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Do Plants Have Cognition?

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Abstrakt (Deutsch)

In den letzten Jahren ist das Interesse an der Vorstellung, dass Pflanzen über kognitive Fähigkeiten verfügen, stark gestiegen. Immer mehr Wissenschaftler und Philosophen vertreten die Ansicht, dass Pflanzen wahrnehmen, sich erinnern, lernen und sogar Entscheidungen treffen können - Behauptungen, die traditionelle Annahmen über die biologischen Grundlagen der Kognition in Frage stellen und kognitive Kategorien über das Tierreich hinaus erweitern. Diese Arbeit überprüft solche Behauptungen kritisch und argumentiert, dass Pflanzen zwar komplexe Formen der Umweltwahrnehmung, des Anpassungsverhaltens und der physiologischen Integration aufweisen, aber keine Kognition im eigentlichen Sinne besitzen. Es wird behauptet, dass Pflanzen über eine grundlegende Art von Handlungsfähigkeit verfügen, die allen lebenden Systemen gemeinsam ist, sowie über eine Form von Intelligenz, die in der metabolischen und entwicklungsbezogenen Plastizität verwurzelt ist. Ihnen fehlen jedoch die neurophysiologischen, repräsentativen und integrativen Strukturen, die der Kognition bei Tieren zugrunde liegen.

Die These argumentiert weiter, dass Pflanzen nicht im eigentlichen Sinne des Wortes kommunizieren, sondern vielmehr durch chemische Signale eine ökologische Kopplung eingehen. Ihre elektrophysiologische Aktivität wird zwar oft mit neuronalen Signalen verglichen, erfüllt jedoch nicht die rechnerischen oder organisatorischen Funktionen eines Nervensystems. Ebenso stellt ihre Reaktionsfähigkeit auf Reize keine Sinneswahrnehmung dar, sondern eher eine subkognitive Form der Umweltempfindlichkeit. Abschließend wird die Frage der Empfindungsfähigkeit von Pflanzen untersucht und argumentiert, dass zwar der noch junge Stand der Bewusstseinsforschung einen endgültigen Ausschluss dieser Möglichkeit verhindert, es jedoch derzeit weder empirische Belege noch theoretische Gründe gibt, Pflanzen Empfindungsfähigkeit zuzuschreiben.

Anstatt sich auf festgelegte Definitionen zu stützen, verfolgt die Arbeit einen informationstheoretischen und pluralistischen philosophischen Ansatz, bei dem Pflanzenphänomene mit Paradigmenfällen aus der Tierkognition verglichen werden, um die biologischen und funktionellen Bedingungen zu identifizieren, unter denen kognitive Fähigkeiten entstehen. Zwar wird anerkannt, dass zukünftige Forschungen noch unbekannte Mechanismen in der Pflanzenbiologie aufdecken könnten, doch deuten die derzeitigen Erkenntnisse auf eine tiefgreifende Diskontinuität zwischen den Fähigkeiten von Pflanzen und denen kognitiver Organismen hin. Die Schlussfolgerung lautet, dass die Zuschreibung von Kognition an Pflanzen die Gefahr birgt, wichtige biologische Unterschiede zu verschleiern und die konzeptionelle Integrität der Kognitionswissenschaft zu untergraben.

Abstract (English)

Recent years have seen a surge of interest in the idea that plants possess cognitive capacities. A growing number of scientists and philosophers argue that plants can perceive, remember, learn, and even make decisions - claims that challenge traditional assumptions about the biological basis of cognition and extend cognitive categories beyond the animal kingdom. This thesis critically examines such claims and argues that, while plants exhibit complex forms of environmental responsiveness, adaptive behavior, and physiological integration, they do not possess cognition in any robust sense. It is maintained that plants have a basic kind of agency shared by all living systems, and a form of intelligence rooted in metabolic and developmental plasticity. However, they lack the neurophysiological, representational, and integrative structures that underlie cognition in animals.

The thesis further argues that plants do not communicate in the proper sense of the term, but rather engage in ecological coupling through chemical signaling. Meanwhile, their electrophysiological activity, while often analogized to neural signaling, does not fulfill the computational or organizational roles of a nervous system. Similarly, their responsiveness to stimuli does not constitute sense perception, but rather a sub-cognitive form of environmental sensitivity. Finally, the question of plant sentience is examined, and it is argued that although the nascent state of consciousness science prevents a definitive exclusion of the possibility, there is at present neither empirical warrant nor theoretical motivation for attributing sentience to plants.

Rather than relying on stipulative definitions, the thesis adopts an information-theoretic and pluralistic philosophical approach, comparing plant phenomena with paradigm cases in animal cognition to identify the biological and functional conditions under which cognitive capacities arise. While it is acknowledged that future research may uncover as-yet-unknown mechanisms in plant biology, current evidence suggests a profound discontinuity between the capacities of plants and those of cognitive organisms. The conclusion is that attributing cognition to plants risks obscuring significant biological distinctions and undermines the conceptual integrity of cognitive science.

Curriculum Vitae

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1 Introduction

1.1 The Emerging Debate on Plant Cognition

In recent years, a growing body of scientific and philosophical literature has advanced the view that plants may possess cognitive capacities. A small but vocal group of researchers has published extensively on the topic, with the aim of establishing plant cognition as a serious domain of inquiry in both biology and philosophy of mind. Drawing on findings from plant physiology, electrophysiology, and behavioral ecology, these authors claim that plants can perceive their environment, process information, learn from experience, and even make decisions (Trewavas 2005; Calvo & Keijzer 2011; Gagliano 2017; Baluška & Mancuso 2008).[1] Some go further, arguing that plants exhibit memory, intentionality, or rudimentary forms of consciousness (Calvo et al. 2017; Segundo-Ortin & Calvo 2021).[2] These proposals are typically framed as part of a broader reconceptualization of cognition – not as a phenomenon confined to animals with nervous systems, but as a fundamental biological process distributed throughout life. It is within this context that the present thesis seeks to intervene.

1.2 Central Question and Thesis

The central question addressed in this thesis is whether plants have cognition. It is argued that they do not. While plants undoubtedly display complex, adaptive, and highly responsive behavior, their capacities do not amount to cognition in the sense employed in the cognitive sciences or in philosophical accounts of mind. Instead, it is maintained that plants possess a kind of intelligence and agency that is characteristic of all living systems – an intelligence rooted in physiological sensitivity and behavioral flexibility, but not in representational processing, sense perception, or sentience. The distinction is a crucial one, and it is the aim of this thesis to make it precise.

1.3 Why the Question Matters

This issue is not merely of botanical interest. The implications of attributing cognition to plants extend into the foundations of cognitive science and philosophy of mind. Expanding the term "cognition" to encompass all forms of environmentally sensitive behavior, regardless of whether they involve sentience, representation, or intentionality, risks eroding the conceptual distinctions

1 Trewavas, A. (2005). Plant intelligence. *The Science of Nature, 92*(9), 401-413. https://doi.org/10.1007/s00114-005-0014-9
Calvo, P., & Keijzer, F. (2011). Plants: Adaptive behavior, root-brains, and minimal cognition. *Adaptive Behavior, 19*(3), 155-171. https://doi.org/10.1177/1059712311409446
Gagliano, M. (2017). The mind of plants: Thinking the unthinkable. *Communicative & Integrative Biology, 10*(2), e1288333. https://doi.org/10.1080/19420889.2017.1288333
Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6

2 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065
Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews Cognitive Science, 13*(2). https://doi.org/10.1002/wcs.1578

that make cognition intelligible as a scientific and philosophical category. It is argued that such conceptual inflation misleads the search for cognition's biological basis by encouraging an undue focus on features – such as signal transduction, growth adaptation, or chemical responsiveness – that are widespread in living systems but are neither constitutive of nor sufficient for cognition. This risks encouraging a reversal of explanatory direction: rather than using paradigm cases of cognition (in humans and animals) to illuminate its evolutionary emergence and material basis, it invites attempts to infer cognition from the mere existence of complexity. Such a move, while rhetorically compelling, is scientifically and philosophically hazardous.

1.4 Methodological Approach

The methodology employed in this thesis is broadly interdisciplinary, combining empirical literature review with philosophical analysis. The primary empirical basis is drawn from current research in plant biology, particularly studies that concern the physiological, electrophysiological, and behavioral capacities of plants – capacities that have been interpreted by some researchers as evidence of cognition. This literature is examined not with the aim of resolving contested empirical questions within plant science, but rather to assess whether the biological data cited in support of plant cognition plausibly warrant such an interpretation. In this respect, the method is not experimental but conceptual: it proceeds by analyzing the empirical claims made in support of plant cognition and evaluating whether these justify the attribution of cognitive capacities in a scientifically and philosophically coherent sense.

In addition, the thesis engages with research in animal cognition and neuroscience, which provides a critical comparative framework. The goal is to assess whether the organizational features and functional capacities found in animals – such as perception, learning, memory, and decision-making – have genuine analogues in plants. Where claims of cognitive similarity are made, attention is paid to whether these similarities are architectural (i.e., concerning the physical mechanisms underpinning cognition), functional (i.e., concerning the kinds of processes carried out), or merely metaphorical. Insights from the study of animal cognition are used not only to clarify what cognition entails, but also to identify the conditions under which it is instantiated in living systems. This dual-level analysis – tracking cognitive phenomena both at the "hardware" level of biological implementation and the "software" level of functional organization – serves as a basis for asking whether plants, though structurally dissimilar, might nevertheless perform equivalent cognitive operations.

Thus, the overall approach combines a critical review of empirical findings in plant biology, animal neurobiology, and cognitive science with conceptual analysis grounded in philosophy of mind and philosophy of biology. The aim is to clarify the boundaries of cognition and assess whether plants plausibly fall within them.

1.5 Theoretical Frameworks

This thesis draws upon a range of theoretical paradigms in philosophy of mind and cognitive science, including some that diverge significantly in their conceptual commitments and explanatory strategies. This pluralistic approach is motivated by a desire to give the case for plant cognition the most comprehensive and philosophically charitable assessment possible. While certain conclusions about plant capacities may appear implausible under specific theoretical frameworks, they may gain traction when examined through alternative lenses. As such, multiple paradigms are considered not with the aim of adjudicating between them, but in order to clarify the conceptual terrain and evaluate the robustness of plant cognition claims across competing perspectives.

The theoretical approaches engaged include representationalism, which treats cognition as fundamentally involving internal representations; enactivism, which emphasizes sensorimotor coupling and the role of embodied interaction with the environment; dynamical systems theory, which focuses on non-linear, time-evolving patterns of activity in coupled systems; and affective valence theory, which considers the motivational and evaluative dimensions of cognitive states. Although these paradigms sometimes diverge or even conflict in their assumptions, each offers conceptual resources for interpreting empirical phenomena and assessing whether cognitive categories may legitimately be applied to plants.

In the discussion of consciousness, the thesis does not treat any single theory as decisively correct, nor does it rest its case on detailed neurobiological models. Instead, it adopts a cautious and largely philosophical stance. The section argues that the science of consciousness remains incomplete and that the very term consciousness is ambiguous, often conflating a state of wakefulness with the presence of subjective experience. Here, the focus is on the latter - on sentience - and the section sketches what a principled case against plant sentience might look like. Rather than asserting that plants categorically cannot be sentient on the basis of their physiology, it examines why claims of plant sentience often conflate responsiveness with experience, and it highlights the need for conceptual clarity and caution in extending the notion of sentience beyond the contexts in which it has explanatory traction.

More broadly, the guiding perspective adopted throughout the thesis is an information-theoretic one. This orientation reflects the nature of the core question: whether plants, despite their radical architectural divergence from animals, can nonetheless instantiate the same functional and informational structures that underlie cognition. Since our concepts of cognition - spanning sensation, perception, memory, learning, and consciousness - are derived from human and animal models, assessing their applicability to plants requires asking whether plants carry out functionally equivalent operations. An information-theoretic lens allows for cross-system comparisons at the level of abstract process and structure, making it especially well-suited to evaluating claims of cognitive equivalence between organisms with vastly different biological substrates.

1.6 On the Avoidance of Definitions

A distinctive methodological feature of this thesis is its avoidance of definitional stipulation as a means of resolving contested questions. It is often assumed – particularly in interdisciplinary debates surrounding cognition – that conceptual clarity requires the introduction of precise definitions at the outset. For instance, one might be tempted to define "consciousness" before considering whether plants possess it, or to settle disputes about "memory" or "intelligence" by appealing to concise formulations. This thesis adopts a different strategy, following the approach advocated by Tyler Burge (2022),[3] who argues that in the philosophy of science, definitions properly belong at the end, not the beginning, of inquiry. Scientific and philosophical investigation aims not to legislate the meanings of terms in advance, but to understand the phenomena those terms aim to describe. Definitions, on this view, are summary formulations that codify the results of substantive inquiry; they should emerge from, not precede, the careful study of empirical and conceptual distinctions.

As Burge notes, the point is not to begin with semantic fiat but rather to investigate the relevant kinds and their properties, and only then arrive at a principled taxonomy. The same holds for cognitive categories. Instead of beginning with a definition of "memory," this thesis examines what is meant when memory is ascribed to plants (e.g., long-lasting epigenetic changes following environmental stimulation) and compares this with paradigmatic forms of memory in animals, which typically involve representational encoding, consolidation, and recall. In many cases, no definition is offered at all; instead, the focus remains on characterizing the phenomena in question and asking whether plants instantiate them in ways continuous with animals or in fundamentally different terms.

Indeed, much of the contemporary case for plant cognition relies on the vagueness or ambiguity of cognitive terms themselves. Concepts such as consciousness, memory, intelligence, learning, communication, agency, sense perception – each examined in the chapters that follow – frequently lack settled definitions, and in many cases this indeterminacy reflects genuine gaps in our understanding of the phenomena involved. The approach taken here is to examine how these terms function in cognitive science, particularly in their application to animals, and to ask whether the phenomena observed in plants are structurally or functionally continuous with those to which the terms ordinarily refer. As the subsequent analysis demonstrates, they typically are not.

The overarching aim of this thesis, once again in line with Burge's view, is to identify what he calls "joints in nature" – the real, empirically grounded distinctions that separate kinds of organisms and their characteristic capacities. The claim advanced here is that such a joint exists between creatures that possess cognition and those that do not. While the exact location of this boundary is difficult to identify and may be obscured by ambiguous or borderline cases, the evidence suggests that the emergence of nervous systems marks a critical inflection point in the evolution of cognition. Organisms like slime molds or plants may exhibit sophisticated forms of problem-

3 Burge, T. (2022). *Perception: First Form of Mind.* Oxford University Press.

solving or adaptive plasticity, but these are argued to be categorically distinct from the kinds of information processing found in animals with nervous systems.

This is not to say that terminological disputes are trivial. On the contrary, how terms are used can shape the trajectory of scientific research and the public understanding of biological phenomena. Nonetheless, the principal concern of this thesis is not to enforce linguistic prescriptions, but to track real distinctions in the natural world. If one chooses to apply the term “cognition” to plants, the more important question becomes whether this usage clarifies or obscures the phenomena in question. The argument developed here is that such usage is both scientifically and philosophically perilous, since it relies on analogical reasoning that elides significant differences in biological structure and function. But at its core, this thesis aims not to legislate language, but to respect the real contours of life by identifying where nature itself draws its boundaries.

1.7 Structure of the Thesis

The structure of this thesis is as follows. Section 2 addresses the concept of intelligence, arguing that while plants exhibit forms of adaptive problem-solving and environmental responsiveness, these should not be conflated with animal intelligence, which often involves associative learning and internal representational states. Section 3 turns to the concept of agency. It is maintained that plants do possess agency in a basic biological sense - an autonomy rooted in homeostasis, self-maintenance, and goal-directed behavior. However, more sophisticated forms of agency, such as intentional or moral agency, are absent in plants and should not be presumed on the basis of analogical reasoning.

Section 4 addresses claims about plant neurophysiology, contending that while plants exhibit bioelectrical signaling, they lack the organized, centralized, and functionally specialized nervous systems characteristic of animals. Assertions that plants have "neurons" or "brains" are shown to rest largely on metaphor and analogy rather than on empirical continuity. Section 5 examines the question of communication. It is argued that plants participate in dynamic ecological coupling with other organisms but do not engage in communication in the strict sense, which presupposes intentionality and the use of signals to influence others' mental states.

Section 6 turns to sense perception, distinguishing this from mere environmental responsiveness. It is argued that plants register information but that this falls short of sense perception, which requires representational and interpretive capacities not found in plants. Section 7 addresses the question of plant consciousness, or more precisely plant sentience. The section argues that claims attributing sentience to plants often conflate complex responsiveness with genuine experience, and that extending notions of consciousness to plants without a principled basis risks obscuring rather than clarifying the phenomena under discussion.

Finally, Section 8 concludes the thesis by recapitulating the main arguments and proposing directions for future research. Emphasis is placed on the importance of preserving conceptual

clarity in debates about cognition, and on the need for further interdisciplinary work in the philosophy of biology, cognitive science, and plant physiology.

2 Intelligence

2.1 Introduction: Clarifying the Question

Assessing the claim that plants possess intelligence is challenging in part because there exists no settled consensus within psychology or cognitive science concerning the nature of intelligence itself (Sternberg et al., 2011).[4] Even within the narrower confines of human cognition, intelligence has long resisted precise definition. Moreover, recent developments in cognitive science and psychometrics have increasingly moved away from the view that intelligence is a singular, unitary faculty. Instead, contemporary frameworks such as the Cattell-Horn-Carroll model (Schneider & McGrew, 2012),[5] the triarchic theory of Sternberg (1985),[6] and network-based theories of intelligence (Barbey, 2018)[7] emphasize the diversity and interdependence of distinct cognitive abilities.

When the scope of inquiry expands beyond the human species, the conceptual terrain becomes even more fraught. Darwin famously proposed a graded view of mental capacities across species, noting that "there is a much wider interval in mental power between one of the lowest fishes… and one of the higher apes, than between an ape and man," an interval he believed to be bridged by "numberless gradations" (Darwin, 1874).[8] While this represented a departure from earlier anthropocentric perspectives, it still presupposed a scale of mental powers anchored in human-like cognition - an approach that has increasingly been displaced in contemporary comparative cognition (de Waal, 1999).[9] Today, as in human cognitive research, investigations into non-human minds have largely abandoned the quest for a singular intelligence, focusing instead on delineating discrete cognitive capacities (Andrews & Monsó, 2021).[10]

Nonetheless, even if intelligence cannot be reduced to any single faculty, it remains a legitimate and important question to ask: What, if anything, unites the various abilities we associate with intelligence? Learning, memory, and anticipation of the future emerge as strong candidates. One might object that this shift merely substitutes one set of elusive concepts for another. While not unfounded, such an objection is mitigated by the fact that proponents of plant intelligence frequently cite plants' purported abilities to retain information about their environments and to adapt behavior accordingly (Gagliano et al., 2017; Trewavas, 2017).[11] Given the centrality of these claims, an analysis of plant learning, memory, and future anticipation is both relevant and necessary.

