non-human animals for that matter—Calvo et al., 2020; Calvo & Trewavas, 2020a, 2020b). Despite the focus being usually placed upon vertebrates (one out of 34 phyla in the kingdom *Animalia*), we may enlarge the picture on "evolutionary continuity" grounds (Griffin, 1976) and consider the evolution of cognitive behaviors in some other of the 96 phyla that compose the tree of

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life. In this review, we shall focus on higher, vascular plants, although the type of considerations herewith presented may well apply more broadly (Baluška & Reber, 2019; Baluška & Reber, 2021).

Cognition and consciousness are standardly thought of as exclusive to some locomoting animals. Yet locomotion appears to be uninformative as a way to draw a plant/animal dividing cognitive line (Linson & Calvo, 2020). To begin with, locomoting and nonlocomoting organisms resort to different strategies to achieve their own ends, these differences being caused by their contingent and differing energy demands. Evolutionarily speaking, animals and plants separated at the single cell stage. Plausibly, behavioral divergences were already found in the first eukaryotic cells. Primordial animal and plant cells found different ways to eke out their living. Whereas the former resorted to locomotion, the latter became photosynthetic through the acquisition of a blue green algal symbiont (Calvo et al., 2017), resulting in their sessile and autotroph lifestyle.[1]

Besides, locomotion is but one form of movement. All higher plants, angiosperms and gymnosperms alike, "move," if only their movement differs from canonical animal locomotion. To move around, plants rely on differential patterns of growth within and across organs, and on turgor-based changes of volume within cells. Growth and turgor changes deliver respectively irreversible and reversible patterns of motion. Together with cell differentiation and development, they allow plants to respond adaptively to their local environments (Hopkins & Hüner, 2008).

Stripped of anthropocentric (and zoocentric) interpretations, a growing body of research indicates that many sophisticated behaviors traditionally assumed to be exclusive to animals are present in the *Plantae* kingdom too, including light and nutrient foraging, competition avoidance, and complex decision-making. Such behaviors take place courtesy of phenotypic plasticity—for example, irreversible directed growth, cellular and tissue differentiation, and so on (Karban, 2008; Silvertown & Gordon, 1989). From a biocentric point of view, many scholars argue that this body of evidence is robust enough to consider plants intelligent or cognitive organisms (Baluška & Levin, 2016; Calvo, 2016, 2018; Calvo et al., 2016, 2020; Calvo & Trewavas, 2020a, 2020b; Karpiński & Szechyńska-Hebda, 2010; Latzel et al., 2016; Lev-Yadun, 2016; Linson & Calvo, 2020; Segundo-Ortin & Calvo, 2019; Trewavas, 2007, 2014, 2017; van Loon, 2016).

For those who believe that plants are cognitive, the subsequent debate pertains whether plants can also be sentient or conscious, where consciousness is marked by the presence of phenomenal experience of some sort (see Baluška & Yokawa, 2021; Calvo, 2017; Mediano et al., 2021; Raja & Segundo-Ortin, 2021). Understood in such minimal terms, consciousness or sentience denotes the occurrence of "feelings, subjective states, a primitive awareness of events, including awareness of internal states" (Baluška & Reber, 2019, p. 2). This notion of consciousness or sentience is to be distinguished from other, more complex kinds, such as self-consciousness or those involving reflection. Sentience or consciousness, as we are using it in the text, involves *just* the presence of some subjective phenomenal experience, be it of the external world or of oneself.[2]

A goal of this article is *not* to provide a positive argument for plant consciousness, although if consciousness boils down to some form of biological adaptation, we should not exclude a priori other biological, yet non-animal, forms of conscious experience. Instead, and with an eye to understanding the evolution of different levels and varieties of subjective awareness throughout biological kingdoms (Baluška & Reber, 2019), our aim is to invite constructive, empirically informed debate about the very possibility of plant consciousness. Evolutionary speaking, we may approach consciousness as a trait that non-animal organisms may possess. Put differently, whether they possess it or not cannot depend on whether they belong to the kingdom of Animalia or not. We shall introduce the reader to the current state of the debate concerning plant consciousness, as well as present a series of approaches to scientifically investigate it.

We begin in the next section by reviewing the current empirical evidence concerning plant cognition. After this, we introduce the reader to the emerging field of Plant Neurobiology (Brenner et al., 2006). The idea here is that if we can understand how sensorimotor integration takes place within plant vascular structures, we will be a step closer to understand what it is like to be a plant (Calvo, 2017). We shall then analyze five highly influential theories of consciousness. Because none of these theories depends on neurocentric postulates, they can offer valuable resources to address the question of plant consciousness from a scientific point of view. Ultimately, the challenge is to find out whether generalizable principles of psychology and the evolution of cognition and consciousness can be drawn out of the comparison of animal and plant behaviors, while paying due respect to their idiosyncrasies.

2 | PLANT COGNITION

The quest for plant consciousness first emerges from observations of cognitive capacities in plants. The consideration of plant cognition does not imply that plants are to be treated as proxies of animals. Cognition in plants can be identified via the type of changes in their behaviors that result in an improvement of their probabilities of survival (Calvo et al., 2020; Calvo & Trewavas, 2020b). Positing cognitive processes in plants is an inference to the best explanation of what can possibly underlie their behavioral repertoire (Karban, 2008; Silvertown & Gordon, 1989), where behavior is understood, non-idiosyncratically, in terms of the "observable consequences of the choices a living entity makes in response to external or internal stimuli" (Cvrčková et al., 2016, p. 3).

Plant cognition, under a biocentric perspective, calls for "the manipulation of the environment in order to enable metabolic functioning" (Calvo, 2018). But not all of plant behavior is cognitive. Overall, we hold that plant cognition encompasses behavioral patterns that are adaptive, flexible, anticipatory, and goal-directed (Calvo, 2016). To consider such adaptive behaviors as indicators of plant cognition, evidence takes the form of observable features established through behavioral and physiological studies, among other types of analyses (Baluška et al., 2006). Plant science can resort, for instance, to time-lapse photography (Brenner, 2017; Stolarz, 2009; Stolarz et al., 2014) or to electrophysiological techniques of observation (Volkov, 2012, 2017)—techniques that can help identify complex morphological and physiological responses (Karban, 2008) that take place during ontogeny, and that would be missed otherwise (Calvo & Trewavas, 2020b). Such techniques reveal that plants are flexible enough and can do more than simply react to the here-and-now in a fixed, hardwired manner (Raja et al., 2020; Segundo-Ortin & Calvo, 2019; Trewavas, 2014, 2017).[3]

We shall review the electrophysiological characteristics that may underlie plant cognition and consciousness in Sections 3 and 4. In the reminder of this section we substantiate the aforementioned points by analyzing how plants fare regarding different cognitive traits.

2.1 | Communication

Plant-level and inter-plant communication takes place via airborne biogenic volatile organic compounds (VOCs), among other mechanisms. VOCs are primary and secondary metabolites that plants exude through their leaves, flowers, fruits and the rest of their plant bodies (Baldwin, 2010; Baldwin et al., 2006; Meents et al., 2019). The release into the air of VOCs is not a physiologically recycled byproduct of the assimilated carbon. Instead, many adaptive interactions are mediated by VOCs (He et al., 2019), where such VOCs operate as informational cues among conspecifics and members of different species alike, and among both mutualists and competitors (Novoplansky, 2019).