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4 Sternberg, R. J., Ackerman, P. L., Rjs, Mackintosh, N. J., Urbina, S., Willis, J. O., Davidson, J. E., Mandelman, S. D., Nickerson, R. S., Fagan, J. F., Rose, L. T., Hertzog, C., Hodapp, R. M., Feldman, D. H., Reis, S. M., Halpern, D. F., Suzuki, L. A., . . . Haier, R. J. (2011). The Cambridge Handbook of Intelligence. In *Cambridge University Press eBooks*. Cambridge University Press. https://doi.org/10.1017/cbo9780511977244

5 Schneider, W. J., & McGrew, K. S. (2012). The Cattell-Horn-Carroll model of intelligence. In D. P. Flanagan & P. L. Harrison (Eds.), *Contemporary intellectual assessment: Theories, tests, and issues* (3rd ed., pp. 99-144). The Guilford Press.

6 Sternberg, R. J. (1985). *Beyond IQ: A triarchic theory of human intelligence*. Cambridge University Press.

7 Barbey, A. K. (2017). Network Neuroscience Theory of Human Intelligence. *Trends in Cognitive Sciences, 22*(1), 8-20. https://doi.org/10.1016/j.tics.2017.10.001

8 Darwin, C. (1874). *The Descent of Man*.

9 de Waal, F. (1999). Anthropomorphism and anthropodenial: Consistency in our thinking about humans and other animals. *Philosophical Topics, 27*(1), 255-280.

2.2 Learning

This section examines the concept of learning in plants, progressing from simple forms of learning like habituation to the more complex associative learning. It argues that despite clever experiments attempting to demonstrate associative learning in plants, the empirical evidence currently does not support the presence of such learning. Further attempts to show associative learning in plants are likely to fail, as plants appear to lack the necessary structures and processes that underlie this capacity. The section also explores edge cases in evolutionary history, concluding that associative learning likely emerged with the development of nervous systems, highlighting the evolutionary divide between organisms with nervous systems and those without.

2.2.1 Behavioral Flexibility

Before turning to specific empirical claims, however, it is worth examining a broader conceptual proposal that surfaces in the literature on plant intelligence. In their 2015 article, "Conditions for minimal intelligence across eukaryota: A cognitive science perspective," Calvo and Baluška argue that consideration of plant environmental adaptiveness may "cast a new light on intelligence in general."[12] As a starting point, they suggest that intelligence consists in "sets of biological functions of organisms that exhibit a degree of flexibility against contingencies in their environment-induced behavioral repertoire." It remains ambiguous whether they intend to define intelligence as behavioral flexibility, or whether they merely take flexibility to be a salient indicator of intelligence. The stronger interpretation - equating intelligence with behavioral or cognitive-behavioral flexibility - has supporters in cognitive psychology (e.g., Birney & Beckmann, 2022).[13] Yet even the more modest view - that behavioral flexibility is at least a reliable marker of intelligence - faces difficulties upon closer scrutiny.

Calvo and Baluška offer a clarifying contrast when they urge us to "discard the hypothesis that the reaction of plants, animals, fungi or protists to environmental inputs is fully accounted for in terms of hard-wired instincts." By opposing flexibility to rigid instinctual behavior, they imply that flexibility involves an organism's capacity to select among multiple possible responses to a given stimulus, rather than being constrained to a singular, predetermined reaction. It is certainly the case that plant behavior exhibits a kind of flexibility: Plants may respond differently to the same stimulus depending on internal physiological states or environmental context. However, this raises

10 Andrews, Kristin and Susana Monsó, "Animal Cognition", The Stanford Encyclopedia of Philosophy (Spring 2021 Edition), Edward N. Zalta (ed.), URL = <https://plato.stanford.edu/archives/spr2021/entries/cognition-animal/>

11 Gagliano, M. (2017). The mind of plants: Thinking the unthinkable. *Communicative & Integrative Biology, 10*(2), e1288333. https://doi.org/10.1080/19420889.2017.1288333
Trewavas, A. (2017). The foundations of plant intelligence. *Interface Focus, 7*(3), 20160098. https://doi.org/10.1098/rsfs.2016.0098

12 Calvo, P., & Baluška, F. (2015). Conditions for minimal intelligence across eukaryota: A cognitive science perspective. *Frontiers in Psychology, 6*, 1329. https://doi.org/10.3389/fpsyg.2015.01329

13 Birney, D. P., & Beckmann, J. F. (2022). Intelligence IS Cognitive flexibility: Why Multilevel models of Within-Individual Processes are needed to realise this. *Journal of Intelligence, 10*(3), 49. https://doi.org/10.3390/jintelligence10030049

a crucial question – does this form of behavioral variability genuinely distinguish plant behavior from reflexive responses?

Reflex actions operate independently of the brain or higher-order cognitive processes, relying instead on localized circuits within the spinal cord (Kandel al., 2013).[14] Notably, such reflexes – including the patellar reflex – can undergo habituation (Hollis, 1971),[15] a form of plasticity that, like the reflex itself, occurs without the involvement of central cognitive systems. This observation is significant, as it reveals that even paradigmatically mindless behaviors exhibit a rudimentary form of flexibility. When Calvo and Balu$ka assert that plant behavior should not be classified as reflexive, their claim must extend beyond the simple observation that such behavior is subject to habituation. The mere fact that a behavior can habituate does not suffice to confer upon it a cognitive or intelligent character, as even spinal reflexes meet this criterion. Thus, if behavioral flexibility is to serve as a meaningful indicator of intelligence, it must involve capacities more robust than those implicated in reflex habituation alone.

This raises a deeper philosophical concern: What distinguishes mere behavioral plasticity from genuine cognition? Some have proposed that cognition requires representational content or the capacity for evaluative control over behavior (Godfrey-Smith, 2003; Burge, 2022).[16] Others, particularly those working in embodied or enactive frameworks, argue that cognition can be identified with sensorimotor patterns of interaction with the world (Clark & Chalmers, 1998; Lyon, 2005).[17] But even within these frameworks, concrete empirical support for imputing learning and memory to plants is required.

2.2.2 Simple Learning

In their 2014 study, "Experience teaches plants to learn faster and forget slower in environments where it matters," Gagliano et al. provide evidence for a complication in plant habituation responses. In their experiment, the researchers demonstrate that the leaf-closing behavior of *Mimosa pudica*, the sensitive plant, is subject to habituation – with an interesting complication related to environmental conditions. When subjected to repeated drops of water, *Mimosa pudica* plants initially closed their leaves – a typical defense mechanism. However, over time, they began to keep their leaves open, indicating habituation to the non-threatening stimulus. Remarkably, the habituated response persisted for at least 28 days, even when plants were transferred to different light conditions. This long-term retention indicates a form of memory in plants, allowing them to adapt their behavior based on past experiences. Furthermore, plants grown under low-light (LL) conditions, which are energetically more demanding, habituated more quickly and retained the learned behavior longer than those in high-light (HL) environments. This

14 Kandel, E. R. (2013). *Principles of Neural Science, Fifth Edition*. McGraw Hill Professional.

15 Hollis, J. H. (1971). Effects of stimulus frequency on habituation: patellar reflex. *Physiology & Behavior, 6*(4), 467-468. https://doi.org/10.1016/0031-9384(71)90187-9

16 Godfrey-Smith, P. (2003). *Theory and Reality: An Introduction to the Philosophy of Science*. University of Chicago Press.
Burge, T. (2022). *Perception: First Form of Mind*. Oxford University Press.

17 Clark, A., & Chalmers, D. (1998). The extended mind. *Analysis, 58*(1), 7-19. https://doi.org/10.1093/analys/58.1.7
Lyon, P. (2005). The biogenic approach to cognition. *Cognitive Processing, 7*(1), 11-29. https://doi.org/10.1007/s10339-005-0016-8

suggests that in energy-scarce settings, plants prioritize conserving energy by not responding to non-harmful stimuli (Gagliano, et al., 2014).[18]

While compelling, the results of this experiment do not resolve the concerns previously articulated regarding behavioral flexibility - specifically, the contention that habituation alone falls short of substantiating claims of intelligence. The results of the experiment demonstrate plant habituation is subject to complications and is modulated by environmental conditions, but the behavioral plasticity implicated by those results is still, at the end of the day, a form of habituation. Although habituation is acknowledged within the cognitive science literature as a basic form of learning, it remains categorically distinct from associative learning, which is more robustly associated with markers of intelligence and cognitive sophistication (Shettleworth, 2009; Domjan, 2014).[19]

2.2.3 Associative Learning

Associative learning - a form of adaptive behavior in which an organism modifies its responses based on the correlation between previously neutral stimuli and biologically significant outcomes - represents a major evolutionary innovation, enabling organisms to adapt far more flexibly to changing environments. Associative learning has long been recognized as a marker of intelligence in animals and has even been suggested to be foundational to intelligence generally (Morand-Ferron, 2017; Enquist, et al., 2016; Heyes, 2012).[20] Unlike non-associative forms of learning such as habituation, associative learning allows animals to predict and respond to complex patterns, enhancing survival and reproductive success. Some theorists have even argued that its emergence has played a crucial role in behavioral diversification and ecological expansion, and may have been a key driver of evolutionary events such as the Cambrian explosion (Ginsburg & Jablonka, 2010).[21]

Discovering that plants are capable of associative learning would be remarkable because it would challenge deeply rooted assumptions about the prerequisites for complex learning - namely, the presence of a nervous system. Associative learning involves forming predictive relationships between stimuli, a cognitive capacity traditionally attributed to animals with centralized brains. If plants, lacking neurons and synapses, could nonetheless exhibit this form of learning, it would not only expand our understanding of intelligence and cognition but also prompt reevaluation of how learning can arise in biological systems, as well as indicate that associative learning emerged in the far more distant evolutionary past than has been typically assumed.

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18 Gagliano, M., Renton, M., Depczynski, M., & Mancuso, S. (2014). Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia, 175*(1), 63-72. https://doi.org/10.1007/s00442-013-2873-7

19 Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*. Oxford University Press.
Domjan, M. P. (2014). *The principles of learning and behavior*. Cengage Learning.

20 Morand-Ferron, J. (2017). Why learn? The adaptive value of associative learning in wild populations. *Current Opinion in Behavioral Sciences, 16*, 73-79. https://doi.org/10.1016/j.cobeha.2017.03.008
Enquist, M., Lind, J., & Ghirlanda, S. (2016). The power of associative learning and the ontogeny of optimal behaviour. *Royal Society Open Science, 3*(11), 160734. https://doi.org/10.1098/rsos.160734
Heyes C. (2012). Simple minds: a qualified defence of associative learning. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 367*(1603), 2695-2703. https://doi.org/10.1098/rstb.2012.0217

21 Ginsburg, S., & Jablonka, E. (2010). The evolution of associative learning: A factor in the Cambrian explosion. *Journal of Theoretical Biology, 266*(1), 11-20. https://doi.org/10.1016/j.jtbi.2010.06.017

2.2.4 Associative Learning in Plants – Current Status of Empirical Evidence

In their 2016 study, Gagliano et al.[22] claim to provide compelling evidence that associative learning – a cognitive process long thought to be exclusive to animals – is also present in plants. Using *Pisum sativum* in a Y-maze apparatus, they demonstrate that plants can form predictive associations between a previously neutral cue (a fan) and a light stimulus, subsequently directing their growth based on the learned association rather than innate phototropic responses. The experimenters trained plants by pairing (fan-generated) wind and light from either the same direction or from opposite directions. When the plants reached a stage where they had to "choose" between two paths, they were exposed only to wind, with no accompanying light. The results showed that wind alone influenced the direction of growth in trained plants: Those trained with wind and light from the same direction grew toward the wind, while those trained with wind and light from opposite directions grew away from it. In contrast, untrained plants showed no consistent pattern and chose directions at random. Interestingly, this learning occurred only when training coincided with the plant's subjective day, implicating a circadian modulation of learning ability.

22 Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. *Scientific Reports, 6*(1). https://doi.org/10.1038/srep38427

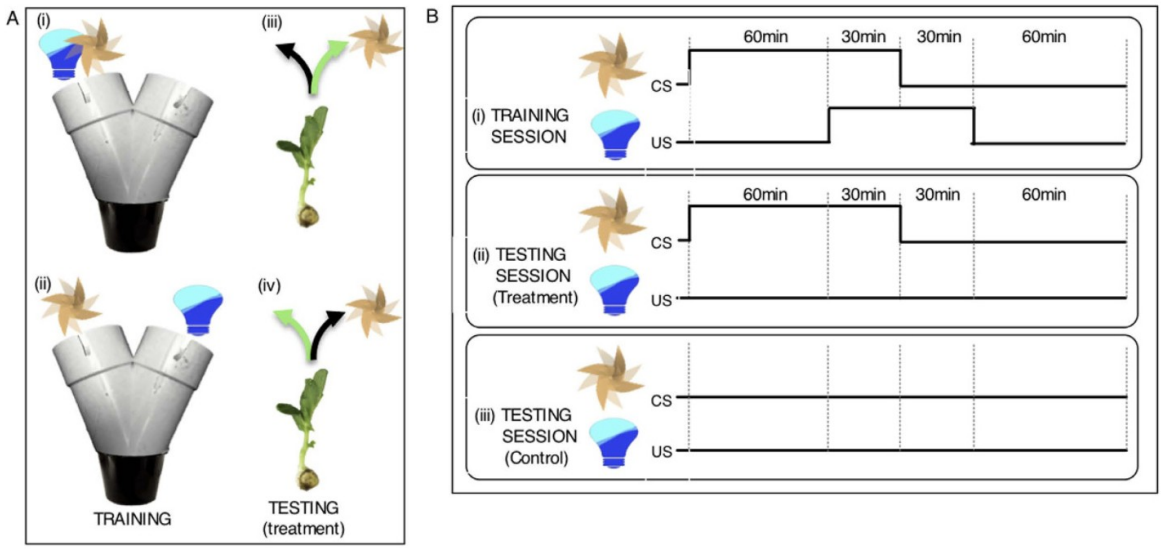

Figure 1. Training and testing protocol for associative learning in pea seedlings. (**A**) During training seedlings were exposed to the fan [F] and light [L] on either the same arm (i) or on the opposite arm (ii) of the Y-maze. The fan served as the conditioned stimulus (CS), light as the unconditioned stimulus (US). During testing with exposure to the fan alone two categories of responses were distinguished. *Correct response*: Seedlings growing into the arm of the maze where the light was "predicted" by the fan to occur [green arrow; iii (corresponding to scenario i) and iv (corresponding to scenario ii)]; *Incorrect response:* Seedlings growing into the arm of the maze where the light was not "predicted" by the fan to occur (black arrow; iii and iv). (**B**) Seedlings received training for three consecutive days before testing. Each training day consisted of three 2-h training sessions separated by 1-h intervals. The 90-min CS preceded the 60-min US by 60 minutes so that there was a 30-min overlap. (i). During the 1-day testing session, seedlings were exposed to the fan alone for three 90-min sessions (ii). Seedlings of the control group were left undisturbed (no fan, no light; iii).

Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. *ScientificReports*, *6*(1). https://doi.org/10.1038/srep38427

Unfortunately, the reproducibility of this study by Gagliano et al. has been challenged by subsequent research. Notably, a 2020 replication attempt by Kasey Markel failed to observe the same associative learning behavior, even when employing a larger sample size and a fully blinded analysis (Markel, 2020).[23] Markel's study suggested that the original findings might have been influenced by specific experimental conditions or uncontrolled variables.

In response, Gagliano and colleagues contended that Markel's replication did not accurately replicate the original conditions, particularly regarding the experimental setup, and therefore could not conclusively refute their findings (Markel, 2020).[24] Further discussions in the scientific community have highlighted the need for more rigorous documentation of experimental parameters, such as light quality and plant growth conditions, to ensure reproducibility in studies of plant learning (Cvrčková & Konrádová, 2021).[25]

23 Markel, K. (2020). Lack of evidence for associative learning in pea plants. *eLife, 9*. https://doi.org/10.7554/elife.57614
24 Markel, K. (2020). Response to comment on "Lack of evidence for associative learning in pea plants." *eLife, 9*. https://doi.org/10.7554/elife.61689
25 Cvrčková, F., & Konrádová, H. (2021). Associative learning in plants: light quality history may matter. *Biocell, 46*(3), 645-649. https://doi.org/10.32604/biocell.2022.018114

Additionally, a case study published in 2023 identified multiple challenges in replicating the original experiment, ranging from seedling germination to apparatus design, underscoring the complexity of reproducing such behavioral studies in plants (Ponkshe et al., 2023).[26] Thus, at present, there is no definitive evidence establishing that plants possess the capacity for associative learning.

2.2.5 Associative Learning - Edge Cases

In spite of current lack of empirical evidence to support a capacity for associative learning in plants, to what extent is it theoretically plausible to think plants possess the necessary physiological architecture to support a capacity for associative learning? It is enlightening to consider some border cases in which associative learning has been claimed to have been demonstrated in creatures possessing decentralized nervous systems - or no nervous system at all.

2.2.5.1 The Box Jellyfish

In a 2023 experiment, Bielecki et al. placed individual box jellyfish in one of three tanks, each differing in wall patterning. One tank featured high-contrast vertical stripes, designed to simulate the visual characteristics of mangrove roots - the natural habitat of these organisms. A second tank displayed low-contrast stripes, while a third had unpatterned, blank walls. In the tank with high-contrast stripes, the jellyfish consistently avoided collisions with the walls. In the blank-walled tank, by contrast, they frequently collided with the boundaries. Notably, in the low-contrast condition, the jellyfish initially exhibited collision behavior similar to that seen in the blank tank; however, over time, they adjusted their movements to avoid the walls. This adaptive shift suggests a rudimentary form of associative learning (Bielecki et al., 2023).[27]

26 Ponkshe, A., Barroso, J. B., Abramson, C. I., & Calvo, P. (2023). A case study of learning in plants: Lessons learned from pea plants. *Quarterly Journal of Experimental Psychology, 77*(6), 1272-1280. https://doi.org/10.1177/17470218231203078

27 Bielecki, J., Nielsen, S. K. D., Nachman, G., & Garm, A. (2023). Associative learning in the box jellyfish Tripedalia cystophora. *Current Biology, 33*(19), 4150-4159.e5. https://doi.org/10.1016/j.cub.2023.08.056

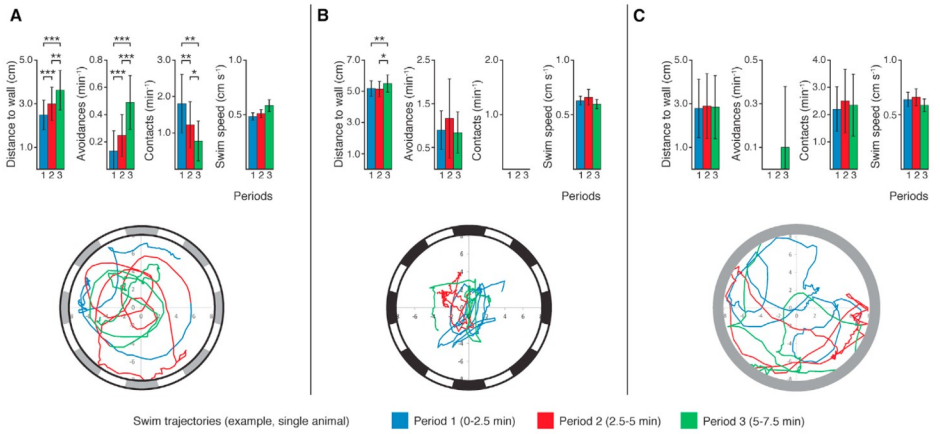

Figure 2. Behavioral evidence of associative learning, operant conditioning, in the box jellyfish *Tripedalia cystophora*

(A) When presented with gray obstacles of a contrast below initial response threshold ($c = 0.39$), the jellyfish initially swam along the arena wall as seen by the trajectory. This provided both visual (gray obstacles) and mechanical (wall contacts) stimuli. Within the 7.5 min trial period, the jellyfish learned to significantly increase the distance to the arena wall and the frequency of avoidances. Importantly, they also more than halved their contacts with the wall. These results suggest associative learning (operant conditioning) in *T. cystophora* by combining visual and mechanical stimuli.