The emission of VOCs can follow, for instance, herbivore attack, permitting plants to adjust their phenotype, and trigger adaptive defense mechanisms. Their reception allows plants to protect themselves against a wide variety of sources of stress. Behavioral responses include attracting the natural predators of herbivores or pathogens, or the priming of their own self-defenses with an eye to deterring future damage (Caruso & Parachnowitsch, 2016; Dicke et al., 2003; Dicke & Baldwin, 2010; Heil & Karban, 2010; Holopainen, 2004; Kalske et al., 2019; Ninkovic et al., 2016; Šimpraga et al., 2016). A well-known illustration of the role that VOCs can play in non-kin relations is provided by *Cuscuta* spp. (dodder)—a genus of parasitic vines that, lacking chlorophyll to photosynthesize their own foodstuff, exploit the VOCs being emitted by potential hosts such as tomatoes (*Lycopersicon esculentum*) and wheat (*Triticum aestivum*) to locate them (Runyon, 2006). We have learnt more recently that dodders combine chemical with light cues to discern the nutritional quality of potential plant–hosts, together with their proximity and shape (Smith et al., 2021).

Although more work is needed, consider, for some other more unexpected forms of communication, the involvement of sensitivity to sound vibrations in plant–invertebrate acoustic interaction (Gagliano et al., 2012). For instance, the model plant *Arabidopsis thaliana* can detect, through epidermal outgrowths (hairs called "trichomes"), the specific vibrations produced by the munching of caterpillars and respond to them by synthesizing toxins (Appel & Cocroft, 2014). Remarkably, *Arabidopsis* can discriminate by their vibrational modes the trichome frequencies caused by chewing from those caused by wind or insect songs. Trichomes thus act as "mechanical antennae" (Liu et al., 2017), enabling *Arabidopsis* to respond in a selective and ecologically meaningful way. Similarly, Veits et al. (2019) report that *Oenothera drummondii* flowers exposed to sounds in the same frequencies as those produced by flying bees produce sweeter nectar, increasing the chances of cross-pollination.

Communication also takes place underground, thanks to the interactions of roots with the mycelial networks of mycorrhizal fungi (Johnson & Gilbert, 2015; Simard, 2018; Simard et al., 2012). Studies have found that the symbiotic exchange of information of fungi and plant roots results in flexible and adaptive changes on the plant's side, including rapid changes in physiology, gene regulation, and defense response (Gorzelak et al., 2015; Song et al., 2015). Similar communication-based symbiotic interactions have been reported to occur between plants and insects (Heil, 2016; Mittelbach et al., 2019), with plants being able to control the behavior of their insect partners via chemical compounds (Grasso et al., 2015).

2.2 | Kin recognition

Evidence of kin recognition, a capacity to discriminate kin from non-kin, and to differentiate between different classes of kin, that plays a fundamental role in animal social cognition (Hepper, 1986), has been found in plants. For instance, studies focusing on root allocation and interaction show that *Impatiens pallida* specimens fight for resources more aggressively if competing with members of different species (Murphy & Dudley, 2009). Similarly, root allocation in *Cakile edentula* increases when a group of strangers shares a pot, but not when groups of kin members do it (Dudley & File, 2007). These findings suggest that root interaction and root-derived chemical exudates play a crucial role as cues for kin recognition and competitive kin discrimination, triggering adaptive behavioral changes (see Biedrzycki et al., 2010; Novoplansky, 2009, 2019; Semchenko et al., 2014).

Subsequent studies point out the importance of photoreceptors in kin recognition. For instance, Crepy and Casal (2015); see also Bais, 2015) report that *Arabidopsis* recognize kin neighbors by detecting red/far-red light and blue light profiles. Further still, exemplars of *Arabidopsis* interacting with kin members yield more seeds compared with plants interacting with non-kin members. This is taken as evidence for cooperative behavior in plants.

2.3 | Decision-making

Plant behavior has been traditionally interpreted as purely reactive and mechanical. The current empirical evidence, however, shows this view to be deeply misleading (see Baluška & Mancuso, 2009b; Segundo-Ortin & Calvo, 2019). Because plants inhabit complex environments, behavioral decision-making, for example, choosing between alternative courses of action such as growth direction and rate, is imperative to them (Reid et al., 2015; Trewavas, 2017). Like animals, plants must decide about where best to forage for light and nutrients (among other resources patchily distributed in different qualities and concentrations), together with repellents to grow away from or that might require an appropriate trade-off (van Loon, 2016). VOCs, for instance, serve to mediate decision-making in *Cuscuta*. Despite the fact that both tomato plants and wheat elicit the directed growth response of this parasite vine (see Section 2.1), experiments have shown that it prefers the former to the latter when both options are presented in tandem (Runyon, 2006). Results indicate that although *Cuscuta* exemplars are sensitive to a variety of VOCs, they preferably respond to those produced by the most nutritive host. For the authors of the experiment, this suggests that parasitic plants, like insect herbivores, are capable of selecting the most viable hosts when foraging.

Decision-making also takes place in the root apparatus (Hodge, 2009). Because high concentrations of salinity can disrupt plants' cellular biochemistry, roots have evolved sensitivity to abnormal saline conditions, adapting their growth accordingly. Li and Zhang (2008) studied salt-avoidance behavior by growing exemplars of *A. thaliana* in a medium with increasing levels of salinity. They found that roots started to bend upward, inverting their natural gravitropic behavior, before reaching the high-salt agar (250 mM NaCl) at the bottom. This indicates that “roots can sense ion gradients [and] make decisions that enable roots to stay away from high salt” (p. 352). Likewise, Trewavas (2014) reports that when exemplars of *Calamagrostis canadiensis* are offered adjacent habitats to grow, they choose the habitat with the best conditions of competition, warmth, and light. However, *C. canadiensis* can also “discriminate these conditions in combination […] choosing light plus warm soil in preference to others” (p. 84).

These empirical findings suggest that plants, similarly to other non-neural organisms (namely, bacteria), can engage in complex decision-making, integrating and weighting information from different parameters, and prioritizing responses to improve the chance of survival (Reid et al., 2015). As Moulton et al. (2020) explicate, “even within a simple plant, multiple environmental cues will combine and overlap in effecting mechanotransducive signals, hormonal response, differential growth, and ultimate change in shape” (p. 32227). As we will see in the following section, the complexity of plant decision-making and multiscale stimulus integration is further exemplified in experiments that involve anticipation and assessment of future states of affairs. We hold that these kinds of behaviors cannot be understood as individual responses to single stimuli.

2.4 | Anticipatory behavior

Getting things wrong can be rather costly when it comes to fitness. Only those organisms that have the ability to “act ahead of time” can survive in a dynamical, ever-changing environment. Furthermore, if we consider that plant behavior takes place across very slow timescales in comparison to animal behaviors, and that changes are often irreversible, we can see why plants cannot afford *not* to be able to anticipate the future (Calvo & Friston, 2017).

For a basic example of anticipatory behavior, consider the leaf laminas of *Lavatera cretica* that reorient during the night in order to face the direction of the sunrise (Garcia Rodriguez & Calvo Garzon, 2010). Heliotropic nocturnal reorientation can be retained for a number of days in the absence of solar-tracking (Schwartz & Koller, 1986). Anticipatory behavior has also been observed at the root level. Consistently with the findings of Dener et al. (2016), Novoplansky (2016) reports that young exemplars of *Pisum sativum* grow different roots if subjected to variable, temporally dynamic, and static nutrient regimes. For instance, when given a choice, plants allocate more root biomass in patches with increasing nutrient levels. The striking fact, however, is that they do so even in the cases when "dynamic" patches were poorer in absolute terms than the "static" ones. For Novoplansky, this indicates that "rather than responding to absolute resource availabilities, plants are able to perceive and integrate information regarding dynamic changes in resource levels and utilize it to anticipate growth conditions in ways that maximize their long-term performance" (p. 63).

Motivated by these findings, plants have been characterized as "anticipatory engines" (Calvo et al., 2016; Calvo & Friston, 2017). Accordingly, plants are constantly monitoring gradients in order to "guess" what the world is like. These predictions allow plants to "minimize surprise" (see Section 4.2), and to adapt to the yet-to-come environmental conditions via phenotypic plasticity.