(B) Presenting the naive jellyfish with high-contrast black obstacles ($c = 0.93$) centered them in the behavioral arena and resulted in a complete lack of collisions with the perimeter wall throughout the trial period. Furthermore, this lack of mechanical aversive stimulation resulted in a constant frequency of avoidances but also in a small (~6%), though significant, increase in the average distance to the obstacles. These results show that learning did not take place with visual stimulation alone.

(C) In the experiments without visual contrast (uniform gray wall), the jellyfish in general failed to perform avoidances and spent most of the time swimming along the arena wall with a high frequency of collisions. This setup with only the aversive mechanical stimulation did not lead to learning, as seen by the lack of significant changes in any of the observed behavioral parameters. Note that for all three visual scenarios the medusae kept the same average swim speed (activity level) through the three periods (Period 1: 0–2.5 min, Period 2: 2.5–5 min, and Period 3: 5–7.5 min; Tables 1 and 2). Asterisks denote levels of significance (*$p < 0.05$, **$p < 0.001$, and ***$p < 0.0001$). Error bars ±SE.

Bielecki, J., Nielsen, S. K. D., Nachman, G., & Garm, A. (2023). Associative learning in the box jellyfish Tripedalia cystophora. *Current Biology, 33*(19), 4150–4159.e5. https://doi.org/10.1016/j.cub.2023.08.056

Unlike organisms with centralized brains, the box jellyfish (class Cubozoa) possesses a decentralized nervous system organized around a ring nerve and a set of specialized sensory structures known as rhopalia. Each rhopalium contains a complex assemblage of sensory organs, including lens-bearing eyes capable of image formation. These structures are embedded within a neural network that supports the integration of visual input with motor output, enabling the animal to perform context-sensitive navigation and obstacle avoidance.

Following the tank-based behavioral trials, the researchers conducted ex vivo experiments to investigate the locus of learning within the box jellyfish. Rhopalia were surgically excised and fitted with electrodes at their tactile sensory input regions. Mild electrical stimuli - intended to simulate the sensory experience of collision - were paired with visual cues presented to the rhopalial eyes. In response, the rhopalia generated motor output signals consistent with object-avoidance behavior. Over repeated pairings, the isolated rhopalia began to generate motor output signals in response to the visual stimulus alone, in the absence of any accompanying shock. This anticipatory motor activation suggests that the rhopalia had acquired an association between the visual cue and the simulated collision, effectively demonstrating a form of associative learning localized within these structures. While the precise mechanisms by which the rhopalia encode and retrieve such associations remain unresolved, the findings compellingly indicate that learning in box jellyfish can occur independently of a conventional brain.

At first glance, the box jellyfish, with its decentralized nervous system, might appear to challenge the notion that centralization is necessary for associative learning. However, a closer examination

reveals a more nuanced picture. While it is true that the box jellyfish lacks a single centralized brain, each of its rhopalia functions as a discrete integrative center - effectively, a kind of localized "mini-brain." Empirical findings from the experiment discussed above indicate that associative learning is localized within these rhopalia. Thus, rather than serving as a counterexample to the necessity of central processing, the case of the box jellyfish may in fact reinforce the idea that associative learning requires some form of centralized neural integration.

2.2.5.2 The Brittle Star

The Brittle star (*Ophiocoma echinata*) presents another interesting case. In a 2023 experiment by Notar, et al.,[28] the Brittle star, a marine invertebrate lacking a centralized brain but possessing a decentralized nerve ring and radial nerve cords, was shown to be capable of associative learning. The experiment employed a classical conditioning paradigm in which food delivery was paired with the dimming of light. Eventually, the brittle stars began to emerge from concealment in response to light dimming alone, demonstrating that they had learned to associate a neutral cue with a biologically salient outcome.

The brittle star's nervous system exemplifies a radically decentralized architecture, composed of a circumoral nerve ring encircling the mouth and five radial nerve cords extending into each arm, enabling coordinated locomotion and sensory integration without a central brain (Clark et al., 2019; Zueva et al., 2018)[29]. This system operates through distributed control, where coordination emerges via signal propagation through the nerve ring, allowing the selection of a leading arm and the organization of complex, context-dependent locomotor behaviors (Matsuzaka et al., 2017).[30] In contrast, the box jellyfish possesses discrete sensory hubs called rhopalia, each containing statocysts and image-forming eyes, as well as neural ganglia that pre-process visual and balance information, effectively localizing sensory-motor integration within modular units (Garm et al., 2007).[31] No comparable organ exists in the brittle star; while recent work has suggested the presence of ganglion-like structures within its radial nerve cords (Zueva et al., 2018),[32] these lack the multimodal sensory and integrative functionality characteristic of rhopalia. Brittle stars rely instead on diffuse sensory input and local processing, including dermal photoreceptors that mediate visually guided behaviors without centralized or modularized sensory centers (Sumner-Rooney et al., 2020).[33]

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28 Notar, J. C., Go, M. C., & Johnsen, S. (2023). Learning without a brain: classical conditioning in the ophiuroid Ophiocoma echinata. *Behavioral Ecology and Sociobiology, 77*(11). https://doi.org/10.1007/s00265-023-03402-x

29 Clark, E. G., Kanauchi, D., Kano, T., Aonuma, H., Briggs, D. E. G., & Ishiguro, A. (2019). The function of the ophiuroid nerve ring: how a decentralized nervous system controls coordinated locomotion. *Journal of Experimental Biology, 222*(2). https://doi.org/10.1242/jeb.192104 Zueva, O., Khoury, M., Heinzeller, T., Mashanova, D., & Mashanov, V. (2018). The complex simplicity of the brittle star nervous system. *Frontiers in Zoology, 15*(1). https://doi.org/10.1186/s12983-017-0247-4

30 Matsuzaka, Y., Sato, E., Kano, T., Aonuma, H., & Ishiguro, A. (2017). Non-centralized and functionally localized nervous system of ophiuroids: evidence from topical anesthetic experiments. *Biology Open, 6*(4), 425-438. https://doi.org/10.1242/bio.019836

31 Garm, A., O'Connor, M., Parkefelt, L., & Nilsson, D. (2007). Visually guided obstacle avoidance in the box jellyfish Tripedalia cystophora and Chiropsella bronzie. *Journal of Experimental Biology, 210*(20), 3616-3623. https://doi.org/10.1242/jeb.004044

32 Zueva, O., Khoury, M., Heinzeller, T., Mashanova, D., & Mashanov, V. (2018). The complex simplicity of the brittle star nervous system. *Frontiers in Zoology, 15*(1). https://doi.org/10.1186/s12983-017-0247-4

33 Sumner-Rooney, L., Kirwan, J. D., Lowe, E., & Ullrich-Lüter, E. (2020). Extraocular vision in a brittle star is mediated by chromatophore movement in response to ambient light. *Current Biology, 30*(2), 319-327.e4. https://doi.org/10.1016/j.cub.2019.11.042

While the brittle star constitutes a potential example of associative learning in an organism with a distributed nervous system, closer scrutiny suggests that it does not, in fact, challenge the view that some form of organized neural architecture is required for such learning. Though the brittle star lacks a centralized brain, its nervous system is not a simple diffuse nerve net but a secondarily reduced and highly structured system, comprising radial nerve cords and a circumoral nerve ring. The organization of this system remains poorly understood, but it is nonetheless clear that it exhibits a degree of integration and coordination far beyond what is found in non-neural organisms such as slime molds.

Importantly, the existing evidence does not support the claim that associative learning in the brittle star is achieved without the mediation of neural circuitry. On the contrary, to the extent that this capacity is present, it appears to depend on the functional dynamics of its decentralized but highly organized nervous system. While further empirical work is needed to clarify the underlying mechanisms, the case of the brittle star does not provide evidence against the necessity of nervous systems for associative learning. Rather than undermining the link between nervous systems and associative learning, it reaffirms the importance of neural organization – however unconventional its form may be.

2.2.5.3 The Slime Mold

The case of the brittle star may represent an instance of associative learning mediated by a distributed nervous system. But what are we to make of organisms that lack a nervous system altogether? A recent study has claimed to demonstrate associative learning in slime molds – a striking and provocative conclusion. However, closer scrutiny of the experimental design and interpretation invites skepticism as to whether such a conclusion is fully warranted. In the interest of exploring the plausibility and character of associative learning in non-neural organisms, it is worth examining the case of the slime mold in greater detail.

In their 2021 study, "Encoding memory in tube diameter hierarchy of living flow network," published in Proceedings of the National Academy of Sciences, Mirna Kramar and Karen Alim[34] investigate how the slime mold *Physarum polycephalum*, a unicellular organism lacking a nervous system, encodes memory through structural changes in its network-like body. The researchers observed that upon encountering a nutrient source, *P. polycephalum* undergoes a reorganization of its tubular network: Tubes proximal to the nutrient source increase in diameter, while others constrict. This alteration in the hierarchy of tube diameters effectively imprints the location of the nutrient source within the organism's morphology. Notably, this structural memory persists beyond the immediate response, influencing future migration decisions by directing cytoplasmic flow toward previously beneficial areas.

The underlying mechanism involves the release of a chemical softening agent at the site of the nutrient, which is transported through the organism's cytoplasmic flow. This agent causes local

34 Kramar, M., & Alim, K. (2021). Encoding memory in tube diameter hierarchy of living flow network. *Proceedings of the National Academy of Sciences, 118*(10). https://doi.org/10.1073/pnas.2007815118

softening and expansion of the tube walls near the nutrient source, while tubes receiving less of the agent shrink due to conservation of volume. Through theoretical modeling and experimental validation, the authors claim to show that this enables *P. polycephalum* to "store and retrieve" information about its environment, which they further claim constitutes a form of "associative memory" without the need for a nervous system (Kramar & Alim 2021).[35]

In his 2021 commentary on Kramar and Alim's study, physicist Robert H. Austin (2021)[36] adopts a cautiously skeptical stance toward the claim that slime molds exhibit memory and associative learning. While acknowledging the elegance and ingenuity of the research, Austin questions whether the behavior observed should be construed as "memory" in any strong or cognitive sense.

He points out that the term "memory" carries conceptual baggage from neuroscience and psychology, and warns against anthropomorphizing or overinterpreting behavior in simple organisms. For Austin, what is being observed may be better understood as a kind of "mechanical hysteresis" – a passive, physical response of a dynamic system to prior inputs – rather than evidence of information encoding in any functional or representational sense akin to memory in animals. Austin further implies that there is a risk in drawing sweeping conclusions about cognition or intelligence from such findings. He underscores the importance of distinguishing between emergent physical properties of a living system and processes that genuinely warrant cognitive attribution. In doing so, he urges the scientific community to remain careful in its terminology and resist the temptation to project higher-level mental functions onto non-neural organisms without rigorous justification.

Austin's careful distinction between mechanical hysteresis and genuine instances of memory or associative learning offers a valuable conceptual clarification. A closer examination of the slime mold's behavior reveals substantive difficulties in interpreting it as a case of associative learning or memory in any robust sense.

To begin with, the application of the term "associative memory" in this context appears to be unwarranted. Associative learning, as traditionally understood, involves the formation of a connection between two or more discrete stimuli – such as in classical conditioning paradigms where a neutral stimulus comes to predict a biologically significant one. In the slime mold case, however, what is observed is a persistent structural modification in response to a single stimulus – the presence of a nutrient gradient. There is no evidence that the organism associates this stimulus with any second, distinct cue. Consequently, the behavior in question lacks the relational component that is central to associative learning.

As for memory, Austin's suggestion that the attribution of memory to slime molds may be more metaphorical or anthropomorphic than literal is a caution worth taking seriously. This reservation will become particularly salient in the ensuing discussion of purported memory phenomena in plants, where similar concerns about conceptual overreach arise.

35 Ibid.

36 Austin, R. H. (2021). A slime mold's remembrance of things past. *Proceedings of the National Academy of Sciences, 118*(14). https://doi.org/10.1073/pnas.2102056118

2.2.6 A Hypothesis About Associative Learning

Where does this leave us? The available evidence indicates that organisms with minimal nervous systems – such as the box jellyfish and the brittle star – exhibit behaviors consistent with associative learning. In contrast, the slime mold, despite its remarkable capacity for goal-directed behavior and problem-solving in the absence of any nervous system, does not convincingly display such learning. This contrast suggests a natural discontinuity: A possible boundary marked by the emergence of nervous systems, with associative learning appearing only on one side of this divide.

A hypothesis emerges: it may be that nervous systems evolved, at least in part, to enable associative learning, serving as the minimal substrate required for such cognitive capacities. In favor of the hypothesis that nervous systems originated – at least in part – to support associative learning, consider what associative learning provides the organisms endowed with it: through associative learning, these organisms are able to detect and respond to complex, non-linear patterns in their environments. This capacity for learning associations – such as correlations between sensory cues and outcomes – offers a powerful mechanism for inferring relevance in dynamic and unpredictable contexts. For motile animals, whose environments vary spatially and temporally as a function of movement, such inferential capacities confer a distinct adaptive advantage: They enable flexible, context-sensitive behavior beyond reflexive or hard-wired responses. In contrast, sessile organisms like plants inhabit relatively stable microenvironments and can rely more heavily on genetically encoded developmental strategies for coping with environmental regularities. Thus, the emergence of the nervous system may be best understood not merely as a means of coordinating movement or processing sensory input, but as a substrate for real-time, experience-dependent updating of behavioral relevance – a function that supports the informational demands of life on the move.

2.3 Memory

This section reviews the purported empirical evidence for memory in plants and critically analyzes the empirical findings to determine how best to conceptualize plant memory, distinguishing it from the types of memory found in animals.

2.3.1 Empirical Evidence for Memory in Plants

This section explores the empirical evidence for four kinds of memory in plants – vernalization memory, stress memory, immune memory, and circadian memory – and examines the biological processes that underpin them.

2.3.1.1 Vernalization Memory

In "Vernalization, Competence, and the Epigenetic Memory of Winter," Richard Amasino (2004)[37] investigates how certain plants perceive, respond to, and remember prolonged cold exposure – a process known as vernalization – in order to ensure that flowering occurs at an appropriate time, typically in spring. Focusing on the model organism *Arabidopsis thaliana*, Amasino outlines the central role of the gene FLOWERING LOCUS C (FLC), a potent repressor of flowering. In non-vernalized plants, FLC is highly expressed and actively suppresses the transition to flowering. Vernalization leads to the repression of FLC, and this repression is maintained even after the return of warmer conditions, enabling flowering to proceed.

Crucially, this repression is not transient but persists through mitotic cell divisions, constituting a form of cellular memory. Amasino explains that this memory is epigenetically mediated – meaning it is encoded through chromatin-level modifications rather than changes in DNA sequence. Specifically, the vernalization process involves histone modifications, such as acetylation of histone H3 (H3K27) and increased methylation of H3K9 and H3K27, which alter the chromatin structure at the FLC locus to a more condensed, transcriptionally silent state. These changes are brought about by the Polycomb Repressive Complex 2 (PRC2) (Nielsen, et al., 2024),[38] which plays a key role in stable gene silencing across eukaryotes (Vijayanathan, et al., 2022).[39]

Another important concept introduced is the idea of competence – the developmental state in which a plant is able to respond to vernalization. Not all tissues or developmental stages are competent to acquire the vernalized state. Thus, vernalization is a temporally regulated and context-sensitive process, integrating developmental stage and environmental cues.

Amasino's work emphasizes that this epigenetic "memory of winter" is reset in each generation. The silenced state of FLC is not transmitted through meiosis, ensuring that each new generation must experience cold to become competent to flower. This dynamic regulatory system enables plants to align reproductive development with seasonal changes, avoiding premature flowering during brief warm spells in autumn or winter.

2.3.1.2 Stress Memory

In "Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics," Crisp et al. (2016) critically re-evaluate the assumption that memory is a pervasive feature of plant stress responses, also using *Arabidopsis* as a primary model system. They argue that while *Arabidopsis* can exhibit molecular and epigenetic signatures of prior stress – such as heat or drought – these instances of memory are relatively rare and often transient. The recovery phase following stress exposure is shown to be a decisive period during which *Arabidopsis* may

37 Amasino, R. (2004). Vernalization, competence, and the epigenetic memory of winter. *The Plant Cell, 16*(10), 2553-2559. https://doi.org/10.1105/tpc.104.161070

38 Nielsen, M., Menon, G., Zhao, Y., Mateo-Bonmati, E., Wolff, P., Zhou, S., Howard, M., & Dean, C. (2024). COOLAIR and PRC2 function in parallel to silence FLC during vernalization. *Proceedings of the National Academy of Sciences, 121*(4). https://doi.org/10.1073/pnas.2311474121

39 Vijayanathan, M., Trejo-Arellano, M. G., & Mozgová, I. (2022). Polycomb Repressive Complex 2 in Eukaryotes—An Evolutionary Perspective. *Epigenomes, 6*(1), 3. https://doi.org/10.3390/epigenomes6010003

either retain stress-induced epigenetic marks, such as histone modifications and DNA methylation, or engage RNA turnover mechanisms that facilitate transcriptomic resetting. The authors emphasize that in *Arabidopsis*, as in other plants, memory formation imposes metabolic costs that can compromise growth and reproduction, and thus may be selectively disadvantageous in fluctuating environments. This leads to the central thesis: That forgetfulness, rather than memory, is often the adaptive default in *Arabidopsis*, underscoring the importance of stress recovery and regulatory reversibility in plant resilience (Crisp, et al., 2016).[40]

Meanwhile, in their comprehensive review, "Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants," Lämke and Bäurle (2017) elucidate the intricate role of chromatin dynamics in mediating plant responses to environmental stressors. Focusing on *Arabidopsis*, they highlight how specific histone modifications, notably H3K4me3, and changes in nucleosome occupancy contribute to somatic stress memory, enabling plants to mount more robust responses upon re-exposure to stress. For instance, genes like RD29B and P5CS1 exhibit enhanced re-induction following dehydration and salt stress, correlating with sustained H3K4me3 enrichment. The authors also discuss the role of transcription factors such as HY5 in integrating environmental signals, like light, into stress memory pathways. Beyond somatic memory, the review explores intergenerational and transgenerational inheritance of stress responses, suggesting that epigenetic mechanisms, including DNA methylation and small RNA pathways, may transmit stress memory to progeny, albeit with varying stability. The authors underscore the adaptive significance of these mechanisms, proposing that while stress memory can confer advantages in recurring stress conditions, the associated metabolic costs necessitate a balance between memory maintenance and resetting (Lämke & Bäurle, 2017).[41]

2.3.1.3 Immune Memory

In his 2011 review, "Molecular aspects of defence priming," Uwe Conrath synthesizes emerging insights into the molecular underpinnings of priming in plant immunity, also using *Arabidopsis* as a model organism. Priming refers to a physiological state wherein plants, upon exposure to specific stimuli - such as pathogen-associated molecular patterns, beneficial microbes, or certain chemical agents - exhibit an enhanced capacity for rapid and robust activation of defense mechanisms upon subsequent stress encounters. Conrath elucidates that this primed state is characterized by the accumulation of inactive mitogen-activated protein kinases (MAPKs), chromatin modifications, and alterations in primary metabolism. These molecular changes do not directly activate defense responses but instead sensitize the plant, enabling a more efficient and potent reaction to future stressors. The review underscores the significance of these mechanisms in conferring immunity and stress tolerance (Conrath, 2011).[42]

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40 Crisp, P. A., Ganguly, D., Eichten, S. R., Borevitz, J. O., & Pogson, B. J. (2016). Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics. *Science Advances, 2*(2). https://doi.org/10.1126/sciadv.1501340

41 Lämke, J., & Bäurle, I. (2017). Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology, 18*(1). https://doi.org/10.1186/s13059-017-1263-6

42 Conrath, U. (2011). Molecular aspects of defence priming. *Trends in Plant Science, 16*(10), 524-531. https://doi.org/10.1016/j.tplants.2011.06.004

2.3.1.4 Circadian Memory

In addition to vernalization memory, stress memory, and immune memory, empirical research has demonstrated that plants possess circadian memory. In their investigation of circadian regulation in *Arabidopsis*, Boikoglou et al. (2011) elucidate the differential integration of photic and thermal cues by the plant's endogenous oscillator, revealing a form of environmental memory that modulates circadian periodicity. Utilizing a recombinant inbred line (RIL) population and a suite of natural accessions, the study demonstrates that prior entrainment conditions - light-dark cycles versus temperature fluctuations - exert lasting effects on the free-running period of circadian rhythms, with thermal entrainment generally resulting in shorter periods compared to photic entrainment. Quantitative trait locus (QTL) mapping identifies distinct genetic loci associated with responses to each *zeitgeber* (an environmental cue, usually photic or thermal), including loci on chromosomes 1 and 5, suggesting partially separable genetic architectures for light and temperature entrainment pathways. Notably, the study uncovers genotype-by-environment interactions and epistatic relationships between QTLs, indicating complex genetic underpinnings for the observed phenotypic plasticity. These findings show how plants integrate multiple environmental signals to fine-tune circadian rhythms, underscoring the role of circadian memory as a dynamic regulatory mechanism through which prior environmental conditions shape current oscillator behavior and thereby modulate adaptive temporal responses (Boikoglou, et al., 2011).[43]

2.3.2 How to Conceptualize Plant Memory

This section explores the distinction between plant memory and memory in animals, emphasizing the non-semantic, adaptive nature of plant memory and the challenges of labeling these processes as "memory" in the traditional sense.

2.3.2.1 The Physiological Basis of Plant Memory

As outlined above, plants exhibit at least four distinct forms of memory - vernalization memory, stress memory, immune memory, and circadian memory. These processes, while legitimately mnemonic in that prior states leave stable, causally efficacious traces influencing subsequent responses, are realized not through neural substrates but through enduring physiological and epigenetic modifications. The mere fact that such traces influence future behavior does not, however, settle the question of whether they are genuinely comparable to the memory systems found in neural organisms. To frame the issue, consider that the annual rings of a tree record environmental history in a way that can be retrospectively “read” to reconstruct aspects of the organism’s past. Yet a similar reconstruction is possible with geological strata, sediment layers, or glacial ice cores, where no one seriously proposes that such formations possess memory in any cognitive sense. The key philosophical question is thus whether plant mnemonic processes should be analogized to the content-rich, representational memory characteristic of nervous systems, or instead to the environmentally induced, structurally embodied traces found in non-living systems -

43 Boikoglou, E., Ma, Z., Von Korff, M., Davis, A. M., Nagy, F., & Davis, S. J. (2011). Environmental Memory from a Circadian Oscillator: The Arabidopsis thaliana Clock Differentially Integrates Perception of Photic vs. Thermal Entrainment. *Genetics, 189*(2), 655-664. https://doi.org/10.1534/genetics.111.131417

persistent records of past events that, while causally potent, lack any intrinsic connection to cognition.

2.3.2.2 Truth vs. Adaptive Value: A Crucial Difference Between Plant and Animal Memory

While it may be reasonable to characterize the stable physiological and epigenetic modifications observed in plants as forms of memory, it is essential to clarify that such memory is categorically distinct from certain kinds of memory enabled by nervous systems. One of the most salient differences lies in the absence of semantic content in plant memory. In organisms with nervous systems, memory often involves the encoding, storage, and retrieval of information that represents features of the world - events, objects, or states of affairs - and thus can be evaluated for truth or accuracy. Such representational or content-laden memory plays a crucial role in belief formation, decision-making, and behavior guided by inference or intentionality. By contrast, the memory capacities observed in plants - while functionally significant - appear to operate without the mediation of representations that refer to or stand in for external states of affairs. Rather, they involve mechanistic adjustments to internal states based on prior exposure to environmental conditions, changes that persist over time and influence future responsiveness. As such, these memory processes are best understood as non-semantic or non-representational - they encode causal regularities, not propositional content, and their efficacy is judged not by truth but by functional adequacy or adaptive value.

To underscore the issue, consider the following question: Can a plant misremember? One might argue that plants can be led to form inaccurate “memories” under experimental conditions - say, by exposing them to artificially cold environments that induce a physiological state resembling a “memory of winter,” despite the absence of actual seasonal change. But how tenable is this analogy? In organisms with nervous systems, evaluating the accuracy of semantic memory involves assessing whether there exists an isomorphic relationship between the organism’s internal representations and its past experiences. In contrast, when considering memory-like phenomena in plants, such as epigenetic or physiological modifications, the notion of representational accuracy becomes inapplicable. These changes do not function as representational states that can be true or false with respect to past events, but rather as causal outcomes of specific environmental triggers. The distinction lies in the nature of what is being assessed - representational fidelity in one case versus causal regularity in the other.

2.3.2.3 Is "Memory" in Plants Merely Metaphorical?

Indeed, one might object that a characterization of plant processes as “memory” is metaphorical at best and misleading at worst. On this view, memory is inherently tied to the conscious recollection or symbolic representation found in animals with nervous systems. Thus, while plants may undergo physiological changes in response to environmental stimuli, describing these changes as memory appears to project cognitive capacities onto organisms that lack the requisite biological infrastructure.

This concern is not without precedent. Historically, the concept of memory has been closely associated with introspective access, deliberative retrieval, and symbolic representation (Tulving, 1972; Squire, 2004).[44] However, cognitive science has increasingly embraced a functionalist and mechanistic conception of memory, defined not by its subjective qualities but by its causal role in retaining and utilizing information over time. For instance, procedural memory – as in skill acquisition – operates independently of conscious awareness (Doyon et al., 2008),[45] and immunological memory describes the long-term adaptation of immune responses to previously encountered pathogens (Murphy & Weaver 2016).[46] Neither case involves representation in the traditional, content-bearing sense, yet both are widely recognized as legitimate forms of memory.

In this light, plant memory – as described in the biological literature – meets the functional criteria for memory: it involves the encoding of past environmental conditions via durable epigenetic or physiological changes, and these changes modulate future responses in context-sensitive ways (Crisp et al. 2016; Gagliano et al. 2014).[47] To call this memory is not to indulge in metaphor but to extend a functional category in light of new empirical findings. This extension is no more metaphorical than the attribution of memory to immune systems, and no less theoretically tractable.

However, while it is not merely metaphorical to speak of plant memory, the analogy to animal memory must be drawn with care. In animals, "memory" denotes a heterogeneous class of phenomena, ranging from non-representational physiological retention to representational systems capable of encoding and retrieving information about the world. Plant memory is comparable to certain non-representational forms of animal memory, in that it operates through physiological changes responsive to environmental regularities, but it is unlike the representational varieties found in some animals. Since not all animal memory is representational, the issue is not simply whether plants lack representational capacity, but whether their memory can be placed within a careful taxonomy that distinguishes functionally similar but cognitively divergent processes. Without such distinctions, the term risks inviting misleading over-analogies to animal memory systems of a more complex kind.

2.4 Anticipation

This section examines the claim that plants' ability to anticipate future environmental conditions – such as nutrient availability or light gradients – serves as evidence of their intelligence. One version of this argument involves the application of the predictive processing hypothesis, which suggests

44 Tulving, E. (1972). *Organization of memory*. Academic Press.
Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory, 82*(3), 171-177. https://doi.org/10.1016/j.nlm.2004.06.005

45 Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., Lehéricy, S., & Benali, H. (2008). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural Brain Research, 199*(1), 61-75. https://doi.org/10.1016/j.bbr.2008.11.012

46 Murphy, K., & Weaver, C. (2016). *Janeway's immunobiology*. Garland Science.

47 Crisp, P. A., Ganguly, D., Eichten, S. R., Borevitz, J. O., & Pogson, B. J. (2016). Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics. *Science Advances, 2*(2). https://doi.org/10.1126/sciadv.1501340
Gagliano, M., Renton, M., Depczynski, M., & Mancuso, S. (2014). Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia, 175*(1), 63-72. https://doi.org/10.1007/s00442-013-2873-7

that organisms anticipate and adjust to future stimuli. While this framework has been used to argue for plant intelligence, the section critically assesses the issues with applying such a model to plants. The section also addresses broader concerns with equating anticipatory behavior in plants with intelligence, highlighting the complexities and risks of anthropomorphizing plant behavior.

2.4.1 The Predictive Processing Hypothesis and Plants

This section critically examines the application of the predictive processing framework, which posits that organisms predict and respond to future stimuli, and evaluates its relevance to plants.

2.4.1.1 The Predictive Processing Hypothesis

The predictive processing (PP) hypothesis has emerged as a unifying framework in cognitive science, positing that the brain is fundamentally a prediction machine, engaged in the hierarchical minimization of prediction error through generative models of sensory input (Friston, 2010; Clark, 2013).[48] Under this view, perception, action, and cognition are deeply intertwined processes governed by the imperative to reduce the discrepancy between expected and actual sensory states. Perception is conceptualized as inference, whereby top-down predictions generated by internal models are continuously updated in light of bottom-up sensory evidence, thereby optimizing beliefs about the world (Hohwy, 2013).[49] Action, in turn, is framed as active inference, wherein organisms act upon the environment to fulfill predictions, thereby minimizing sensory uncertainty (Friston et al., 2011).[50] This approach dissolves traditional boundaries between perception and action and provides a parsimonious account of a broad array of cognitive phenomena, including attention, learning, and the sense of agency. The PP framework thus offers a deeply integrative, mechanistic explanation of cognition grounded in principles of Bayesian inference and the free-energy minimization imperative.

2.4.1.2 A Claim for Predictive Processing in Plants

In their provocative 2017 article, "Predicting Green: Really Radical (Plant) Predictive Processing," Calvo and Friston advance the thesis that predictive processing (PP) - a framework traditionally reserved for neurocognitive systems - can be meaningfully applied to plant behavior. Challenging the anthropocentric and neurocentric assumptions of mainstream cognitive science, the authors argue that plants engage in cognition-like processes through mechanisms compatible with the free-energy principle, namely, the minimization of prediction error via active and passive inference. Rather than interpreting plant reactivity as mere stimulus-response, Calvo and Friston conceptualize plant-environment interaction as fundamentally inferential, guided by endogenous models that anticipate environmental changes. On this view, plants continuously regulate their

48 Friston, K. (2010). The free-energy principle: a unified brain theory? Nature Reviews. *Neuroscience, 11*(2), 127-138. https://doi.org/10.1038/nrn2787
Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences, 36*(3), 181-204. https://doi.org/10.1017/s0140525x12000477

49 Hohwy, J. (2013). *The predictive mind*. Oxford University Press.

50 Friston, K., Mattout, J., & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics, 104*(1-2), 137-160. https://doi.org/10.1007/s00422-011-0424-z

internal states by making predictions about future environmental inputs and adjusting their physiological processes to reduce discrepancies between expected and actual inputs – thereby maintaining homeostasis and adaptive viability. The article thus marks a radical departure from conventional views of cognition, extending PP to a domain devoid of nervous systems and suggesting that predictive engagement with the environment may be a fundamental biological principle rather than a uniquely neural one (Calvo & Friston, 2017).[51]

To substantiate their claims, Calvo and Friston draw upon detailed examples of plant behavior that exhibit features consistent with predictive processing and inference-based regulation. Circumnutation – the helical or oscillatory growth movement observed in shoots and tendrils – is presented not merely as a mechanical byproduct of growth, but as a structured exploratory strategy enabling plants to sample their environment and anticipate future contact points with supports, in ways that resemble active information-seeking behavior. Phototropism, the directional growth of plants toward light sources, is argued to involve more than a reactive gradient-following mechanism; instead, it exhibits predictive characteristics insofar as plants adjust growth trajectories in anticipation of future light availability, integrating past light exposure to guide future orientation. Similarly, root-foraging patterns are cited as evidence of predictive environmental modeling: Roots do not grow randomly but preferentially extend toward regions that are likely to contain nutrients, often altering their growth direction before actual contact with resources – suggesting the existence of internal probabilistic models that infer the presence of underground targets. Calvo and Friston interpret these behaviors as expressions of both active inference, where growth and movement are deployed to confirm hypotheses about the environment, and passive inference, where internal states are updated in light of prediction errors. Together, the authors claim these examples support the view that plant behavior is not merely reactive but governed by anticipatory, model-based engagement with a dynamic environment, in line with the predictive processing framework.

2.4.1.3 Problems with Attributing Predictive Processing to Plants

While the application of predictive processing (PP) to plant behavior presents an intriguing expansion of cognitive theory, significant conceptual and empirical concerns caution against such an interpretation. First and foremost, the theoretical apparatus of PP – including hierarchical generative models, precision-weighted prediction error minimization, and active inference – was developed to account for neurocognitive systems characterized by rapid, plastic, and recursive signal processing. Extending this framework to plants, which lack neurons, centralized control structures, or synaptic communication, risks diluting the mechanistic specificity that makes PP explanatory. Plant behaviors such as circumnutation, phototropism, and root foraging, while undeniably complex and adaptive, can be parsimoniously explained by well-established physiological and biochemical mechanisms. Auxin gradients, hormone transport, and cellular turgor dynamics offer sufficient accounts of these phenomena without invoking the computational machinery of predictive modeling. As such, the inference to internal probabilistic models or

51 Calvo, P., & Friston, K. (2017). Predicting green: really radical (plant) predictive processing. *Journal of the Royal Society Interface, 14*(131), 20170096. https://doi.org/10.1098/rsif.2017.0096

prediction error minimization in plants may be unwarranted, reflecting a tendency to anthropomorphize functionally effective but non-cognitive biological processes.

Moreover, the methodological criteria for attributing predictive processing to a system remain underdeveloped in the context of non-neural organisms. While behaviors that are anticipatory or flexible are sometimes taken as indirect evidence of internal modeling, this inference is equivocal without demonstrable error-corrective feedback characteristic of PP. In neural systems, predictions are updated through precision-weighted signals in well-mapped hierarchical architectures; in plants, by contrast, signal transduction is largely distributed, slow, and constrained by physical growth processes. Without empirical markers of prediction error correction - such as reversals of expected trajectories in response to violated predictions - or independent evidence of model-based anticipation, the attribution of PP risks becoming metaphorical. Instead of offering a genuinely radical extension of cognitive science, such interpretations may collapse under their own theoretical promiscuity, failing to distinguish between adaptively tuned behavior and inferential cognition. A more cautious and biologically grounded approach would seek to clarify the boundary conditions of PP rather than extending it to all organized, environment-responsive systems.

Indeed, if the predictive processing (PP) hypothesis offers an accurate account of cognition, then the emergence of nervous systems may be understood not merely as an evolutionary convenience for information transmission, but as a structural innovation precisely tailored to support hierarchical generative modeling and rapid prediction error minimization. Neural architectures, with their capacity for high-bandwidth bidirectional signaling, modular organization, and dynamic precision-weighting, appear exceptionally well-suited for implementing the computational requirements of PP, including temporally deep inference and counterfactual reasoning. On this view, the nervous system does not merely instantiate predictive processing - it may have evolved *for* predictive processing, providing the specialized substrate necessary for the efficient execution of inferential control in uncertain, fast-changing environments. Consequently, the attempt to ascribe PP to plants - organisms that lack the speed, structural hierarchy, and recursive processing capacities of neural systems - may conflate evolutionary convergence in adaptive behavior with computational equivalence.

2.4.2 General Issues with Citing Anticipation in Plants as Evidence of Plant Intelligence

This section discusses a paradigmatic example of the attribution of future anticipation to plants, critically examining the concept of anticipation in the context of plant behavior. The discussion clarifies what it might mean to accurately claim that plants anticipate the future. It then addresses the broader issue of using plant anticipation as evidence of plant intelligence.

2.4.2.1 A Paradigmatic Example of How Plants Are Claimed to Anticipate the Future

In the article “What Plant Roots Know,” Novoplansky (2019)[52] explores the remarkable sensory and decision-making capabilities of plant roots and in doing so mentions their capacity for anticipatory behaviors. The author argues that plant roots possess sophisticated information processing systems that enable them to navigate and adapt to their environment. This involves not only responding to immediate environmental cues but also predicting future conditions to optimize growth and resource acquisition. Novoplansky highlights how roots exhibit behaviors such as foraging and nutrient sensing that suggest an advanced form of anticipatory action, where roots adjust their growth trajectories based on both current and predicted future conditions. This anticipatory capacity, the author suggests, reveals a level of cognitive sophistication previously underappreciated in plants. The study challenges the conventional view that plant behavior is purely reactive and supports the notion that plant roots engage in a form of proactive, future-oriented decision-making akin to the anticipatory strategies seen in higher organisms.

2.4.2.2 General Issues with Attributing Anticipation to Plants

The concept of anticipation in plants presents a significant challenge, particularly when attempting to avoid conflating plant behavior with that of humans or other animals. In colloquial usage, anticipation in humans typically involves a mental representation of future possibilities, where future events are imagined or predicted based on past experiences. This process requires cognitive faculties and a model of the world that plants clearly lack. In contrast, when we speak of anticipation in plants, we are referring to behavior that is adaptive to future conditions likely to follow from present ones, without the need for mental representation or a cognitive model of the world. This distinction is crucial, as it highlights that plant "anticipation" involves adaptive behavior driven by environmental cues rather than the kind of cognitive foresight we attribute to humans.