2.5 | Learning and memory

The literature on plant learning and memory can be traced back to the 19th Century (see Abramson & Chicas-Mosier, 2016). Consider, for instance, habituation. Habituation occurs when the response to a repeated stimulus decreases and such decrease is not due to, say, sensory adaptation or motor fatigue. An early study on habituation was conducted by Pfeffer (1873) on *Mimosa pudica*, and it demonstrated that repeated mechanical stimulation led to a decrease in leaflet closure (see also Bose, 1906).

More recently, Gagliano et al. (2014) have studied habituation in *Mimosa* in the context of light foraging and risk predation. Rather than simply confirming Pfeffer's discoveries, two striking facts about this phenomenon were reported. First, that leaf-folding habituated behavior was more persistent for *Mimosa* exemplars growing in energetically costly environments (e.g., environments where light is scarce). This indicates that habituation is responsive to environmental conditions. Second, that the habituated reflex could last for up to 28 days. This evinces the acquisition of long-lasting memory in *Mimosa*.

Subsequent studies have sought for more sophisticated forms of learning, such as classical conditioning. This takes place when a conditioned stimulus (CS) is paired with an unconditioned stimulus (UC) that elicits a reflex. After a number of CS–US pairings, the response previously elicited by the US is now elicited by the CS. Recent research by Gagliano et al. (2016) showed that, after training, pea plant (*P. sativum*) specimens associated the presence of a fan (CS) with the onset of light (US). Besides, measuring expressional changes in heat-responsive genes, Bhandawat et al. (2020) have reported the occurrence of aversive conditioning in *A. thaliana*. Finally, Mittelbach et al. (2019) report that *Nasa poissoniana* adjust the timing of their pollen presentation based on previously experienced pollinator visitation intervals.

All these experiments suggest that plants can learn from past experience, eliciting changes at the level of behavior and phenotype for the sake of maximizing fitness. Needless to say, the research on plant learning and memory is just flowering, and further independent replications are needed before we can robustly claim that plants are able to learn (Abramson & Chicas-Mosier, 2016). In fact, the literature yields a mixed bag of negative (Holmes & Gruenberg, 1965; Holmes & Yost, 1966), positive (Armus, 1970), and unclear results (Haney, 1969; Levy et al., 1970—see Adelman (2018) for a review, and Gagliano et al., 2016; Markel, 2020a, 2020b for the latest exchanges on the evidence, or lack of, for associative learning in plant). In light of the inconsistent results being reported, at the Minimal Intelligence Lab, we currently aim to test independently the capacity for replication of Gagliano et al.'s (2016) results. Likewise, it is important that we further improve the research designs by taking these experiments out of the lab if we aim to yield ecologically meaningful conclusions (Abramson & Calvo, 2018; Affifi, 2018).

2.6 | Foraging and competition

The capacity of plants to integrate information from different vectors plays an essential role in their ability to develop different strategies for nutrient foraging (de Kroon et al., 2009). For instance, Latzel and Münzbergová (2018) report that clones of *Fragaria vesca* can associate locations of soil nutrients with particular light intensities and that they can use this previous experience to anticipate the presence of nutrients in a new environment. This experiment confirms previous evidence that epigenetic memory of previous interactions provides clonal plants with an advantage to forage in not yet occupied environments (González et al., 2016, 2017).

Foraging is also affected by competition. Cahill et al. (2010) measured patterns of root growth in *Abutilon theoprasti* while manipulating both competition and resource allocation, and reported different foraging behaviors depending on the conditions. When plants grew alone, they displayed both maximum root distribution and breadth independently of resource distribution. However, when competitors were present, plants adopted different foraging strategies depending on the allocation of resources. Similarly, Gruntman et al. (2017) conducted a series of experiments with *Potentilla reptans* where they simulated different light competition settings. They found that *P. reptans* can tailor its phenotype—namely, inducing changes in the vertical inclination, leaf area, and so on—according to the relative stature and densities of their opponents. The studies of Gruntman et al. demonstrate that plants "pick up" information from their competitors in order to make decisions about appropriate foraging strategies (Novoplansky, 2009).

Recent studies have been performed at the level of root interaction. For instance, Cabal et al. (2020) have successfully applied game theoretical models—models originally designed to predict strategic interactions between decision-makers in zero-sum competition games—to predict the behavior of exemplars of *Capsicuum annum* competing for soil resources.

2.7 | Risk sensitivity

Sensitivity to variability in nutrients has been documented in many animal species, showing how this sensitivity affects whether they switch between risk proneness and risk aversion. In a series of experiments with *P. sativum*, Dener et al. (2016) have demonstrated that root growth can show risk sensitivity too. For their experiment, Dener et al. used split-root pea plants—plants whose root tips grow in separate containers—and allocated different nutrient regimes to both pots: one pot received constant while the other one received variable nutrient concentration. Experimenters found that if the nutrient concentration in the first pot was enough for the plants to meet their metabolic needs, they grew roots in this pot. However, if the concentration of nutrients was insufficient, plants allocated more roots in the pot that receives the variable nutrient concentration. For Dener et al., these findings suggest that plants "respond strategically to patches varying in their average of nutrient availability" (p. 1765), and that they can switch between risk-prone and risk-averse behavior as a function of resource availability.

Commenting on these empirical findings, Schmid (2016) goes as far as to claim that they indicate that when faced with choices concerning different environmental conditions, plants make rational decisions in favor of the option that maximizes their fitness. For him, this implies that "theories of decision making and optimal behavior developed for animals and humans can be applied to plants" (p. R677).

2.8 | Mimicry

Mimicry refers to the adaptive similarity or resemblance between a mimic organism and its model. Whereas mimicry is a well-known phenomenon in the animal kingdom, examples of true plant mimicry are less frequent (Niu et al., 2018; Williamson, 1982), with documented cases in the plant literature being scarce (Lev-Yadun, 2016). An illustration nonetheless is provided by Gianoli and Carrasco-Urra (2014), who report that the leaves of *Boquila trifoliolata* can mimic the leaves of its supporting host, including size, shape, orientation, color, and petiole length, among other features. Moreover, the same individual can mimic two different hosts in a series. For Gianoli and Carrasco-Urra, mimicry behavior in *B. trifoliolata* is related to predation avoidance, for they gain protection against herbivores by climbing onto trees whose leaves are mimicked.

Mimicry by *B. trifoliolata* has also been observed to take place in full absence of touch. Although this has been previously observed in other species such as Australian mistletoes, in the case of *B. trifoliolata*, the lack of (physiological) connections in between vine and support, together with the impressive serial mimicking, somewhat reduces the alternative hypotheses as to what the mechanism that underlies mimicry in this species is (although see Pannell, 2014). In line with previous research, two alternative hypotheses are VOCs airborne communication and horizontal gene transfer (Gianoli & Carrasco-Urra, 2014). However, taking into account that physical contact is not needed for mimicry to take place, a more radical hypothesis has been recently advanced: a plant-specific form of proto-vision akin to the ocelloid-based type of vision found in cyanobacteria and some dinoflagellates (Baluška & Mancuso, 2016, 2017). According to Baluška and Mancuso, the vine may be able to perceive shapes and colors via somewhat primitive image-forming mechanism (although see Gianoli, 2017).

Finally, Schaefer and Ruxton (2009) studied deception by orchids *Ophrys exaltata* and *Epipactis helleborine*, and distinguished between plants relying on mimicry to achieve pollination and those relying on the exploitation of perceptual biases of animals. According to the researchers, since the exploitation of perceptual biases is a less restrictive strategy than mimicry, the former could be a precursor for the evolution of the later. As they explain, "if distinct plants exploit similar sensory biases, they can be "within reach" in animals' perceptual world for mimicry to evolve gradually" (p. 682).