The issue becomes more complex when considering non-human animals. It is not clear whether animals possess the ability to imagine or represent the future in the same way humans do, and indeed, it is likely they do not. However, animals, like plants, exhibit behavior that is adaptive to likely future circumstances. In this sense, animal "anticipation" of the future may be more akin to plant anticipation than to human anticipation, as it does not necessarily involve the mental construction of future possibilities. Nevertheless, as argued earlier, animals - but not plants - possess the capacity for associative learning, which allows for a greater degree of flexibility in adapting to future conditions. This capacity enables animals to form more complex and dynamic responses based on past experiences, distinguishing animal anticipation from the more limited, direct adaptive responses seen in plants.

Ascribing anticipation to plants brings attention to important features of their behavior that are shaped by evolutionary pressures. However, it also risks blurring the distinctions between human, animal, and plant capacities by relying too heavily on analogy. It is essential to maintain precision in our descriptions and to qualify use of terms like "anticipation" to avoid oversimplifying complex differences across species. By doing so, important distinctions are preserved - distinctions that

52 Novoplansky, A. (2019). What plant roots know? *Seminars in Cell and Developmental Biology, 92*, 126-133. https://doi.org/10.1016/j.semcdb.2019.03.009

better reflect the diverse ways in which living systems interact with and adapt to their environments.

It is not strictly inaccurate to attribute anticipation to plants, so long as the term is used with appropriate conceptual precision. In Robert Rosen's sense, all living systems are anticipatory systems, including plants (Rosen 1985).[53] However, this usage departs significantly from standard interpretations of anticipation as a representational or cognitive act. For Rosen, anticipation does not require a symbolic model or internal representation of future states. Rather, a system is anticipatory insofar as its internal organization gives rise to present behavior that is functionally oriented toward future conditions. In this sense, what constitutes a "model" within the system is not an abstracted or isomorphic depiction of the environment, but a set of internal dynamics that produce outcomes which are adaptively suited to what has not yet occurred. A clear example of this is vernalization, the cold-induced epigenetic changes in plants that enable flowering only after prolonged exposure to low temperatures. The plant does not "know" that winter has occurred or that spring is imminent; instead, its internal state has been shaped by prior exposure in a way that predisposes it to initiate flowering at a later time. Here, the internal physiological organization functions as a kind of non-representational model in Rosen's sense: not because it encodes future events, but because it is structured to bring about behavior that is adaptively aligned with predictable environmental regularities. In this limited but meaningful sense, plants may be said to be anticipatory systems - but only if the term is carefully qualified to avoid conflating functional anticipation with representational foresight.

2.4.2.3 Levels of Analysis and Issues with Citing Anticipation as Evidence of Plant Intelligence

Having established conceptual clarity about what is meant by anticipation in plants, it is crucial to consider whether this form of anticipation warrants its use as evidence of plant intelligence. In Novoplansky's article, he notes - accurately - that the problem-solving involved in determining what kind of developmental plasticity or growth patterns a plant should exhibit in order to be well-adapted to future conditions, is not a function of the plant itself. Rather, he attributes this adaptive capacity to the process of natural selection itself, which has shaped the plant's behaviors over evolutionary time.

This distinction reveals a critical issue with citing anticipation as evidence of plant intelligence - it conflates different levels of analysis. While plants do exhibit behaviors that prepare them for future conditions, the underlying intelligence at play is the intelligence of evolution, embodied in the process of natural selection, rather than intelligence at the level of the individual organism. When we preserve these levels of analysis - distinguishing between the evolutionary intelligence that shapes behaviors and the potential cognitive capacities of individual plants - it becomes clear that attributing intelligence to plants based on their anticipatory behaviors is misguided. The behaviors in question are evolutionary adaptations, not manifestations of cognitive processes akin to those that characterize intelligence in animals or humans.

53 Rosen, R. (1985). *Anticipatory Systems: Philosophical, Mathematical, and Methodological Foundations*. Pergamon Press.

2.5 Conclusion

This concluding section summarizes the discussion on plant intelligence. It contrasts plant intelligence, such as it is, with the absence of associative learning and semantic memory, arguing for a nuanced understanding of intelligence that distinguishes between non-neural forms and cognitive capacities in animals.

2.5.1 Plants Have a *Kind* of Intelligence

From an evolutionary perspective, it is plausible that plants have developed functionally complex behaviors to navigate environmental challenges. As living organisms, plants must rely on adaptive strategies - adjusting growth and physiology in response to cues concerning light availability, soil conditions, predation, and competition. These behaviors, while lacking a neural basis, can nonetheless exhibit context-sensitive plasticity, goal-directedness, and environmental attunement. In this sense, plants possess a form of non-neural intelligence: they respond adaptively to patterns in their environments in ways that promote survival and reproductive success.

2.5.2 Limits to Plant Intelligence: Associative Learning and Semantic Memory

However, current empirical evidence indicates that this intelligence does not extend to associative learning or semantic memory. Associative learning - minimally defined as the capacity to modify behavior through the formation of predictive associations between stimuli or between actions and outcomes - appears to require some form of nervous system architecture, even in its most rudimentary forms. Organisms such as *Tripedalia cystophora* (Box jellyfish) and *Ophiocoma wendtii* (Brittle star) lack centralized brains but nevertheless exhibit behaviors consistent with associative learning. In contrast, while plants display remarkable forms of responsiveness and plasticity, no conclusive evidence has demonstrated that they can form associations between temporally separated stimuli in a way that meets the operational criteria for associative learning. Similarly, claims about plant memory tend to invoke physiological or epigenetic persistence rather than representational storage in the cognitive sense.

This emerging asymmetry suggests the presence of a natural discontinuity - a joint in nature – that divides the non-neural forms of intelligence found in plants from the associative and semantic memory-based forms of cognition found in animals with nervous systems. Recognizing this divide does not diminish the cognitive interest of plant behavior; rather, it underscores the need for conceptual precision when attributing cognitive capacities across biological systems.

2.5.3 Plant Intelligence as Akin to Swarm Intelligence

Considering the limits of plant intelligence, it may be helpful to draw a parallel with swarm intelligence, which operates without central processing but can solve complex problems within an ecological niche. Like plant intelligence, swarm intelligence lacks associative learning or memory in any semantic sense. Swarm systems, such as slime molds (discussed earlier), are composed of

identical cells that collectively exhibit emergent problem-solving properties, but they too lack the kind of memory or learning seen in animals with nervous systems. While plants are not literal swarms, their behavior exhibits a similar decentralized, emergent structure. Growth patterns in plants emerge from the interaction of countless individual cells, with no central control center guiding decisions. This decentralized decision-making in plants mirrors how swarm behavior emerges from individual agents within a group. As such, plant intelligence shares limitations with swarm intelligence - both are adaptive and capable of solving problems, but both lack the sophisticated cognitive processes associated with organisms that have nervous systems. Therefore, while it's valid to ascribe intelligence to plants, it's crucial to be precise about the kind of intelligence we are attributing, much like we must do when discussing swarm intelligence.

2.5.4 Philosophical Implications

The broader philosophical implication is that intelligence need not be confined to creatures with brains or to systems capable of conscious deliberation. It may instead be treated as a functionally defined capacity: the ability of an organism to modulate its behavior in response to structured and recurring features of its environment. Framed in this way, intelligence appears as a graded and heterogeneous phenomenon, one that can be realized across diverse biological substrates. Yet such pluralism does not collapse the distinctions that matter for theories of cognition. Associative learning and representational memory mark substantive thresholds, enabling the detection of higher-order relations among stimuli and the stabilization of internal states that guide future action. Their presence in animals with rudimentary nervous systems, and their consistent absence in plants despite extensive investigation, sharpens rather than blurs our cognitive taxonomies.

The study of plant behavior thus poses a constructive challenge to established assumptions in the philosophy of mind. It encourages a reconceptualization of intelligence that is inclusive in recognizing non-neural adaptive capacities, yet discriminating in identifying the functional markers that underwrite genuine cognition. Philosophical analysis has an important role here, not by settling empirical questions prematurely, but by clarifying which behavioral and physiological capacities warrant classification as cognitive and which do not.

Seen from this perspective, plant behavior offers a valuable vantage point from which to reconsider the boundaries of cognition without erasing them. A framework that accommodates non-neural intelligence while withholding attributions of associative learning and representational memory allows for a more ecologically and evolutionarily informed account of mind. Such a framework treats plant intelligence as an adaptive strategy for managing environmental complexity, but not as evidence of cognition in the paradigmatic sense exemplified by animals. In this way, we can acknowledge the sophistication of plant behavior while preserving empirically grounded distinctions that continue to structure our understanding of cognitive life.

3 Agency

3.1 Introduction: Rethinking Agency in Living Systems

What does it mean to call something an agent? In both everyday and scientific contexts, "agency" is typically associated with intentional action: behavior guided by internal representations, decision-making processes, and a capacity for choosing between alternatives (Bratman, 1987; Dennett, 1989).[54] Under this model, agents are beings who act for reasons, whose behavior is not merely reactive but governed by cognitive mediation. This conception of agency fits well with paradigmatic human cases and is often extended to many nonhuman animals. But what becomes of the concept when we turn to organisms that lack nervous systems, centralized control, or any plausible analogues to mental representations?

Plants raise this question in a striking way. Although they are sessile, lack neurons and brains, and operate on timescales that are often imperceptible to human observers, they exhibit highly coordinated and adaptive behavior. They grow directionally toward light and nutrients, adjust their development based on environmental cues, avoid mechanical obstacles, initiate systemic defense responses to localized damage, and engage in both intra- and interspecies signaling (Trewavas, 2003; Karban, 2015).[55] Such behaviors are neither fixed nor mechanical in a simple sense. They display sensitivity to context, plasticity, and a functional organization suggestive of autonomy and goal-directedness. For these reasons, several researchers and philosophers have proposed that plants exhibit a genuine form of agency - one that is non-representational and non-intentional, but nonetheless real (Calvo & Friston, 2017; Trewavas, 2014; Segundo-Ortin & Calvo, 2021).[56]

This view has not gone unchallenged. Critics argue that the attribution of agency to plants risks anthropomorphism, concept-stretching, or conceptual confusion. Mallatt, et al. (2020)[57] warn that we must distinguish mere biological responsiveness from agential behavior properly so-called. They argue that agency implies a form of decision-making, however rudimentary, which plants lack. On this view, plant behavior, however complex, remains the output of evolved regulatory mechanisms rather than the expression of agential capacities.

This thesis takes a middle path. It defends the idea that plants do indeed possess a kind of agency - one grounded in their autonomy, responsiveness, and self-maintaining organization - while clearly distinguishing it from the intentional, representational agency characteristic of animals. On

54 Bratman, M. (1987). *Intention, Plans and Practical Reason*. University of Chicago Press.
Dennett, D. (1989) *The Intentional Stance*. MIT Press.

55 Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1-20. https://doi.org/10.1093/aob/mcg101
Karban, R. (2015). *Plant sensing and communication*. University of Chicago Press.

56 Calvo, P., & Friston, K. (2017). Predicting green: really radical (plant) predictive processing. *Journal of the Royal Society Interface, 14*(131), 20170096. https://doi.org/10.1098/rsif.2017.0096
Trewavas, A. J. (2014). *Plant Behaviour and Intelligence*. Oxford University Press.
Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews Cognitive Science, 13*(2). https://doi.org/10.1002/wcs.1578

57 Mallatt, J., Blatt, M. R., Draguhn, A., Robinson, D. G., & Taiz, L. (2020). Debunking a myth: plant consciousness. *Protoplasma, 258*(3), 459-476. https://doi.org/10.1007/s00709-020-01579-w

this account, agency is not a unitary phenomenon but a spectrum or family of related capacities that manifest differently across biological systems. In this pluralist view, plant agency is not a primitive or failed form of animal agency, but a distinct expression of the self-organizing powers of life. At the same time, the emergence of intentional agency in early animals represents a real qualitative shift: a developmental joint in nature that builds upon but exceeds minimal agential capacities.

3.2 Against Mechanistic Reduction: Defending Plant Agency

Skeptics of plant agency often assume that any complex plant behavior can ultimately be explained in terms of underlying mechanisms – photoreceptors, hormonal gradients, or genetically encoded reaction chains – and therefore lacks the spontaneity, evaluative flexibility, or autonomy typically associated with agents. On this view, plants may be intricate machines, but machines nonetheless, without anything resembling the action capacities attributed to animals or humans. While this mechanistic perspective correctly emphasizes the biochemical and physiological basis of plant activity, it overlooks the possibility that agency may emerge from, rather than be excluded by, mechanistic processes – provided those processes are organized in the right way.

3.2.1 The Basis of Agency in Living Systems

Agency, at its most fundamental level, does not require cognition or representation but emerges from the self-organizing and self-manufacturing nature of living systems. Organisms regulate their internal processes and selectively engage with their environment in ways that reflect what matters to their continued existence. This section examines two key interrelated features of such biological agency: autopoietic organization and the capacity for relevance realization. Together, these provide the groundwork for understanding how plants instantiate a minimal but genuine form of agency.

3.2.1.1 Self-Organization and Self-Manufacture

What distinguishes an agent from a mere mechanism may not be the absence of mechanistic parts but the particular way those parts are organized and maintained. Central to theories of biological autonomy is the concept of organizational closure: an agent is a system whose components recursively depend on one another for their generation, regulation, and continued functioning (Moreno & Mossio, 2015).[58] In such systems, the whole is not externally imposed but internally constituted – a self-organizing unity that maintains itself through the dynamic interdependence of its parts.

Yet self-organization alone does not capture the full picture. Living agents are not merely systems that maintain internal order; they are self-manufacturing systems. This is the core insight of the concept of autopoiesis as developed by Maturana and Varela (1992)[59] – living beings are systems

58 Moreno, A., & Mossio, M. (2015). *Biological Autonomy: A Philosophical and Theoretical Inquiry*. Springer.
59 Maturana, H. R., & Varela, F. J. (1992). *Tree of knowledge: The Biological Roots of Human Understanding*. Shambhala.

that produce and regenerate the very components of which they are composed, through a closed network of metabolic processes. The boundary of the organism – its membrane, tissues, organs – is not fixed by external scaffolding, but produced and maintained by internal activity. In other words, the living system is both the producer and the product of its own organization. It is this capacity for self-production that grounds the organism's identity as a unified, individuated whole.

Crucially, this self-manufacturing organization confers a kind of normativity on the organism's activity. Because the system is responsible for its own maintenance, perturbations from the environment are not neutral – they are encountered as problems or opportunities relative to the system's organizational needs.

Thus, agency, understood at its most basic level, emerges from the autonomous organization of the living system itself. A self-manufacturing organism is not merely alive – it is a center of activity oriented toward the preservation of its own form. It regulates its interactions with the world in ways that express an implicit concern for its own continued existence. This, it is suggested, is the minimal condition for agency.

3.2.1.2 Relevance Realization

In their 2024 article, "Naturalizing relevance realization: why agency and cognition are fundamentally not computational," Jaeger et al.[60] propose that cognition is best understood as the dynamic process of relevance realization – the organism's capacity to attune to what matters in a given situation. Drawing on enactivism, ecological psychology, and autopoietic theory, they argue that cognitive agents are not passive processors of information but active sense-makers that regulate their engagement with a complex world of affordances. Relevance realization, on this view, is not computational but emergent from the embodied agent's situated interaction with its environment, allowing for the flexible selection and modulation of affordances according to shifting goals and contexts. The authors thus offer a naturalized account of cognition as an ongoing coordination of attention and action, grounded in the organism's embodied orientation toward relevance within a field of possibilities.

Relevance realization, as articulated by Jaeger et al., need not be restricted to organisms traditionally considered cognitive. While the authors frame relevance realization as central to cognition, their account makes clear that what underpins this capacity is not mental representation or internal models of the world, but the self-organizing, self-maintaining nature of living systems capable of dynamically responding to environmental affordances. On this view, relevance realization is not exclusive to animals or organisms with nervous systems – it is a fundamental feature of life itself. Plants, for example, need not possess cognition in any robust sense in order to realize relevance; rather, by virtue of being autopoietic, environmentally embedded systems, they are continuously engaged in modulating their responses to what matters for their survival and flourishing. In doing so, they exhibit a form of basic agency – distinct from intentional, deliberative,

60 Jaeger, J., Riedl, A., Djedovic, A., Vervaeke, J., & Walsh, D. (2024). Naturalizing relevance realization: why agency and cognition are fundamentally not computational. *Frontiers in Psychology, 15*. https://doi.org/10.3389/fpsyg.2024.1362658

or moral agency, but nonetheless real – shared across the domain of living systems and arguably definitive of life itself.

3.2.2 How Plants Instantiate Basic Agency and Realize Relevance

If agency is not the exclusive domain of animals with nervous systems, then we must ask how it is instantiated in other forms of life, such as plants. The answer lies in understanding how relevance is dynamically realized by living systems – how organisms selectively respond to features of their environment that matter to them, not by means of cognition or representation, but through the metabolic and developmental organization that underpins life itself. Drawing on Jaeger et al.'s (2024)[61] account of relevance realization as a dynamic, non-computational process, it is argued that plants qualify as agents in virtue of their capacity to modulate their own environmentally situated activity in accordance with internal norms of viability. This section examines the physiological and interactive mechanisms through which this basic form of agency is enacted in plants.

3.2.2.1 Metabolic Organization and the Norms of Viability

Relevance, for a living system, is defined by what contributes to or threatens its ongoing self-maintenance. Unlike representationalist accounts that tie agency to internal models or explicit goals, this perspective understands agency as emerging from the organism's capacity to regulate its own internal coherence in response to changing conditions. Homeostatic regulation is key: through coordinated physiological processes, the organism keeps itself within a viable operational range.

Plants exhibit this capacity through complex, context-sensitive adjustments that preserve metabolic balance. Under drought stress, for instance, they close stomata to reduce water loss, alter growth patterns to increase water uptake, and activate hormonal signaling networks such as abscisic acid to coordinate these changes systemically (Tardieu & Simonneau, 1998; Calvo, et al. 2017).[62] These processes are neither reflexive nor computational; they are enacted by a living system that, by virtue of its organization, enacts what counts as relevant. In such cases, water becomes meaningful not because the plant represents it as such, but because the plant's self-organizing dynamics make water a condition for continued existence. It is through this metabolic organization that plants instantiate basic agency: they regulate their activity in ways that reflect their own viability-based norms.

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61 Ibid.

62 Tardieu, F., & Simonneau, T. (1998). Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany, 49*(Special), 419-432. https://doi.org/10.1093/jxb/49.special_issue.419
Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065

3.2.2.2 Developmental Plasticity and Environmental Coupling

Beyond metabolic regulation, plants also realize relevance through structural coupling with their environment. This process involves a mutual shaping of organism and surroundings over time, such that the plant's structure and behavior reflect a history of adaptive engagement. Enactivist theorists describe this as a form of sensorimotor coordination – though in the case of plants, this coordination is expressed through developmental plasticity rather than locomotion.

Plants grow toward light (phototropism), modulate root architecture in response to nutrient availability, and alter stem strength and leaf orientation based on mechanical feedback (Trewavas, 2003; Novoplansky, 2015).[63] These are not mere stimulus–response patterns; they are the result of distributed regulatory systems that integrate spatial, temporal, and chemical cues in a way that is sensitive to local and global context. By adjusting their growth and internal organization, plants actively shape the conditions of their own perception and response. They do not passively receive information from the world – they enact it through morphology and physiology. In this respect, the plant's engagement with affordances is both autonomous and adaptive: the environment is made relevant through the organism's history of interaction with it (Calvo & Keijzer, 2011).[64]

3.2.3 Locating Plants on the Agency Continuum

Taken together, these forms of metabolic and developmental responsiveness show that plants are capable of realizing relevance and exhibiting agency in a basic but genuine sense. This agency is non-representational and non-intentional, yet normatively structured and organized around the active maintenance of viability. Plants are not passive organisms that merely endure their surroundings; they are self-organizing systems that selectively modulate their engagement with a complex world of affordances.

While this establishes that plants instantiate the minimal form of agency characteristic of living systems, it also raises a broader question: how does this form of agency relate to those found elsewhere in the tree of life? As we move from sessile organisms like plants to motile animals, new layers of complexity are added – nervous systems, internal sensory maps, anticipatory motor planning, and eventually, cognitive representation. These enriched forms of agency do not replace the basic agency found in plants but build upon it. The following discussion examines how such capacities emerge and scaffold one another across evolutionary time, situating plant agency within a broader continuum that extends from metabolic regulation to representational cognition.

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63 Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1-20. https://doi.org/10.1093/aob/mcg101
Novoplansky, A. (2015). Future perception in plants. In *Cognitive systems monographs* (pp. 57-70). https://doi.org/10.1007/978-3-319-22599-9_5

64 Calvo, P., & Keijzer, F. (2011). Plants: Adaptive behavior, root-brains, and minimal cognition. *Adaptive Behavior, 19*(3), 155-171. https://doi.org/10.1177/1059712311409446

3.3 A Step Up: The Emergence of Intentional Agency in Animals

In the previous section, the shared biological foundations of agency across life forms were identified - autopoiesis, homeostasis, and self-maintenance - as the scaffolding for organismic responsiveness. These features are already robustly present in plants, which are capable of highly plastic, context-sensitive behavior. But a divergence was also noted: in the animal lineage, agency takes a distinctive turn. In this section, that turn is explored by identifying the biological and philosophical features that characterize the emergence of intentional agency, and distinguish it from the basic organismal agency possessed by plants.

3.3.1 Intentional Agency

The key features of intentional agency are: (1) perceptual representation of environmental features, (2) the capacity to act on the basis of those representations, and (3) the selection of actions from among multiple behavioral possibilities. The hallmark of this agency is not merely behavioral complexity or reactivity, but representational control over action - a capacity enabled by perceptual constancy, internal evaluations, and neural structures that support anticipatory, choice-based behavior. This section traces the evolutionary appearance of these features in early animals and argues, following Tyler Burge (2022), that the development of perceptual constancy marks the beginning of representational mind - and with it, a new form of agency (Burge, 2022).[65]

Plant behavior, though often complex and goal-directed, remains structurally and developmentally coupled to environmental stimuli. Plants do not initiate action independently of present conditions; their responsiveness is real, but it is always context-embedded, shaped by gradients of light, water, gravity, and touch. By contrast, animals with nervous systems can decouple behavior from immediate stimuli and instead use internal representations to guide action. This decoupling allows for deliberation, anticipation, and action selection - core dimensions of intentional agency.

The minimal form of this shift can be seen in the evolution of perceptual constancy - the capacity to track an object or property as the same across variable conditions (e.g., recognizing prey as prey whether it is in shadow, partially occluded, or at different distances). As Burge argues, perceptual constancies are non-conceptual forms of representation that underlie objective perception. Crucially, they allow organisms to discriminate environmental regularities as such, rather than merely react to momentary configurations. When an organism can treat an object as the same despite superficial changes, it no longer behaves in lockstep with stimuli but instead interprets the world in terms of stable features that persist across contexts, marking the beginning of representational mind (Burge, 2022).[66]

65 Burge, T. (2022). *Perception: First Form of Mind.* Oxford University Press.
66 Ibid.

3.3.2 Arthropods and the Origin of Representational Mind

According to Burge, arthropods are the first creatures for which we have strong evidence of perceptual constancy, and thus the first to possess a representational mind in the minimal, biologically grounded sense. Bees, ants, and spiders all show capacities for invariant tracking, context-sensitive navigation, and learning – behaviors that are difficult to explain without appealing to object- or feature-constancy representations.

Honeybees (*Apis mellifera*), for example, exhibit color constancy, continuing to recognize the same flowers under different lighting conditions (Giurfa et al., 1996).[67] They also show configural learning: they can be trained to discriminate complex visual patterns and even abstract relationships such as symmetry. This kind of flexible behavior suggests that bees are not simply reacting to fixed stimuli but are representing patterns and categories that underlie those stimuli – a hallmark of perceptual constancy.

Desert ants (*Cataglyphis*), similarly, navigate across vast, featureless terrain using a combination of path integration, celestial compass orientation, and landmark memory. When displaced during foraging, ants initiate systematic search behavior rather than blindly follow previous paths. This behavior indicates the presence of an internal model of spatial relations – a way of representing the world that goes beyond stimulus-response mechanisms (Wehner, 2003).[68]

Perceptual constancy, in which an organism can track features or objects independently of immediate sensory input, marks the onset of representational mind, and with it, the groundwork for intentional agency. This is because the ability to form stable representations enables the organism to select among potential actions, grounded in an internal, representational understanding of the environment. Intentional agency, unlike mere reactive behavior, requires that an agent possesses a plan – a mental blueprint for action. Representations are essential for this because they provide the content for any plan. Even if these representations are non-conceptual, they are still crucial, as they allow the agent to hold an action in mind before carrying it out intentionally, rather than as a mere physiological reaction to external stimuli.

It is important to recognize that action plans that underlie intentional agency do not need to be conscious. In fact, they likely operate unconsciously for much of the time – perhaps even most of the time. The Libet experiment (Libet, 1985)[69] has often been interpreted in various ways regarding free will, but its core finding reinforces what we already know from ordinary experience – much of decision-making occurs outside of conscious awareness. Whether or not this implies that the will is free remains a matter of philosophical debate, but that issue is not relevant to the current discussion. In other words, what is at issue is the will itself, irrespective of its freedom. What is noted here is the distinction that the capacity for intentional action – what we refer to as

67 Giurfa, M., Vorobyev, M., Kevan, P., & Menzel, R. (1996). Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *Journal of Comparative Physiology A, 178*(5). https://doi.org/10.1007/bf00227381

68 Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A, 189*(8), 579-588. https://doi.org/10.1007/s00359-003-0431-1

69 Libet, B. (1985). Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behavioral and Brain Sciences, 8*(4), 529-539. https://doi.org/10.1017/s0140525x00044903

"will" – does not require consciousness. This distinction becomes relevant when considering plants: It is not that plants lack intentional agency because they lack consciousness – the question of plant consciousness is addressed in a later section – but because they do not possess representations. Without representations, there can be no intentional agency.

3.3.3 The Human Case: Moral Reflection and Higher Forms of Agency

The pluralistic account of agency we have developed invites us to place not only plants and nonhuman animals on an evolutionary continuum but also to consider human agency as a further elaboration of this spectrum. In ordinary usage, "agency" often refers to the uniquely human capacity for self-reflective deliberation, rational choice, and moral responsibility – a use that is clearly distinct from the sense in which we attribute agency to plants or even to most nonhuman animals. Understanding the evolutionary and conceptual distinctiveness of human agency helps underscore the broader point that agency is not a single natural kind but rather a layered, developmental, and evolutionarily scaffolded phenomenon.

Human beings display a form of agency marked by the capacity to reflect on one's own reasons for action, to recognize and revise motivations, and to engage in moral evaluation – both of oneself and of others. Philosopher Harry Frankfurt (1988) has argued that human agency is uniquely characterized by our ability to form second-order volitions, or desires about our desires, and to identify with or reject our own motives (Frankfurt, 1988).[70] Christine Korsgaard, following the same line, considers this reflective capacity to be constitutive of normative self-governance: to act as a human agent is not merely to respond to reasons, but to recognize oneself as the source of one's reasons through self-legislated reflection (Korsgaard, 2009).[71]

This form of agency, while central to ethics and moral philosophy, is not innate in its full form. Developmental psychologists and philosophers alike have noted that children gradually acquire the ability for moral reasoning, self-regulation, and perspective-taking, and that these capacities develop in stages throughout childhood (Gopnik, 2009; Tomasello, 2018).[72] This developmental trajectory builds on the evolutionary progression we have traced, from reactive to representational to reflective forms of agency.

Recognizing the special features of human agency does not entail a strict divide between humans and other animals. On the contrary, edge cases abound. Nonhuman animals such as elephants, dolphins, and great apes have been observed to engage in behaviors that suggest elements of empathy, grief, cooperative planning, and possibly even rudimentary norm-following. Dogs in particular have drawn philosophical interest for their apparent capacity to track social expectations and express guilt-like behavior in response to human feedback. Peter Railton (2014) discusses dogs as proto-moral creatures that participate in a kind of affective normativity, responding to social cues and forming attachments in ways that support proto-ethical interaction. These animals

70 Frankfurt, H. G. (1988). *The importance of what we care about: Philosophical Essays*. Cambridge University Press.
71 Korsgaard, C. (2009). *Self-Constitution: Agency, Identity, and Integrity*. Oxford University Press.
72 Gopnik, A. (2009). *The philosophical baby: What Children's Minds Tell Us About Truth, Love, and the Meaning of Life*. Macmillan.
Tomasello, M. (2018). *A natural history of human morality*. Harvard University Press.

may not engage in propositional moral reasoning, but they may still possess proto-reflective evaluative capacities, marking them as nearer to humans on the agential spectrum (Railton, 2014).[73]

Such cases complicate any sharp boundary between “moral” and “non-moral” agency. Rather than a categorical divide, the distinction between animal and human agency may reflect a difference in degree, structure, and representational sophistication. What distinguishes human moral agency, then, is not just the ability to act for reasons, but the ability to make one's reasons themselves the object of evaluation, to hold oneself accountable, and to deliberate about what kind of agent one wishes to be. This kind of reflexivity gives human agency a recursive depth that is, as far as we know, unique in the biological world.

In light of this expanded spectrum – from the metabolic autonomy of plants to the representational perception of insects and mammals, and finally to the self-reflective, norm-sensitive agency of adult humans – it becomes clear that "agency" operates as a family resemblance concept, not a fixed property. It is a structure that ramifies across life, not a feature that cleaves the living world neatly into agents and non-agents. Human agency, far from being the definition of agency itself, is just one – albeit particularly rich – form within a diverse and evolving field of living self-organization and action.

3.4 Conclusion: Rethinking Agency as a Plural Concept

This section has argued for a pluralistic, evolutionary account of agency – one that resists reductionism while avoiding uncritical anthropomorphism. By recognizing plant agency as a genuine but non-representational form of life-based self-organization and goal-directedness, we expand our understanding of what it means to act in the world. At the same time, plant agency has been situated within a continuum of increasingly complex forms of agency.

Rather than treating agency as a threshold concept – present or absent – this discussion has shown it to be a family of related phenomena rooted in the structural and functional organization of living systems. Autopoiesis, perception, representation, norm-responsiveness, and moral self-reflection each mark evolutionary developments that give rise to qualitatively different forms of agential life. Acknowledging this diversity not only sharpens our conceptual tools but also fosters a more inclusive and accurate account of cognition, behavior, and normativity across the tree of life.

Ultimately, this framework allows us to affirm the distinctive agential nature of plant life without collapsing it into animal or human categories. It also allows us to better appreciate the deep biological and philosophical continuities that bind even the most alien forms of life to our own.

73 Railton, P. (2014). The affective dog and its rational tale: intuition and attunement. *Ethics, 124*(4), 813-859. https://doi.org/10.1086/675876

4 Neurophysiology

4.1 Introduction: The Rise of “Plant Neurophysiology”

This section introduces the terms "plant neurophysiology" and "plant neurobiology," which emerged in the early 2000s as part of an effort to better understand plant signaling and responsiveness. It highlights the growing debate over the accuracy and appropriateness of these terms, given the significant differences between plant signaling and animal nervous systems. By examining the implications of applying "neurophysiology" to plants, this section sets the stage for a critical analysis of whether these terms are scientifically valid or whether they risk misrepresenting plant biology.

4.1.1 Historical background and terminology

The terms “plant neurophysiology” and “plant neurobiology” emerged in the early 2000s as part of a growing effort to reframe how plant signaling and responsiveness are understood. In particular, a 2006 paper by Brenner et al[74]. advocated for a new interdisciplinary approach under the banner of plant neurobiology, aiming to highlight the complexity of plant behavior and the presence of signaling molecules traditionally associated with animal nervous systems. These included neurotransmitters such as glutamate, GABA, serotonin, and dopamine, along with the capacity for action potentials and calcium-based signaling cascades - features previously thought to be largely confined to animal physiology.

However, the coining of the term was immediately controversial. In 2007, a group of prominent plant scientists - including A. Baluška, F. W. Baluška-Staiger, and E. D. Brenner himself - received pushback from another cohort of researchers, who published an open letter in Trends in Plant Science explicitly rejecting the “plant neurobiology” label (Alpi et al., 2007).[75] These critics argued that the analogy to animal neurobiology was deeply misleading, both because plants lack neurons and because the kinds of signaling they exhibit are not structured in ways that permit comparison with nervous system function. They warned that metaphoric overreach could distort biological understanding and mislead the public.

The term “plant neurobiology” has persisted nonetheless - largely in a small but vocal minority of researchers (Trewavas, 2007; Baluška & Mancuso, 2008; Calvo, 2016).[76] More recently, popular

74 Brenner, E. D., Stahlberg, R., Mancuso, S., Vivanco, J., Baluška, F., & Van Volkenburgh, E. (2006). Plant neurobiology: an integrated view of plant signaling. *Trends in Plant Science, 11*(8), 413-419. https://doi.org/10.1016/j.tplants.2006.06.009

75 Alpi, A., Amrhein, N., Bertl, A., Blatt, M. R., Blumwald, E., Cervone, F., Dainty, J., De Michelis, M. I., Epstein, E., Galston, A. W., Goldsmith, M. H. M., Hawes, C., Hell, R., Hetherington, A., Hofte, H., Juergens, G., Leaver, C. J., Moroni, A., Murphy, A., . . . Wagner, R. (2007). Plant neurobiology: no brain, no gain? *Trends in Plant Science, 12*(4), 135-136. https://doi.org/10.1016/j.tplants.2007.03.002

76 Trewavas, A. (2007). Response to Alpi et al.: Plant neurobiology - all metaphors have value. *Trends in Plant Science, 12*(6), 231-233. https://doi.org/10.1016/j.tplants.2007.04.006
Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6
Calvo, P. (2016). The philosophy of plant neurobiology: a manifesto. *Synthese, 193*(5), 1323-1343. https://doi.org/10.1007/s11229-016-1040-1

science writers and philosophers of mind have picked up on the term to support claims about the cognitive or even sentient capacities of plants. Thus, the issue is no longer purely terminological or confined to botany – it touches on broader questions in the philosophy of biology, cognition, and the nature of intelligence across life forms.

4.1.2 Why this matters

At stake in the plant neurobiology debate is more than a matter of scientific classification. The terminology used to describe plant signaling profoundly shapes how both scientists and philosophers conceptualize plant behavior. For philosophers interested in plant cognition, the temptation to describe plants as possessing a form of "neurophysiology" raises urgent questions about what kinds of organizational and functional criteria should be required for attributing cognitive capacities.

On one hand, the analogy with animal neurophysiology can help challenge anthropocentric biases. It brings attention to the chemical and electrical complexity of plant signaling systems, which are often unjustly dismissed as passive or automatic (Trewavas, 2003).[77] On the other hand, the term "neurophysiology" carries with it a dense cluster of theoretical associations – intentionality, information processing, representation, and agency – that may be inappropriate when applied to plants. The risk is that by borrowing terminology from neuroscience, we inadvertently smuggle in assumptions about internal models and central coordination that may not be warranted.

From an interdisciplinary perspective, then, the stakes are high. If the term "plant neurophysiology" is used incautiously, it can collapse important distinctions between types of biological organization. For philosophers, this can lead to conflated accounts of cognition across radically different life forms; for scientists, it can obscure empirical differences that matter for understanding how plants regulate their lives. In both cases, conceptual clarity is needed to distinguish metaphorical analogies from functional homologies.

4.2 The Neuron as a Functional Unit

This section explores the distinct features of neurons and their role as information-integrating devices within nervous systems, emphasizing the specialized architecture and functional capacities that allow neurons to process and represent information. It then contrasts this with plant signaling, which, despite similarities such as neurotransmitter-like molecules and electrical signals, lacks the organizational structures and integrative dynamics seen in animals. By examining the absence of neurons, centralized integration, and representational networks in plants, the section argues that the term "plant neurobiology" risks misrepresenting plant signaling by conflating it with animal neurophysiology.

77 Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1-20. https://doi.org/10.1093/aob/mcg101

4.2.1 Neurons as information-integrating devices

To assess whether it is appropriate to describe plant signaling as a form of "neurophysiology," one must first understand the distinctive features of neurons as biological structures. Neurons are not merely conduits for transmitting bioelectrical signals. Rather, they are morphologically and functionally specialized cells whose defining feature is the capacity to integrate multiple sources of input into a coherent, temporally structured output. This integrative function is made possible by a highly specific architecture that includes dendrites for receiving signals, a soma (or cell body) for integrating them, and an axon for transmitting the resulting output to other neurons or effector cells (Kandel, et al. 2013).[78]

The neuronal membrane is not a passive boundary; it actively modulates incoming signals through changes in membrane potential, gated ion channels, and synaptic plasticity. Crucially, synapses permit the selective modulation of input strength and timing, allowing neurons to weight different signals and combine them through processes of spatial and temporal summation. Moreover, synaptic transmission is chemically mediated and directional: neurotransmitters are released from presynaptic terminals and bind to receptors on postsynaptic membranes, enabling highly regulated and context-sensitive communication. This directionality, combined with the compartmentalized architecture of the neuron, creates the possibility for circuit-level organization, in which information can be processed, filtered, and transformed (Dayan & Abbott, 2001).[79]

It is this combination of morphological specialization and biochemical adaptability that allows neurons to function as computational units. The neuron, in this sense, is not simply a switch but a dynamic processor that contributes to the emergence of complex functional properties at the network level. As Bickle (2003)[80] emphasizes, such units are necessary for the construction of explanatory bridges between neurophysiological mechanisms and cognitive phenomena.