Note that we are focusing exclusively on mimicry as occurring within one lifetime, not over evolutionary time. As we see it, what makes these instances of mimicry cognitively interesting is that they involve adaptations to the current contingencies of the environment. That the same exemplar of *Boquila* can tailor its phenotype to mimic different hosts (from different taxa) consecutively (Gianoli & Carrasco-Urra, 2014) invites explanations that prima facie resemble those invoked to account for the behaviors of some animal species (Lev-Yadun, 2016).

2.9 | Numerosity

As research in animal cognition shows, numerical competence, the ability to estimate and process quantitative magnitudes such as the number of times an event occurs (Anobile et al., 2021), is shared across a wide variety of phyla. Number-space mapping in chicks (Rugani et al., 2017) or numerosity by honeybees (Howard et al., 2019a; Howard et al., 2019b) first come to mind in non-mammalian species. As Rapp et al. (2020) observe, insects can use action potentials to encode basic numerical concepts non-symbolically. Yet, if insects can help themselves to the number of action potentials to solve numerosity-related tasks, the roots of "numerical competence" can be traced further down the tree of life.

Plants may well benefit from numerical competence during "hunting." The carnivorous plant *Dionaea muscipula* (Venus flytrap) can keep track of the number of times that the trigger hairs located in the inner side of the snap trap are stimulated (Böhm et al., 2016; Hedrich et al., 2016). When an insect lands on the trap and tilts the mechanoreceptors in the hairs, it induces the firing of action potentials (APs) responsible for the closing of the trap. Yet, for the trap to close, a second stimulation must be repeated within 20s-30s of the first one. Otherwise, the cycle resets. Besides, it appears that *Dionaea* is able to store information bio-electrically for short periods of time, discriminating the number of stored signals even further. When trapped, panicking insects repeatedly touch the trigger hairs, inducing the release of acidic enzymes that decompose them. However, once the trap has been shut and the prey is trapped, *Dionaea* keeps counting episodes of mechanical stimulation until it reaches five before it releases its digestive enzymes (Böhm et al., 2016).

Even though further empirical studies are needed before we can claim that plants exhibit numerosity-related abilities, and before we can tell how sophisticated such abilities are in relation to those exhibited by animals, Nieder (2020) speculates that plant sensitivity to numerical quantity, even if rudimentary, may play a crucial role in enhancing adaptive decision-making in various ecologically meaningful contexts. In fact, more recently, it has been reported that the Venus flytrap can fine-tune its carnivorous skills to different preys, being able to snap shut its trap after one single stimulation that would serve to elicit two consecutive action potentials (Burri et al., 2020).

2.10 | Swarm intelligence

Swarm intelligence—this is, the collective adaptive behavior of a decentralized group of individuals in response to sensory input in the vicinity—is common in bird flocking, ant colonies, fish schooling, bacterial colonies, and even human communities (Krause et al., 2010). Recent empirical evidence suggests it could be present in plants as well.

As aforementioned, growing root apices exhibit complex behavior and decision-making about where to grow. Yet, for Ciszak et al. (2012), complex root systems deploy coordinated growing for the sake of resource optimization and competition too. According to their studies, individual roots can induce a change in the direction of growth in the roots of their vicinity, giving rise to episodic patterns of coordinated activity among individual root apices. Swarm behavior of this kind proves crucial for adaptive success, for it helps maize roots to scan the soil structure collectively, enhancing their ability to detect nutrient patches. Elaborating on this, Baluška, Lev-Yadun, and Mancuso (2010), Baluška, Mancuso, et al., 2010) speculate that information transmission between individual root apices can take place via the combination of different mechanisms, including internal, neuron-like electrical activity, segregated chemical volatiles, and, finally, electric fields generated by each individual root (see Section 3).

Leaving aside the mechanisms that make swarm behavior possible in plants, all these researchers agree that the study of root behavior indicates that roots can solve problems collectively. However, for Taiz et al. (2019), this does not qualify for swarm intelligence, as the reported cases of collective behavior in plants occur between "individuals" with no genetic conflict, unlike those that occur in insect colonies, for instance.

3 | PLANT NEUROBIOLOGY: A SCIENTIFIC FRAMEWORK FOR THE STUDY OF PLANT INTELLIGENCE AND SENTIENCE

Plant neurobiology (PN) studies plant signaling with the aim of providing an explanation of how plants, *qua* information-processing systems, perceive, and act in an integrated and purposeful manner (Baluška et al., 2006; Brenner et al., 2006; Calvo, 2016). The rationale that underlies this scientific endeavor is that intelligent behavior requires information to be integrated with an eye to coordinating physiological needs among the different plant structures.

Decision making, kin recognition, learning, and the rest of competencies reviewed in Section 2, call for the informational integration of the plant body as a whole (Cahill et al., 2010; Souza et al., 2017). To alter traits in the phenotype and achieve flexible global behavior, plants cannot rely on a single source of information. To make, say, foraging decisions, plants must process incoming information concerning a panoply of parameters simultaneously (Novoplansky, 2016). These comprehend biotic and abiotic parameters alike, ranging from light, temperature, mechanical or vibrational cues to variations in supply of water and humidity, the distribution of resources in the soil, the presence of volatile and non-volatile chemicals, and many others (see Calvo & Trewavas, 2020a). All these informational resources get combined in order to maximize fitness and decision-making (van Loon, 2016).

Uncovering the fine-tuned integration of information signaling mechanisms across the root and shoot systems that give rise to intelligent behavior in plants is the goal of PN.[4] To achieve this goal, several disciplines are called for, including molecular biology, electrophysiology, biochemistry, evolutionary and developmental psychology, and plant ecology, among others (Heras-Escribano & Calvo, 2020).

As the reader may have guessed, the very idea of plant *neuro*biology is not free from controversy. Since the term was first coined in 2006 (Brenner et al., 2006), different authors have reacted against it. For instance, Alpi et al. (2007, see also Struik et al., 2008) argued that the concept is based on vague analogies, and adds nothing to our current understanding of plant physiology, ecology, and metabolism. Brenner et al. (2007) then responded that PN "creates an important and yet unfilled niche for plant biology," and that "the use of neurobiological terms and our understanding of plant behavior [has] generated ideas about how to understand the broader picture of plant signaling" (p. 286). Similarly, Trewavas (2007) argued that neurobiology concepts are "an essential adjunct to the imaginative scientific mind in confronting some of the most recalcitrant problems in plant biology" (p. 232). Far from settled, these disputes remain alive as of today (see Baluška & Mancuso, 2020, 2021; Baluška & Yokawa, 2021; Calvo et al., 2020; Calvo & Trewavas, 2020a, 2020b; Mallatt et al., 2020; Baluška & Reber, 2021; Robinson et al., 2020; Taiz et al., 2019, 2020).

We agree with critics that the price of using metaphors and analogies is eternal vigilance, if only to avoid being carried away by their implications. So, what justifies researchers' use of concepts from animal neurobiology to characterize plant signaling and behavior? For one thing, even though plants do not have neurons that could give rise to a nervous system, there are many molecular-level functional similarities between animal and plant substrates. For one thing, neurotransmitters such as acetylcholine, glutamate, dopamine, histamine, noradrenalin, serotonin, and g-aminobutyric acid (GABA) are also found in plants (Volkov, 2017; Žárský, 2015). This is no surprise, as a vast array of molecular mechanisms (including ion channels) evolved prior to the emergence of animal nervous systems (Baluška & Levin, 2016). Plant cells further resemble neurons in many other aspects (Baluška, 2010), responding electrically to many different environmental factors. Most notably, and among other types of electric potentials specific to plants, vegetable cells are capable of producing and supporting action potentials (APs) akin to those produced by animal cells, exhibiting in turn the standard three-fold phase of depolarization, repolarization, and hyperpolarization (Favre & Agosti, 2007; Felle & Zimmermann, 2007).[5] In addition, plants make use of both chemical and electrical synapses (Volkov, 2017) with plasmodesmata channels being functionally equivalent to animal gap junctions.