4.2.2 Neural networks and representational dynamics

The significance of neurons becomes even more apparent when they are considered in their natural context - that of organized neural networks. Nervous systems exhibit hierarchical and modular architectures, in which sensory information is progressively abstracted and integrated across multiple levels of processing. For example, in the mammalian visual system, neurons in early visual areas (such as V1) respond to simple features like orientation or spatial frequency, while neurons in higher-order areas (like V4 or IT) are selectively tuned to complex patterns, including objects and faces (Churchland & Sejnowski, 1992; DiCarlo et al., 2012).[81] These receptive fields are often organized into topographic maps, such that spatial relations in the environment are mirrored

78 Kandel, E. R. (2013). *Principles of Neural Science, Fifth Edition*. McGraw Hill Professional.

79 Dayan, P., & Abbott, L. F. (2001). *Theoretical neuroscience: Computational and Mathematical Modeling of Neural Systems*. Mit Press.

80 Bickle, J. (2003). *Philosophy and neuroscience: A ruthlessly reductive account*. Springer.

81 Churchland, P. S., & Sejnowski, T. J. (1992). *The computational brain*. MIT Press.
DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron, 73*(3), 415-434. https://doi.org/10.1016/j.neuron.2012.01.010

in the spatial layout of neural representations – a principle evident in retinotopy, somatotopy, and tonotopy (Kandel, et al. 2013).[82]

Such network architectures support representational dynamics that go beyond immediate reactivity. Through recurrent connectivity, feedforward and feedback loops, and long-range projections, nervous systems are capable of integrating multimodal information, maintaining internal states, and generating predictions about future inputs. These dynamics enable a form of representation in the philosophical sense: internal structures that bear informational content about distal features of the world and can guide behavior in their absence (Gładziejewski 2016; Shea 2018).[83]

Furthermore, many nervous systems feature centralized structures – such as brains and ganglia – that coordinate sensorimotor activity across the organism. These central structures serve as hubs of integration, allowing for the flexible regulation of behavior, the formation of memory, and the capacity for selective attention (Flavell, et al. 2022).[84] The central–peripheral distinction is thus not merely anatomical but also functional: it reflects an underlying division of labor between local responsiveness and global control.

Such features are not incidental to the designation of neurophysiological function. They are constitutive of what it means to have a nervous system capable of cognitive processing. Without discrete excitable units (neurons), specialized intercellular junctions (synapses), and an organized network structure that enables integration and representation, the use of the term "neurophysiology" becomes conceptually strained.

4.2.3 What plants lack

Advocates of plant neurobiology often point to the presence of neurotransmitter-like molecules – such as glutamate, GABA, and serotonin – as evidence that plants share core signaling mechanisms with animals (Baluška & Mancuso, 2008; Calvo, 2016).[85] Similarly, they highlight the existence of electrical signals in plants, such as action potentials and variation potentials, as further evidence of neural-like activity (Fromm & Lautner, 2006).[86] However, these similarities are superficial. What plants lack is not simply the presence of particular molecules or signals, but the organizational framework that gives those molecules their cognitive significance in animals.

Plants do not possess neurons – there are no cells with dendritic trees, axonal projections, or synaptic junctions specialized for electrical integration and directional communication. Instead,

82 Kandel, E. R. (2013). *Principles of Neural Science, Fifth Edition*. McGraw Hill Professional.

83 Gładziejewski, P. (2016). Predictive coding and representationalism. *Synthese, 193*(2), 559-582. https://doi.org/10.1007/s11229-015-0762-9
Shea, N. (2018). *Representation in cognitive science*. Oxford University Press.

84 Flavell, S. W., Gogolla, N., Lovett-Barron, M., & Zelikowsky, M. (2022). The emergence and influence of internal states. *Neuron, 110*(16), 2545-2570. https://doi.org/10.1016/j.neuron.2022.04.030

85 Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6
Calvo, P. (2016). The philosophy of plant neurobiology: a manifesto. *Synthese, 193*(5), 1323-1343. https://doi.org/10.1007/s11229-016-1040-1

86 Fromm, J., & Lautner, S. (2006). Electrical signals and their physiological significance in plants. *Plant Cell & Environment, 30*(3), 249-257. https://doi.org/10.1111/j.1365-3040.2006.01614.x

signaling occurs through vascular tissues such as the phloem, where electrical changes propagate in a diffuse manner, often with slow kinetics and without spatial specificity (Volkov, 2010).[87] Unlike the rapid, directional, and spatially organized signaling of neurons, plant electrical signals are systemic, analog, and often non-specific in their effects.

Moreover, there is no evidence of centralized integration in plants. While some researchers have proposed the root apical meristem as a potential coordination center (Baluška et al., 2004),[88] there is little to suggest that this region performs functions comparable to those of animal brains or ganglia. Plants also lack the topographic organization characteristic of neural representations. There are no receptive fields, no hierarchical processing stages, and no apparent capacity for predictive or decoupled representation of environmental features.

Thus, even if plants are capable of complex, adaptive behavior, their underlying signaling architecture is fundamentally different from that of organisms with nervous systems. As Alpi et al. (2007)[89] argue in their widely cited open letter, the term "plant neurobiology" risks conflating metaphorical analogy with functional equivalence. While plants clearly possess sophisticated mechanisms for environmental responsiveness, there is no compelling evidence that these mechanisms instantiate anything like the integrative, representational dynamics characteristic of neurons and neural systems.

4.3 Signal Propagation Does Not Equate to Information Processing

A common motivation for describing plant physiology in neurobiological terms is the documented presence of rapid electrochemical signaling in plant tissues. The discovery of action potentials in *Dionaea muscipula* (the Venus flytrap) and other species capable of rapid movements has inspired claims that plants possess signal propagation mechanisms analogous to those found in animal nervous systems (Volkov, 2010; Hedrich et al., 2016).[90] However, while the existence of fast electrical signals in plants is not in dispute, what remains controversial is whether these signals perform anything like the information-processing functions characteristic of nervous systems. In this section, it is argued that the conflation of signal propagation with information processing is a central conceptual error in the attribution of "neurophysiological" function to plants.

4.3.1 Electrochemical signaling in plants

Plants are capable of transmitting signals over long distances using a variety of physiological mechanisms. Electrical signals in plants include action potentials (APs), variation potentials (VPs),

87 Volkov, A. G. (2010). *Plant Electrophysiology: Theory and Methods*. Springer.

88 Baluška, Frantisek & Mancuso, Stefano & Volkmann, Dieter & Barlow, P.W.. (2004). Root apices as plant command centres: The unique 'brain-like' status of the root apex transition zone. *Biologia 59*. 9-17.

89 Alpi, A., Amrhein, N., Bertl, A., Blatt, M. R., Blumwald, E., Cervone, F., Dainty, J., De Michelis, M. I., Epstein, E., Galston, A. W., Goldsmith, M. H. M., Hawes, C., Hell, R., Hetherington, A., Hofte, H., Juergens, G., Leaver, C. J., Moroni, A., Murphy, A., . . . Wagner, R. (2007). Plant neurobiology: no brain, no gain? *Trends in Plant Science, 12*(4), 135-136. https://doi.org/10.1016/j.tplants.2007.03.002

90 Volkov, A. G. (2010). *Plant Electrophysiology: Theory and Methods*. Springer.
Hedrich, R., Salvador-Recatalà, V., & Dreyer, I. (2016). Electrical wiring and Long-Distance plant communication. *Trends in Plant Science, 21*(5), 376-387. https://doi.org/10.1016/j.tplants.2016.01.016

and system potentials (SPs), often mediated by changes in ion fluxes – particularly calcium (Ca^{2+}) waves – and accompanied by hydraulic and chemical signals such as reactive oxygen species and phytohormones (Zimmermann et al. 2009; Gilroy et al. 2016).[91] These signals are usually initiated by physical damage, herbivory, or mechanical stimulation, and are typically propagated through the phloem, xylem, or apoplast.

The functions of these signals are primarily physiological and systemic: they coordinate wound responses, regulate stomatal closure, induce the production of defensive compounds such as jasmonic acid, and modulate turgor pressure involved in rapid plant movements (Mousavi et al., 2013; Toyota et al., 2018).[92] For example, when a leaf is wounded, a wave of calcium-dependent signaling can travel to distal tissues and trigger the activation of defensive genes. In the Venus flytrap, the summation of multiple action potentials within a short time interval triggers trap closure – an impressively rapid movement by plant standards, yet one that reflects a simple threshold mechanism rather than fine-grained environmental discrimination (Scherzer et al., 2019).[93]

These signaling capacities are undoubtedly impressive. Yet the mere presence of electrical or chemical signal propagation does not, in itself, imply cognitive processing. To suggest otherwise risks mistaking physiological coordination for information-processing in the cognitive sense.

4.3.2 Comparison with nervous systems

In animals, the transmission of electrochemical signals is tightly coupled with representational structure. Sensory neurons transduce specific features of the environment – such as light wavelength, pressure, or chemical composition – into neural codes that preserve distinctions among those features. In the visual system, for instance, motion-sensitive neurons in the retina and early visual cortex encode the direction, speed, and location of moving stimuli (Livingstone & Hubel, 1988; DiCarlo et al., 2012).[94] These signals are not mere triggers for reaction; they form a structured internal representation of external features, which can be modulated, integrated with other modalities, or held in working memory.

By contrast, the signals transmitted in plants do not appear to encode information about the structure of the environment in any similarly differentiated way. Electrical or calcium waves in

91 Zimmermann, M. R., Maischak, H., Mithöfer, A., Boland, W., & Felle, H. H. (2009). System Potentials, a novel electrical Long-Distance apoplastic signal in plants, induced by wounding. *Plant Physiology, 149*(3), 1593-1600. https://doi.org/10.1104/pp.108.133884
Gilroy, S., Białasek, M., Suzuki, N., Górecka, M., Devireddy, A. R., Karpiński, S., & Mittler, R. (2016). ROS, calcium, and electric signals: key mediators of rapid systemic signaling in plants. *Plant Physiology, 171*(3), 1606-1615. https://doi.org/10.1104/pp.16.00434

92 Mousavi, S. a. R., Chauvin, A., Pascaud, F., Kellenberger, S., & Farmer, E. E. (2013). Glutamate receptor-like genes mediate leaf-to-leaf wound signalling. *Nature, 500*(7463), 422-426. https://doi.org/10.1038/nature12478
Toyota, M., Spencer, D., Sawai-Toyota, S., Jiaqi, W., Zhang, T., Koo, A. J., Howe, G. A., & Gilroy, S. (2018). Glutamate triggers long-distance, calcium-based plant defense signaling. *Science, 361*(6407), 1112-1115. https://doi.org/10.1126/science.aat7744

93 Scherzer, S., Federle, W., Al-Rasheid, K. a. S., & Hedrich, R. (2019). Venus flytrap trigger hairs are micronewton mechano-sensors that can detect small insect prey. *Nature Plants, 5*(7), 670-675. https://doi.org/10.1038/s41477-019-0465-1

94 Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science, 240*(4853), 740-749. https://doi.org/10.1126/science.3283936
DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron, 73*(3), 415-434. https://doi.org/10.1016/j.neuron.2012.01.010

plants typically vary in amplitude or duration in response to the magnitude or intensity of a disturbance, such as wounding or mechanical pressure (Zimmermann & Mithöfer, 2013).[95] These signals thus reflect stress gradients or threshold-exceeding perturbations but lack the specificity characteristic of neural coding. A given calcium spike or voltage fluctuation does not indicate what happened in the environment - only that something sufficiently disruptive occurred.

Moreover, there is no evidence that plant signals are integrated across multiple modalities or coordinated in a way that reflects abstract environmental features. While plant responses can be context-sensitive - such as differing hormonal responses to herbivory depending on the time of day (Fowler et al., 2005)[96] - this contextualization appears to be managed by biochemical state dependencies rather than centralized processing of diverse informational inputs. The signaling is closer to a distributed physiological cascade than to the integrated perceptual representations seen in even relatively simple animal nervous systems.

4.3.3 No evidence of internal modeling

Perhaps the clearest difference between neural and plant signaling lies in the absence, in plants, of any evidence for internal models. In cognitive science and neuroscience, internal modeling refers to the capacity of a system to construct and manipulate representations of the environment that guide behavior in the absence of direct stimuli (Friston, 2010; Clark, 2016).[97] Such models support prediction, error correction, and abstraction, and are increasingly understood as central to perception and action in animals.

Plant signaling, by contrast, does not appear to exhibit any of these hallmarks. There is no known plant structure or process that maintains a stable, decodable representation of environmental features. While plants can exhibit complex responsiveness - such as differential growth toward light or away from toxins - these behaviors do not require internal modeling. Instead, they are best understood as the result of dynamic but non-representational feedback loops between environmental inputs and physiological outputs.

Calcium and electrical signaling in plants lacks semantic content; it does not function as a "code" in the sense used in neuroscience to describe population-level encoding of stimulus features (Panzeri et al., 2015).[98] Nor do we see any evidence of abstraction or categorization in plant responses - no plant behavior has yet been shown to generalize across stimulus tokens or to involve the manipulation of internal variables decoupled from immediate input. As Gagliano et al. (2016)[99]

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95 Zimmermann, M. R., & Mithöfer, A. (2013). Electrical Long-Distance signaling in plants. In *Long-Distance Systemic Signaling and Communication in Plants* (pp. 291-308). https://doi.org/10.1007/978-3-642-36470-9_15

96 Fowler, S. G., Cook, D., & Thomashow, M. F. (2005). Low temperature induction of arabidopsis CBF1, 2, and 3 is gated by the circadian clock. *Plant Physiology, 137*(3), 961-968. https://doi.org/10.1104/pp.104.058354

97 Friston, K. (2010). The free-energy principle: a unified brain theory? Nature Reviews. *Neuroscience, 11*(2), 127-138. https://doi.org/10.1038/nrn2787
Clark, A. (2016). *Surfing uncertainty: Prediction, Action, and the Embodied Mind*. Oxford University Press.

98 Panzeri, S., Macke, J. H., Gross, J., & Kayser, C. (2015). Neural population coding: combining insights from microscopic and mass signals. *Trends in Cognitive Sciences, 19*(3), 162-172. https://doi.org/10.1016/j.tics.2015.01.002

99 Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. *Scientific Reports, 6*(1). https://doi.org/10.1038/srep38427

acknowledge in their more ambitious interpretations of plant learning, the cognitive status of such behaviors remains controversial precisely because the internal mechanisms lack the structure typical of information-processing systems.

It is worth noting that the term "model" itself is used in divergent ways across theoretical frameworks. In cognitive science and computational neuroscience, internal models typically refer to explicit, often probabilistic, representations of environmental structure that support inferential processes such as prediction, simulation, and error correction. This is the sense in which the term is used here. By contrast, in Robert Rosen's relational biology, a system may be said to possess a model insofar as its internal dynamics give rise to behavior that is appropriately oriented toward future environmental states, even in the absence of representation or computation (Rosen, 1985).[100] In this broader, more pragmatic sense, plants may be described as modeling their environments through functional organization that supports adaptive outcomes. However, this usage of "model" departs sharply from its more common, representational meaning in the cognitive sciences. The purpose of the present discussion is precisely to preserve that distinction. While plants may qualify as anticipatory systems in Rosen's terms, they do not exhibit the kind of internal modeling that characterizes information-processing in organisms with nervous systems.

In sum, while plants do indeed propagate signals, often rapidly and adaptively, the structure and function of those signals is not equivalent to information-processing in animals. The language of "plant neurophysiology" risks obscuring this crucial distinction by importing assumptions about representational content and internal modeling that are not supported by empirical evidence.

4.4 Category Inflation and the Dangers of Metaphor

The notion of "plant neurophysiology" derives part of its appeal from the evocative power of the "neuro-" prefix. But this same rhetorical potency poses philosophical and scientific dangers. In this section, it is argued that referring to plant signaling systems in neurobiological terms tends to obscure critical organizational differences, facilitates conceptual slippage from analogy to homology, and invites anthropomorphic assumptions that are at odds with both biological evidence and contemporary enactivist philosophy. The cost is not merely terminological - it is theoretical confusion that may distort our understanding of cognition, agency, and biological organization.

4.4.1 The rhetorical power of "neuro-" language

The language of neuroscience carries considerable conceptual weight. Terms such as "neurophysiology," "neurotransmission," and "neural processing" are closely associated with intelligence, subjectivity, and agency. To describe a system as "neuro-" is implicitly to suggest that it partakes in the functional and perhaps even experiential capacities associated with animal nervous systems - perception, decision-making, and integrated behavioral control. This rhetorical power has been mobilized in the promotion of "plant neurobiology," where the use of

100 Rosen, R. (1985). *Anticipatory Systems: Philosophical, Mathematical, and Methodological Foundations*. Pergamon Press.

neurotransmitter analogues and action potentials is often taken to imply the existence of neural-like functions (Baluška & Mancuso, 2008; Segundo-Ortin & Calvo, 2021).[101]

Yet the persuasive force of such language frequently exceeds the evidential basis for its use. The presence of molecules such as glutamate, GABA, or serotonin in plants is often cited as evidence of neurophysiological continuity. However, as Robinson et al. (2023)[102] caution, molecular similarity does not entail functional equivalence. Glutamate may trigger calcium fluxes in plant cells, but this is not equivalent to its role in excitatory synaptic transmission in animal nervous systems. The invocation of "plant synapses" or "neural circuits" risks conflating shared biochemical substrates with convergent or even homologous cognitive mechanisms, when no such homology has been established.

4.4.2 Conceptual slippage: from mechanism to meaning

One of the most insidious consequences of "neuro-" metaphorics is the way analogies become misread as indicators of deep functional similarity. This process of conceptual slippage - from superficial mechanism to implied meaning - is evident in how plant glutamate receptors (GLRs) have been interpreted. In plants, GLRs are implicated in long-distance calcium signaling and systemic wound responses (Toyota et al., 2018),[103] yet these functions are a far cry from the role of glutamate in vertebrate synaptic transmission, where it contributes to complex encoding of spatial, temporal, and semantic information across interconnected neural networks (Kandel et al., 2013).[104]

The problem is not the use of analogy per se, but the failure to maintain awareness of its limits. As Love (2007)[105] argues, biological analogies are epistemically useful only when we remain attuned to the structural and functional contexts from which they arise. In the case of plant neurobiology, analogies with animal systems are often abstracted from vastly different organizational frameworks - distributed versus centralized control, excitable tissues versus neurons, ion channels versus synaptic vesicles. Without these distinctions, the metaphor of plant "neural" activity begins to imply a kind of cognitive depth that is neither warranted by empirical findings nor supported by theoretical rigor.