On the other hand, these electrical signals are propagated in the membrane of plant cells, and are transmitted along vascular conduits distributed throughout the whole plant body via a complex network of bundles of phloem, xylem, and cambium (Baluška & Mancuso, 2009a, 2009b; Brenner et al., 2006; Hellmann et al., 2018; Huber & Bauerle, 2016;

Souza et al., 2017; Trebacz et al., 2006; Volkov, 2012). Contemporary plant electrophysiology (Hedrich et al., 2016; Volkov, 2012; 2017) shows the phloem to be the primary carrier of such electric potentials from sensor to effector sites over long distances. The vascular system thus acts effectively as an inter-organ, long distance communication system (Calvo et al., 2020; Lucas et al., 2013).

Plant electrophysiology can reveal the underpinnings at work in the plant (Calvo et al., 2014). Searching the vascular bases of natural behavior provides the opportunity to correlate the behavior of plants and phyto-neural activity. Even though a thorough understanding of plant signaling is yet to be achieved, the current working hypothesis is that cellular electric excitability and propagation are partially responsible for the capacity of plants to respond to the changing environmental conditions as globally organized and coherent units, instead of an amalgamate of stimulus–response mechanisms.[6] Producing such an integrated approach of plant intelligent behavior is the ultimate goal of PN, and, so the advocates of the new discipline argue, "it would be a mistake to assume that plant physiology, when informed by plant ecology, can deliver the goods" (Calvo & Trewavas, 2020a, p. 215).

Moreover, some authors (Baluška, 2016; Calvo, 2017; Calvo et al., 2017; Trewavas et al., 2020) have defended that the emerging field of PN can also provide a new way to approaching plant sentience scientifically. According to Calvo et al. (2017), besides the obvious differences between the nervous systems of animals and the vascular system of plants, "plants lack none of the functional structures that are supposedly needed [to have consciousness]" (p. 205). Following this view, Trewavas et al. (2020) hypothesize that "changes in levels of plant sentience will be consistently linked to changes in long-distance electrical signaling and vascular complexities" (p. 217). Consequently, these authors propose to look at time-lapse observations of plant behavior, electrophysiological recordings, and phytohormone secretion as indicators for the ascription of consciousness to plants (see Calvo et al., 2017).

One promising way to investigate plant sentience involves the use of anesthetics in plants. For one thing, plants do not only produce anesthetic chemical compounds when stressed, but they can be subject to anesthetic treatments too. For instance, *Venus flytrap* snap-shutting behavior ceases under general anesthesia, and the same occurs with the leaf-folding response after mechanical stimulation of *M. pudica* (Yokawa et al., 2018). The current working hypothesis is that anesthesia could affect plants in a similar way as it affects animals: by acting upon the action-potential-inducing glutamate and GABA, thus inhibiting the production of electrical signals. Even though the underlying mechanisms that explain how anesthetics disrupt plants behavior and responsiveness remain to be elucidated, Baluška and Yokawa (2021) suggest that since "[a]nesthesia in humans induces a loss of awareness" this "could also be hypothesized to occur for plants" (Baluška and Yokawa, 2021, p. 2; see also Mediano et al., 2021). It is possible that anesthetics not only disrupt plant behavior, but plant sentience or awareness altogether.

The idea of plant consciousness has nonetheless recently been contested by Taiz et al. (2019, 2020, see also Mallatt et al., 2020). Their argument is two-fold. On the one hand, they claim that "the capacity to process environmental information for adaptive behavior and subjective awareness of the environment are two different things" (Mallatt et al., 2020, p. 219), whereby the latter depends on the presence of complex nervous systems and brains. Consequently, they assert that whereas vertebrates (including fish), arthropods, and cephalopods, are probably conscious, plants are not (Mallatt et al., 2020, p. 684). On the other hand, they argue that plants do not need consciousness, for their behavior is purely reactive and hardwired: "Instead of subjective consciousness, plants evolved adaptive behavior that is genetically determined by natural selection and epigenetically determined by environmental factors" (Mallatt et al., 2020, p. 218).

Two caveats are in order here. First, as shown in Section 2, the view that plant behavior is completely determined either by genetic or environmental factors is highly debatable in light of the empirical evidence. Second, even if we cannot rule out the possibility that consciousness emerges from the activity of a sophisticated nervous system, we have no scientific or empirical reasons to exclude the possibility that other forms of life have evolved different structures for subjective awareness (see Section 4). Hence, even if we agree that ascribing sentience to plants may be too premature, inasmuch as there is no consensus on what biological features are required for consciousness (Godfrey-Smith, 2017, p. 219), concluding that plants do not have it because they lack brains is a matter of presumption and begs the very question we are trying to address.

4 | PLANT SENTIENCE: REDUCTIVE AND NON-REDUCTIVE APPROACHES

Sentience is not necessarily granted by the presence of intelligent behavior. In fact, it is possible that consciousness bottoms-out at some point, and that plants mark such borderline. On the other hand, any theory of consciousness must be "evolutionarily sound," and it is precisely paying due respect to evolutionary considerations what brings to the fore the very idea of plant consciousness. Insofar as sentience may ease goal-directed behaviors and decision-making, there is a biological adaptive function to it that we cannot turn a blind eye to (Pennartz et al., 2019). The quest for plant consciousness thus first emerges from observations of complex behavior in plants. If consciousness happens to facilitate informational exchanges for the sake of the intelligent control of behavior, then contemporary research on consciousness can set the agenda by revising the candidate systems that we may ascribe sentience to.

Can we then rely upon scientifically grounded indicators for the ascription of sentience to plants? The purpose of this section is to present different theoretical candidates for the scientific study of plant consciousness. We believe these theoretical frameworks are apt to the task because they do not depend on the assumption that a brain (or a nervous system, more broadly) is necessary for having consciousness.

The study of plant sentience can be effectively approached both functionally and structurally. Taking function first, sentience plausibly has to do with enabling interaction with the surroundings. In the case of neural-based agents, this could well be its function, first and foremost (Morsella et al., 2016). Functionally speaking we may focus on the behavioral repertoire of plants. We may then find justification for the ascription of consciousness to plants on the grounds that it provides the most robust explanation of the available behavioral data. Alternatively, we may opt for structural (physical) criteria, and pay attention to the underlying mechanisms of (plant) natural behavior that may suffice to give rise to subjective awareness, shedding thus a distinctive light upon their alleged experience.

In what follows, we divide theories into reductive and non-reductive ones, whereby the former aim to identify the biophysical mechanisms and material substrates (neuronal and non-neural correlates of subjective phenomena alike) that may allow us to infer plant sentience from the available data. Accordingly, the most basic forms of consciousness may be reduced to the activity of a series of cellular and or subcellular structures, and it is on the basis of these processes that other, more sophisticated forms of consciousness may have evolved. The latter, non-reductionist approach aims likewise to identify the type of non-mechanistic principles that can possibly underlie plant sentience as an emergent phenomenon. All in all, the questions we are interested in in this section are: How can we determine whether plants are conscious? And, if they are, what are the physical principles behind it?

4.1 | Reductive approaches

4.1.1 | The cellular basis of consciousness

The cellular basis of consciousness (Reber, 2018) hypothesis, CBC for short, rejects the view that consciousness restricts to a small subset of creatures. Instead, according to CBC, consciousness is a fundamental property of cellular life, having emerged as an inherent feature of the very first life-forms. Subjectivity effectively dates back to the origins of life itself. If so, *all* biological organisms must be equipped with some sort of sentience, whereby its complexity is tailored to the specific necessities of the species in question. The rationale is as follows. Since all organisms need to interact with the environment to survive, "all adaptive functioning organisms, from the earliest on, must be sentient [...]. A non-sentient organism [...] would be an evolutionary dead-end" (Baluška & Reber, 2019, p. 1).

To make sense of this proposal, defenders of CBC hypothesize that consciousness is a fundamental property of cellular life, and that it emerged as an inherent feature of the very first life-forms, including prokaryotes. Besides biopsychism,[7] CBC is also an openly reductionist approach. Accordingly, the most basic forms of consciousness can be reduced to the activity of a series of cellular structures, and it is on the basis of these processes that other, more sophisticated forms of consciousness have evolved (Reber, 2018, pp. 5–6). If so, we may in principle attempt to trace the evolution of consciousness by taking into account existing phylogenetic relationships between groups of organisms, within and across kingdoms and clades. Ultimately, and according to CBC, consciousness could have been acquired through a distant evolutionary event that took place already at the time of LECA, the Last Eukaryotic Common Ancestor. However, there is no reason not to trace it back to unicellularity, to the Last Universal Common Ancestor, LUCA (Reber, 2018).

Baluška and Reber (2019; 2021) offer a tentative list of the subcellular structures that could be responsible for the emergence of consciousness. First is the excitable membranes. Excitable membranes appeared early in the biological evolution of cells and are present both in prokaryotic species and eukaryotic organelles. As we saw before, current plant electrophysiology shows that plant excitable cells produce their own specific electrical signals that are transmitted through the phloem (Volkov, 2012, 2017). A second option is the dynamic cytoskeleton, including microtubules and actin filaments. Finally, structurally flexible proteins, particularly those that have fivefold symmetries and quasicrystal properties. All these properties, Baluška and Reber explain, act as "bioelectronic devices" and "contribute to subjectivity within single cells" (p. 4).

In order to understand how individual cellular consciousness can give rise to consciousness in multicellular organisms, Baluška and Reber suggest paying attention to synaptic principles within eukaryotic cells. Apart from such synaptic principles, they also recommend paying attention to mechanisms by which adjacent cells interact via extracellular electric and electromagnetic fields, forming ephaptic units. It is suggested that, in plants, "the best candidate for such an ephaptic unit is the oscillating zone of the root apex" (p. 5), also known as the "transition zone" (TZ), a special root area in which electrical fields are maximal and synchronized oscillatory signal crosstalk occurs (Masi et al., 2009). Placed in between the apical root meristem and the subapical elongating area of the root, TZ constitutes a truly "hot spot" (Kong et al., 2018) that allows the root apparatus to integrate sensorimotor pathways, determining in turn differential growth, and allowing for flexible and global patterns of root growth and development. It is possible that the temporal structuring of transition zone patterns of electrical activity furnishes the plant body with specific areas in which to integrate sensory-motoric signaling circuits (Baluška et al., 2004).

In sum, from the point of view of CBC, consciousness is co-extensive with life (thus biopsychism) and emerges out the electrical activity of cellular organelles (see Baluška & Mancuso, 2021; Baluška & Reber, 2021). Therefore, it is by studying the activity of these cellular structures, and their integration in larger-scale mechanisms, that we can uncover the particularities of subjective awareness in complex, multicellular organisms.

4.1.2 | Information integration theory

The second theoretical candidate we present is Information Integration Theory, or IIT (Tononi, 2004, 2008; Tononi et al., 2016; Tononi & Koch, 2015). The core idea of IIT is that consciousness has to do with the capacity of a physical system to integrate information. In particular, IIT lays the stress on the role that complex interactions between the parts of the system play in bringing about system-level sentience. This idea needs further unpacking.

For one thing, IIT states that the quantity of consciousness a system possesses can be measured as the value Φ of integrated information within a complex of elements, C. Φ represents the amount of causally efficacious information that is contained in the interaction between a subset of elements of a complex, but not within the parts *themselves* (Balduzzi & Tononi, 2008). The notion of a complex, in turn, serves to determine the location within the system where information happens to be integrated (a maximally integrated subset). We may say that a complex constitutes a "local maximum" of integrated information, Φ (see Mediano et al., 2021).

According to IIT then, a complex C possesses consciousness if: (a) the amount of Φ in C is higher than 0, and (b) C is not part of another complex with higher Φ. Besides, the theory also postulates that the quality of consciousness is determined by the informational relationships between the elements of the complex. This informational relationship is captured by the values of causally effective information among them. With these notions at hand, the fundamental assumption of IIT can be stated as follows: A particular experience is identical to a complex structure, and each property of the experience must correspond to an informational interaction between the elements of the complex.

Even though there are substantial disagreements on how to compute Φ (see Mediano et al., 2018), proponents of IIT defend that the theory provides the means needed to investigate the physical substrate of consciousness. This investigation has been conducted primarily in the context of cognitive neuroscience (Tononi et al., 2016), but there is no reason to suppose that information integration can only take place over neural structures.[8] Instead, consciousness could emerge from the phyto-neural features of the vascular system of higher plants (Calvo et al., 2017); features that underlie plant-specific forms of informational integration under general IIT principles.

With this premise at hand, Mediano et al. (2021) offer some suggestions as to how to apply IIT to the study of plant consciousness. They do so under PLANT-IIT principles—that is, the vegetable extension of IIT denoting the research programme and experimental and analysis tools needed to investigate integrated and information in plants. Adapting IIT, they contend that the quest for plant consciousness may rest upon architectural and topological features of plants' vascular system. In particular, two features must be honored: the existence of a non-feedforward, reentrant architecture, and of maximally irreducible conceptual structures (MICS). As they suggest, vascular cells in higher plants may have the means to build up complex electrical network-like structures (Zamski, 1979), providing in turn the type of reentrant "dynamic core" that IIT calls for (Edelman & Tononi, 2000; Tononi & Edelman, 1998). The physiological basis for plant consciousness could be found, Mediano et al. (2021) propose, in the complex formed by the meristematic tissues, this is, the embryonic regions of cell division that serve to construct the overall plant body, and the vascular system itself (see also Calvo et al., 2020). In their own words: "As its human counterpart focuses on the electrical activity of neurons, PLANT-IIT shines the spotlight on plant electrophysiology [...] and, in particular into the role of the vascular system as a long-distance communication network that orchestrates the activities of the merismatic tissues in different plant regions to achieve goal adaptive behavior at the whole-plant level" (p. 6).

One advantage of IIT is that, should consciousness be equal to information integration, IIT allows us to identify different degrees of sentience among different plant species, represented by gradable measures within a Φ metric space. In fact, the analysis of vascularity in mature stems and trunks (Carlquist, 1975; Dobbins, 1971; Horak, 1981; Wheat, 1977) reveals rather complex multi-layered structures with vascular tissues nesting one within the other. As it turns out, we may discover that some plant species possess an intricate vascular system complex enough to support a higher degree of information integration, yielding higher Φ values. Other species, by contrast, would enjoy a lower degree of sentience as quantified within such Φ metric space, insofar as they possess a less integrated and differentiated vascular activity (Mediano et al., 2021). This is consistent with adopting an evolutionary approach to consciousness, according to which different species have evolved different grades of sentience tailored to their specific needs and the characteristics of their econiches (see Calvo, 2017; Trewavas et al., 2020).

4.1.3 | Quantum-based approaches

Taking sentience to be a state of matter, reductionist theories of consciousness can likewise resort to a more fundamental quantum level beyond neural activities. Most notably, Penrose (1989, 1994) has placed the origin of consciousness at the level of quantum phenomena. According to him, consciousness relates to the behavior not just of neural tissue but to their quantum-mechanical properties—this is, with states posited at the quantum level.

The "orchestrated objective reduction" (Orch OR) model of consciousness (Hameroff, 1998; Hameroff & Penrose, 1996, 2014) has served in the last two decades to epitomize such an idea.[9] According to the Orch OR model, sentience arises through states of quantum computation as a result of the wave function collapse (reduction) of quantum superpositions into single definite states. In Orch OR jargon, it is the objective collapse of the wave function that consciousness itself consists of.[10]

In animals, the emergence of states of protoconsciousness takes place in the tubulin molecules within neural microtubules that play the information-processing role of biological quantum computers or resonators (see Hashimoto, 2015). States of protoconsciousness occur when the microtubule quantum superposition collapses into a single definite state or specific choice (Woolf & Hameroff, 2001). As objective quantum reduction is fine-tuned (i.e., becomes orchestrated), the quantum system develops states of long-lasting coherence across neural populations.[11] As a result, richer states of consciousness are delivered out of more basic and punctual OR events and protoconscious experiences.

Quantum coherence and quantum state reduction may in principle be applicable to the study of plant consciousness (see Barlow, 2015). Under Orch OR principles, plant sentience could arise from quantum effects of the sort hypothesized to underlie the emergence of consciousness in animals. For one thing, it goes without saying that resonating, long-lasting quantum phenomena take place in bacteria, plants, and other non-neural systems (Jedlicka, 2017). In the case of plants, macroscopic quantum phenomena may well be connected to their vascular, phyto-neural activity. Besides, microtubules are shared across eukaryotic cells (Celler et al., 2016; Hashimoto, 2015) forming "dense and organized arrays" (Mirabet et al., 2018) that may play the role of quantum resonators for the sake of orchestrating their own plant-based OR events. In like vein, and beyond quantum coherence, other quantum features serving different purposes such as non-local quantum entanglement and quantum superposition may find a plant-based correlate. One way or another, whether we shall be able to identify robust enough correlates of plant sentience at the quantum level awaits further investigation.[12]

4.2 | Non-reductive approaches

4.2.1 | Free-energy principle and predictive processing

Although the free energy principle (FEP) and predictive processing (PP) are logically independent, they are most commonly presented in tandem (see, e.g., Clark, 2016; Hohwy, 2013). This is also true of so-called plant predictive processing (PPP) (Calvo et al., 2017; Calvo & Friston, 2017; Sims, 2019).

According to FEP, all self-organizing systems must minimize free energy to avoid disintegration (Allen & Friston, 2016; Friston, 2009, 2010). Free-energy is an information-theoretic measure that sets the upper bound of surprise, where surprise refers to the amount of discrepancy between the expected sensory inputs of a system and the actual inputs the system receives. Because FEP regards surprise as being formally equivalent to entropy, it follows that systems must minimize surprise to avoid disintegration.

Given that free energy is equivalent to prediction error, PP is usually considered to be the way FEP is implemented in cognitive systems (van Es, 2020). PP states that the primary aim of cognitive systems is to minimize prediction error. Prediction errors must be minimized if behavior is to remain adaptive. To achieve such error-minimization, organisms possess a hierarchically structured generative model of their environment. The mission of this generative model is to generate top-down predictions about the most likely causes of the bottom-up sensory samples. Hence, rather than inferring the causal structure of the environment from the bottom-up sensory stimuli, as in classical theories of perception, organisms estimate the probability that a particular stimulus is caused by some environmental event or property. Previous successful predictions act as empirical priors for subsequent predictions. Likewise, the disparity between predictions and sensory samples results in prediction errors, which propagate upwards and laterally, updating the probability distribution of the priors. This process is called "perceptual inference." Another way to minimize prediction error is to actively act upon the environment to generate the expected sensory observations—a process called "active inference." Over the long term, prediction error minimization is said to approximate Bayesian belief optimization.

Calvo and Friston (2017) have applied the theoretical machinery of PP to plant behavior. According to them, plants' vascular systems and plasmodesmata could allow for the kind of hierarchical and lateral informational processing required by PP. They propose, for instance, that the vascular cells in deep phloem could serve to encode a probabilistic model of the environment, whereas apical cells can convey prediction errors. Likewise, the assessment of competing hypotheses can be possible courtesy of the horizontal and tangential anastomoses and PD. Like in the case of animals, Calvo and Friston argue that plants can control their behavior once prediction error is minimized and the vascular network settles on a preferred hypothesis.

PP has also been applied to the study of consciousness. For instance, on the assumption that the information required for expressing conscious experience can be encoded in the generative model, Hobson and Friston (2014) write: "we consider consciousness to be the process of perceptual inference about the states of the world causing sensations. […] In other words, we consider consciousness as finding the best (in a Bayes optimal sense) probabilistic explanation for our sensorium" (p. 7). In the same vein, Hohwy (2012) tell us that conscious experience occurs when the system "selects" a hypothesis that accounts for the current sensory evidence (see also Clark, 2018). If these arguments are on the right track, then understanding plant consciousness would amount to understanding how plants engage in probabilistic, action-oriented guessing. This would require expanding on the work already initiated by Calvo and Friston (2017).

Others have argued that PP can provide the basis for an embodied-embedded theory of consciousness. Accordingly, conscious experience emerges from the organism–environment interaction, and thus cannot be studied by focusing on how predictions are generated uniquely. This is the case of Kirchhoff and Kiverstein (2018), for whom "[u]nder active inferences, conscious experience has its roots in embodied activity, coupling the agent—that is, the generative model—to the world" (p. 2). If that is the case, understanding plant sentience would require combining PP with a more ecological approach—one that focuses not only in understanding how prediction takes place within plant vascular systems, but how prediction is translated into behavior (see Section 4.2.2).

4.2.2 | Ecological-enactive theories

The sensorimotor theory provides the most clear-cut example of a non-reductive, embodied-embedded theory of consciousness (Noë, 2010; O'Regan, 2007, 2011, 2014; O'Regan & Noë, 2001). Directly inspired by Gibson's ecological theory of perception (Chemero, 2009; Gibson, 1966, 1979), the sensorimotor theory states that conscious experience emerges from the activity of the whole system coupled with the environment.[13] Of course, this is not to deny that internal structures and processes causally enable consciousness. What this position reacts against is the assumption that consciousness can be understood by considering these internal structures and processes in isolation.

To make sense of this view, defenders of the sensorimotor theory propose that the qualities of experience are to be explained in terms of "sensorimotor contingencies." Sensorimotor contingencies take the form of objective laws that link actions to resulting sensory changes, both proprioceptive and exteroceptive. Accordingly, "feeling is not something that can be located in some circuit, or which is generated by some mechanism. Instead, feel is a way to doing things" (O'Regan, 2007, p. 339). It follows that what determines the phenomenal differences between sensory modalities is the fact that they depend on the enactment of different sensorimotor contingencies—different cycles of perception and action. For instance, because we do different things when we explore a glass visually and haptically, these sensory modalities yield different experiences of the glass. Likewise, the soft feeling of a sponge derives from the fact that it squishes when I press it, and it is thus made possible by a particular sensorimotor interaction (O'Regan, 2011, p. 25). Sensorimotor theory thus focuses on studying how different organisms interact with the environment, enacting different sensorimotor contingencies.

It follows from sensorimotor theory that insofar as plants behave in their environment, this is, insofar as they exploit sensorimotor feedback loops to negotiate the external world, they have phenomenal consciousness. Indeed, Heras-Escribano and Calvo suggest that principles of sensorimotor theory "fit hand in glove with the idea of phenotypic plasticity enabling metabolic functioning through the manipulation of the environment. Under this light, plants could have sensory awareness of their surrounding via active exploration" (Heras-Escribano & Calvo, 2020, p. 540). Investigating plant consciousness under the principles of sensorimotor theory thus requires looking for plant-specific sensorimotor contingencies—the laws that determine the ways their behavior correlates with sensory changes. To do so, we must begin by investigating how plants exploit the sensory information derived from exploratory actions to access the properties of the environment and control growth and development. As a preliminary example of this, consider research concerning how the common bean explores the surroundings via circumnutation in order to find out a climbable surface nearby (Frazier et al., 2020; Raja et al., 2020). Nutation movements elicit plant-specific sensorimotor contingencies that the common bean can exploit to control adaptive behavior.

But, what is the role of the vascular system of plant consciousness according to sensorimotor theorists? As mentioned before, the hypothesis here is that consciousness is not something that *happens* inside the organism; rather, it is a situated activity, something that the organism as a whole *does*. It follows from this perspective that if we aim to understand how the vascular system of plants contributes to consciousness, we need to look at the vascular systems' job in relation to the plant body and environment.

One way to do this is to supplement sensorimotor theory with PP (see Kirchhoff & Kiverstein, 2018, chap. 5). Here we suggest looking at Gibsonian neuroscience for an alternative route. For instance, Raja (2018, 2019) has recently fleshed out the notion of "resonance" to describe the activity of the central nervous system concerning what happens at the scale of the organism-environment system (the ecological scale). According to him, when a system detects a particular sensorimotor pattern—namely, optic flow—, the dynamics at the level of the CNS get temporally constrained by the dynamic at the ecological scale. To investigate resonance, Raja proposes to look at the coupling between the ecological and the neural level in terms of fractals—namely, "pink noise" at both scales.[14]

We hypothesize that a similar analysis can be run for plants (Frazier et al., 2021). Once we have discovered the sensory information the climbing bean exploits in guiding nutation, we should be able to find whether the dynamics at the vascular level of the plant "resonate" to the dynamics at the scale of the plant-environment scale (for an analysis of the dynamics underlying plant nutation see Raja et al., 2020). In light of this idea, Hardcastle (2020) has already suggested the possibility that "[t]he pink noise of our cognitive synergy indexes our phenomenal experience" (p. 26).

5 | CONCLUSION

Is there any objective reason to justify the ascription of consciousness to plants? Whether plants have consciousness and, if so, what it might be like to be a plant are not only philosophical but also scientific questions. In order to face these questions, we must engage with the empirical research being conducted within plant biology, ecology, neurobiology, and cognitive science, more broadly.

One reason to defend that plants are *not* conscious is that plant behavior is genetically and environmentally determined. If consciousness is a biological adaptation that evolved to facilitate intelligent, adaptive behavior, then there is no in principle reason to believe that plants are not sentient. This assumption, however, conflicts with the empirical evidence. Contrary to what it is commonly assumed, plants seem to be capable of many of the cognitive abilities traditionally assumed to be exclusive to animals. Hence, the behavioral evidence thus suggests that plants could qualify to be sentient organisms. A second argument concerns the lack of a nervous system in plants. If having a nervous system is a pre-requisite for being conscious, then plants are automatically excluded. The reason why this second argument is debatable is two-fold. Firstly, the assumption that having a nervous system is a sine qua non condition for consciousness is unjustified, for we do not have a scientific consensus regarding what physical structures need to be in place for consciousness to appear. Secondly, if plants have evolved their own means to behave adaptively—by means of phenotypic plasticity, instead of locomotion as in the case of animals—there is no reason to suppose that they could not have evolved their own physical structures for consciousness. Regarding this second argument, we submit to the reader the idea that the empirical research of plant neurobiology can help shed light onto the physical processes and structures that could give rise to plant sentience. Despite the obvious functional and structural divergences, we believe that the question of whether phyto-nervous systems can cause consciousness in plants is not unlike the question concerning the neural correlates of consciousness in animals. Furthermore, we contend that this empirical research can be combined with currently existing non-neurocentric theories of consciousness.

However, research on plant consciousness and cognition is only at the onset. Some questions for future research include, for instance: Can we fully understand the cognitive processes of plants by using the models, theories and techniques we use in cognitive science? Can comparative studies be useful to reveal aspects such as decision-making, learning, and anticipatory behavior in plants? Can they be useful to understand plant consciousness? Can techniques of overt behavior observation—for example, time-lapse—become a starting point in attempting to discover the biological principles of plant consciousness and cognition? Can consciousness be implemented in vascular systems, and, if so, how? And, finally, how can the study of plant consciousness help illuminate our broad understanding of consciousness itself?

ENDNOTES

[1] Considering that photosynthetic products are osmotically active, plants' rigid cell walls serve the purpose of controlling volume, pressure and shape. As a result, movement akin to the form it takes in animal cells is hindered. With light being ubiquitous, such an evolutionary constraint did not result in an urge to locomote (Calvo et al., 2017).

[2] We acknowledge that the terminology is problematic here. Authors such as Godfrey-Smith (2017), for instance, propose to use "sentience" to refer to the subjective phenomenal experience, while "consciousness" denotes one form of sentience (see also Nani et al., 2021). Nonetheless, he sometimes uses "consciousness" as a broad umbrella term to cover both (Barron & Klein, 2016). We choose to remain neutral about this controversy, and use "sentience" and "consciousness" interchangeably to refer to the basic presence of subjective experience (see also Calvo, 2017; Ginsburg & Jablonka, 2019).

[3] A traditional assumption used to exclude plants from being cognitive resorts to the Aristotelian distinction between motion and self-motion (Linson & Calvo, 2020). According to this view, one reason as for why plants do not qualify as cognitive creatures is that they lack the capacity to control their movement endogenously. Recent empirical research has shown this assumption to be misled. For instance, in a recent study on the patterns of growth of common bean shoots (*Phaseolus vulgaris*), researchers discovered that the bending this vine exhibits is influenced by the presence of a nearby climbable pole (Raja et al., 2020). If the vine fails in its attempt to reach the pole, it straightens out and tries again. The fact that the vine's movements are continuously reconfigured in the different attempts to reach the pole suggests that they are not ballistic but endogenously controlled by the plant in order to attain a specific goal.

[4] For a historical review of the research on plant electrical signaling see Stahlberg (2006).

[5] Plant cells also support variation and system potentials (Choi et al., 2016; Debono & Souza, 2019; Huber & Bauerle, 2016; Souza et al., 2017; Vodeneev et al., 2016; Zimmermann et al., 2009; Zimmermann et al., 2016). For the significance of electrical excitability and signaling overall in the physiology of plants, see Fromm & Lautner, 2007, and more recently Debono (2020).

[6] In order to get a complete knowledge of how electrical conduction takes place in vascular cells, we must elucidate how electrical, hydraulic and chemical signaling pathways interact, triggering integrated and synergistic responses at the level of the plant system (see Huber & Bauerle, 2016).

[7] According to biopsychism, some form of sentience is present in all living organisms (Godfrey-Smith, 2016).

[8] In fact, some authors regard IIT as being compatible with panpsychism (Godfrey-Smith, 2016; Tononi, 2008). As Van Gulick (2018) explicates, "even a simple system such a single photo diode will be conscious to some degree is it is not contained within a larger complex."

[9] For a recent attempt to combine Orch OR and IIT see Chalmers and McQueen (2021).

[10] Penrose and Hameroff hypothesize that this "objective collapse" does not necessitate an external observer interacting with the system. Rather, it is caused by the specific conditions of the internal environment of microtubular structures (see below).

[11] Bose–Einstein condensates provide the canonical illustration of the transition towards a unifying wave function (Woolf & Hameroff, 2001).

[12] The Orch OR model of consciousness has nonetheless been objected for not being biologically feasible (Mckemmish et al., 2009).

[13] For an analysis of the relationship between sensorimotor theory and Gibson's psychology see Silberstein and Chemero (2012) and Heras-Escribano and Calvo (2020).

[14] "Pink noise" is an indication of nested, self-similar structures occurring over time. It is usually taken to be characteristic of soft-assembled cognitive synergies (Dotov et al., 2010; Orden et al., 2005; Van Orden et al., 2011).

CONFLICT OF INTEREST

The authors have declared no conflicting interests.

AUTHOR CONTRIBUTIONS

Miguel Segundo-Ortin: Conceptualization (equal); formal analysis (equal); methodology (equal). **Paco Calvo:** Conceptualization (equal); formal analysis (equal); methodology (equal).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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FURTHER READING

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