4.4.3 Philosophical caution: respecting organizational difference

More fundamentally, the overextension of neurocentric metaphors risks reintroducing anthropomorphic assumptions that enactivist and ecological approaches to cognition have worked

101 Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6
Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews Cognitive Science, 13*(2). https://doi.org/10.1002/wcs.1578

102 Robinson, D. G., Blatt, M. R., Draguhn, A., Taiz, L., & Mallatt, J. (2023). Plants lack the functional neurotransmitters and signaling pathways required for sentience in animals. *Animal Sentience, 8*(33). https://doi.org/10.51291/2377-7478.1782

103 Toyota, M., Spencer, D., Sawai-Toyota, S., Jiaqi, W., Zhang, T., Koo, A. J., Howe, G. A., & Gilroy, S. (2018). Glutamate triggers long-distance, calcium-based plant defense signaling. *Science, 361*(6407), 1112-1115. https://doi.org/10.1126/science.aat7744

104 Kandel, E. R. (2013). *Principles of Neural Science, Fifth Edition*. McGraw Hill Professional.

105 Love, A. C. (2007). Functional homology and homology of function: biological concepts and philosophical consequences. *Biology & Philosophy, 22*(5), 691-708. https://doi.org/10.1007/s10539-007-9093-7

hard to deconstruct. Enactivism, for instance, emphasizes the co-constitution of cognition and biological embodiment. Minds are not defined by the possession of certain neurochemical compounds but by the structured organization of sensorimotor loops that generate meaningful world-relations (Thompson, 2010; Di Paolo et al., 2017).[106] On this view, the mere presence of chemical signaling does not indicate cognition unless embedded in a form of life that integrates those signals into ongoing patterns of adaptive regulation and interactive sense-making.

Applying enactivist insights to plant biology thus calls for a different kind of sensitivity - not one that projects neural capacities onto plants, but one that attends to their distinctive forms of embodied organization. Plants are sessile, autotrophic, and developmentally plastic organisms whose behavioral repertoire and environmental engagement are profoundly shaped by their architectural and metabolic constraints. Their intelligence, if one wishes to call it that, emerges not from neuronal computations but from the modulation of growth, hormonal cross-talk, and decentralized responsiveness across modular structures (Trewavas, 2014).[107]

To respect these organizational differences is not to deny plant capacities, but to understand them on their own terms. The temptation to frame plant responsiveness in neurophysiological language may stem from a desire to elevate plant agency to cognitive status. Yet such elevation should not come at the cost of conceptual clarity. If we are to expand our understanding of cognition beyond animals, we must resist the pull of familiar metaphors and instead cultivate conceptual frameworks appropriate to the biological forms we study.

4.5 Conclusion: Toward a More Accurate Conceptual Vocabulary

The argument advanced thus far has not aimed to diminish the sophistication of plant signaling, nor to deny the deep evolutionary continuities among living systems. Rather, it has sought to clarify the categorical distinctions necessary for a precise and philosophically coherent understanding of plant life. If plants do not possess neurophysiology in any strict or homologous sense, then what terms should we use to describe their impressive signaling capabilities? This concluding section proposes alternative conceptual frameworks that do justice to plant complexity without importing neural assumptions - particularly through the lens of non-neuronal bioelectricity, electrophysiology, and a refined model of agency.

4.5.1 Plants as bioelectric organisms

Although plants lack neurons, they are indisputably bioelectrical organisms. They generate action potentials, display variation potentials in response to damage, and exhibit long-distance electrical signaling that coordinates systemic physiological responses (Fromm & Lautner, 2006; Zimmermann & Mithöfer, 2013).[108] This electrochemical responsiveness is not unique to plants.

106 Thompson, E. (2010). *Mind in life: Biology, phenomenology, and the sciences of mind*. Belknap Press/Harvard University Press.
Di Paolo, E. A., Buhrmann, T., & Barandiaran, X. E. (2017). *Sensorimotor life: An Enactive Proposal*. Oxford University Press.

107 Trewavas, A. J. (2014). *Plant Behaviour and Intelligence*. Oxford University Press.

108 Fromm, J., & Lautner, S. (2006). Electrical signals and their physiological significance in plants. *Plant Cell & Environment, 30*(3), 249-257. https://doi.org/10.1111/j.1365-3040.2006.01614.x

Indeed, many early-diverging metazoans – such as sponges and cnidarians – exhibit excitable cells or tissues without possessing nervous systems per se (Leys, 2015; Moran & Zakon, 2014).[109] These cases highlight the existence of pre-neural bioelectrical architectures that operate independently of neuronal organization but nevertheless enable coordinated, whole-organism responses to environmental stimuli.

Understanding plants in this light situates them within a broader class of organisms that use excitable membranes and ion-based signaling to maintain physiological coherence and environmental responsiveness. This does not require positing neurons, synapses, or centralized processing units. Rather, it affirms the diversity of bioelectric strategies in the living world and allows us to place plant signaling within a comparative framework that includes, but is not limited to, neural systems.

4.5.2 Signaling without neurophysiology

A more accurate term for what plants do may be "plant electrophysiology." This label captures the real and measurable bioelectrical phenomena observed in plant tissues – action potentials, membrane depolarizations, and calcium waves – without implying homology with animal neural processing (Volkov, 2010; Salvador-Recatalà et al., 2014).[110] It allows for specificity about the mechanisms involved while remaining neutral about their functional equivalence to neural computation.

This terminological shift is not merely semantic. "Neurophysiology" carries with it a conceptual history rooted in the study of perception, cognition, and motor coordination in animals. To apply this term to plants encourages a misleading inference: that similar molecular mediators entail similar functional architectures. By contrast, electrophysiology" avoids smuggling in assumptions about information processing, representation, or subjective experience. It focuses our attention on the dynamic regulation of physiological states, rather than suggesting the presence of minds or nervous systems where there are none.

Zimmermann, M. R., & Mithöfer, A. (2013). Electrical Long-Distance signaling in plants. In *Long-Distance Systemic Signaling and Communication in Plants* (pp. 291-308). https://doi.org/10.1007/978-3-642-36470-9_15

109 Leys, S. P. (2015). Elements of a 'nervous system' in sponges. *Journal of Experimental Biology, 218*(4), 581-591. https://doi.org/10.1242/jeb.110817
Moran, Y., & Zakon, H. H. (2014). The evolution of the four subunits of Voltage-Gated calcium channels: ancient roots, increasing complexity, and multiple losses. *Genome Biology and Evolution, 6*(9), 2210-2217. https://doi.org/10.1093/gbe/evu177

110 Volkov, A. G. (2010). *Plant Electrophysiology: Theory and Methods*. Springer.
Salvador-Recatalà, V., Tjallingii, W. F., & Farmer, E. E. (2014). Real-time, in vivo intracellular recordings of caterpillar-induced depolarization waves in sieve elements using aphid electrodes. *New Phytologist, 203*(2), 674-684. https://doi.org/10.1111/nph.12807

5 Communication

5.1 Introduction: Varieties of Plant Communication and the Discourse of Plant Intelligence

This section introduces the topic of plant communication, exploring the various claims made in the scientific literature about how plants interact with one another and their environment. It reviews the different mechanisms through which plants are said to communicate, including chemical, electrical, and mycorrhizal signaling. The section then highlights the key questions about the nature of plant communication, setting the stage for a deeper discussion in the following sections about whether these interactions can truly be considered communication in the same sense as seen in animals.

5.1.1 Claims for Plant Communication

In recent decades, the biological sciences have increasingly emphasized the complexity, sensitivity, and adaptiveness of plant life. Central to this reevaluation is the claim that plants are capable of communication – a term now used across a broad spectrum of empirical studies involving inter- and intra-organismic signaling. Whether through airborne chemical cues, soil-mediated nutrient exchange, electrical pulses, or physical contact, plants have been shown to produce, transmit, and respond to diverse signals across space and time. These signaling phenomena are often grouped under the expansive heading of "plant communication," and have become a touchstone in contemporary arguments for plant intelligence, behavioral plasticity, and even cognition (Trewavas, 2014; Calvo & Keijzer, 2011; Karban, 2015).[111]

5.1.2 Varieties of So-Called Plant Communication

Among the most extensively studied modes of plant signaling are those involving volatile organic compounds (VOCs), released in response to abiotic or biotic stressors, especially herbivore attack. Many plants, including poplar, sagebrush, and maize, emit complex blends of VOCs when their tissues are damaged, which neighboring conspecifics or even heterospecifics can detect and respond to by upregulating their own defensive pathways (Heil & Karban, 2009; Frost et al., 2008).[112] This so-called “eavesdropping” on volatile cues has been interpreted as a form of warning signal or priming, leading to questions about whether such emissions are merely incidental or serve a selected communicative function. Some studies suggest that the emitted VOC blends are context-sensitive, varying with herbivore identity or tissue type, hinting at a potential specificity or

111 Trewavas, A. J. (2014). *Plant Behaviour and Intelligence*. Oxford University Press.
Calvo, P., & Keijzer, F. (2011). Plants: Adaptive behavior, root-brains, and minimal cognition. *Adaptive Behavior, 19*(3), 155-171. https://doi.org/10.1177/1059712311409446
Karban, R. (2015). *Plant sensing and communication*. University of Chicago Press.

112 Heil, M., & Karban, R. (2009). Explaining evolution of plant communication by airborne signals. *Trends in Ecology & Evolution, 25*(3), 137-144. https://doi.org/10.1016/j.tree.2009.09.010
Frost, C. J., Mescher, M. C., Carlson, J. E., & De Moraes, C. M. (2008). Plant Defense Priming against Herbivores: Getting Ready for a Different Battle. *Plant Physiology, 146*(3), 818-824. https://doi.org/10.1104/pp.107.113027

"semantic" content (Mithöfer & Boland, 2012).[113] Yet whether this context sensitivity reflects genuine signal modulation or merely biochemical constraint remains contentious.

Belowground, root exudates represent another prolific avenue of plant signaling. These exudates include sugars, amino acids, organic acids, flavonoids, and secondary metabolites that shape microbial communities in the rhizosphere, attract symbionts, inhibit competitors, or facilitate kin recognition (Bais et al., 2006; Mommer et al., 2016).[114] Some legumes, for instance, exude flavonoids that specifically induce nodulation genes in compatible rhizobia, triggering a cascade of mutualistic development. Meanwhile, plants like *Arabidopsis thaliana* and *Zea mays* show differential root allocation when grown in the presence of kin vs. non-kin, suggesting a chemical basis for identity recognition (Dudley & File, 2007).[115] These processes often blur the boundary between physiology and communication, and have fueled philosophical debates about intentionality and individuality in plant systems.

Recent attention has also been directed at mycorrhizal networks, or common mycorrhizal networks (CMNs), in which symbiotic fungi form vast subterranean connections between the roots of multiple plant individuals. Through these networks, plants can exchange not only carbon, phosphorus, and nitrogen, but also allelopathic compounds and stress-related cues (Simard et al., 2012; Song et al., 2010).[116] For example, drought-stressed plants have been shown to alter the root architecture and water uptake of their neighbors via CMNs, even in the absence of direct root contact. There is growing evidence that such networks can support asymmetric transfer (from larger to smaller plants, or from parents to offspring), suggesting a non-trivial ecological logic to their functioning. These networks complicate the classical notion of the autonomous plant individual and invite new metaphors of distributed coordination or even fungal-mediated "conversation" (Sheldrake, 2020),[117] though again, whether such processes qualify as communicative in any strong sense is philosophically unclear.

5.1.3 Questions Concerning Plant "Communication"

These signaling systems display a remarkable degree of sensitivity, specificity, and functional integration. It is no surprise, then, that many theorists have interpreted them as evidence for intelligent behavior or minimal cognition. The ability to initiate and respond to cues across diverse modalities, sometimes in a coordinated and seemingly goal-directed fashion, has been enlisted to support a vision of plants as communicative agents, participating in what some call a

113 Mithöfer, A., & Boland, W. (2012). Plant defense against herbivores: Chemical aspects. *Annual Review of Plant Biology, 63*(1), 431-450. https://doi.org/10.1146/annurev-arplant-042110-103854

114 Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology, 57*(1), 233-266. https://doi.org/10.1146/annurev.arplant.57.032905.105159
Mommer, L., Kirkegaard, J., & Van Ruijven, J. (2016). Root-Root interactions: towards a rhizosphere framework. *Trends in Plant Science, 21*(3), 209-217. https://doi.org/10.1016/j.tplants.2016.01.009

115 Dudley, S. A., & File, A. L. (2007). Kin recognition in an annual plant. *Biology Letters, 3*(4), 435-438. https://doi.org/10.1098/rsbl.2007.0232

116 Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., & Teste, F. P. (2012). Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biology Reviews, 26*(1), 39-60. https://doi.org/10.1016/j.fbr.2012.01.001
Song, Y. Y., Zeng, R. S., Xu, J. F., Li, J., Shen, X., & Yihdego, W. G. (2010). Interplant Communication of Tomato Plants through Underground Common Mycorrhizal Networks. *PLOS One, 5*(10), e13324. https://doi.org/10.1371/journal.pone.0013324

117 Sheldrake, M. (2020). *Entangled life: How Fungi Make Our Worlds, Change Our Minds & Shape Our Futures*. Random House.

"phytosemiosis" – a plant-based form of semiosis or meaning-making (Mancuso & Viola, 2015; Hoffmeyer, 2008).[118]

However, this expansion of communicative attributions invites critical scrutiny. Do these signals rise to the level of genuine communication, or are they better understood as causally efficacious cues within structurally coupled biological systems? Are plants capable of modulating their signals in light of inferred states in other organisms, or do they merely produce context-bound responses to environmental regularities? Is there a layer of interpretation involved in how such signals are received and acted upon, or are responses pre-patterned and stimulus-bound?

These questions lead to deeper conceptual issues that demand clarification before strong analogies to animal communication can be justified. If "communication" is to retain any analytical precision – especially in comparative biology and philosophy of mind – we must ask what theoretical conditions it presupposes. In what follows, a principled account of these conditions is provided along with an argument that while plant signaling is biologically complex and ecologically consequential, it is not communicative in the intentional, symbolic, or interpretive sense typically associated with animal or human cognition.

5.2 Conceptual Foundations: Communication, Signaling, and Indexicality

This section delves into the indexical nature of plant signaling, distinguishing it from true communication. It argues that plant signals, such as the emission of volatile organic compounds or root exudates, function as causal, environmentally contingent cues rather than intentional messages. By examining the ecological consequences of plant signaling, the section emphasizes that these signals are better understood as part of an ecological system of interdependence, where responses are driven by evolutionary adaptations, not by cognitive or representational intent. This framework of indexicality clarifies the distinction between plant signaling and animal communication.

5.2.1 Indexicality of Plant Signaling

The intricate and diverse signaling behaviors observed in plants – from the emission of volatile organic compounds (VOCs) to the secretion of root exudates, and from hydraulic changes to electrical signaling – have prompted a growing number of researchers to describe these phenomena as "plant communication." However, such characterizations require careful conceptual scrutiny to avoid conflating fundamentally distinct processes. To clarify, it is essential to distinguish between signaling understood broadly as any causally effective exchange of information in ecological systems, and communication conceived narrowly as intentional or representational interaction. This section develops this distinction and proposes a working definition of plant signaling as the environmentally and physiologically contingent production of indexical cues. It is argued that while plant signaling can have important ecological consequences,

118 Mancuso, S., & Viola, A. (2015). *Brilliant Green: The Surprising History and Science of Plant Intelligence*. Island Press.
Hoffmeyer, J. (2008). *Biosemiotics: An Examination Into the Signs of Life and the Life of Signs*. University of Scranton Press.

it does not meet the criteria for genuine communication, and is better understood as non-representational, causally linked outputs embedded within an ecological network of structural coupling.

In ethology and evolutionary biology, the difference between cues and signals has long been recognized. A cue is any feature of an organism or its behavior that can be exploited by another organism to guide its own behavior, irrespective of whether the cue evolved for that function. A signal, on the other hand, is a trait shaped by natural selection precisely because it changes the behavior of receivers to the benefit of the sender (Smith & Harper, 2003).[119] For example, the bright plumage of male birds often functions as a sexual signal, evolved to attract mates by exploiting female sensory biases.

5.2.2 Communication and Intention

In philosophy of communication and language, an even more demanding standard is often applied, rooted in intention. Following Grice (1957),[120] communication requires that a signaler produce a sign with the intention that the receiver recognize that very intention. While few nonhuman animals meet the full Gricean criterion, many demonstrate flexible signaling behaviors that adjust to social context (Tomasello, 2010).[121]

By contrast, there is little evidence that plant signaling meets this standard. Signals in plants appear as largely automatic, physiologically driven responses to environmental and internal stimuli, lacking the hallmarks of directedness or flexible modulation in response to audience. For instance, when a leaf is damaged by herbivory, the plant releases methyl jasmonate and other VOCs as part of a systemic defensive cascade (Wasternack & Hause, 2013).[122] These compounds can induce defensive responses in neighboring plants or attract predatory insects that consume herbivores. However, this emission is not a chosen act of expression or an attempt to convey information, but rather an inevitable consequence of the plant's metabolic and signaling pathways responding to injury. Although such signals have clear ecological effects, they are not produced with the aim of communication or coordinated interaction.

Some might object that such a narrow, intention-based definition of communication is unnecessary, arguing that the term can simply be extended to cover any process in which a signal from one organism affects another. Yet the point of maintaining a stricter standard is precisely to avoid conflating two radically different kinds of phenomena. When one person speaks to another, the act is embedded in a web of intentional states, guided by the aim that the hearer recognize the speaker's intention to be understood. By contrast, when a plant emits volatile compounds that alter the behavior of a neighbor, there is no comparable mental state or aim at comprehension. To be sure, one could call both cases "communication" in a purely descriptive, effect-based sense, but

119 Smith, J. M., & Harper, D. (2003). *Animal signals*. Oxford University Press.
120 Grice, H. P. (1957). Meaning. *The Philosophical Review, 66*(3), 377. https://doi.org/10.2307/2182440
121 Tomasello, M. (2010). *Origins of human Communication*. MIT Press.
122 Wasternack, C., & Hause, B. (2013). Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in Annals of Botany. *Annals of Botany, 111*(6), 1021-1058. https://doi.org/10.1093/aob/mct067

doing so risks obscuring the categorical distinction between behavior underwritten by a mind and behavior that is not. The term "communication" carries strong cognitive connotations, making it all too easy to slide from the uncontroversial claim that plants signal to the unwarranted conclusion that they converse or engage in exchanges akin to human dialogue—something plainly absent, as evidenced by the fact that plants do not have conversations at all. It is for this reason that conceptual discipline in the use of the term is not pedantic, but necessary to prevent the inadvertent attribution of cognitive capacities where none exist.

5.2.3 A Philosophically Sound Characterization of Plant Signaling

To capture these features, a working definition is proposed that casts plant signaling as the production and transmission of physiological outputs - chemical, electrical, or mechanical - that are causally linked to internal or environmental states and may influence other organisms, but which are not produced with the aim of affecting those organisms or coordinating shared behavior. This definition acknowledges that plant signals are neither accidental nor arbitrary. Rather, they are shaped by evolutionary pressures that optimize the plant's responsiveness to stressors and environmental variables. However, these outputs do not constitute expressions or messages intended for other organisms. Rather than chosen acts of expression, they are contingently modulated outputs whose production is contingent on environmental and physiological conditions.

Semiotic theory, especially the Peircean framework, provides further insight. Peirce (1932)[123] distinguishes between icons, which resemble their referents; symbols, which are connected to their referents by social convention; and indices, which have a causal or physical connection to what they indicate. Plant signals fit clearly into the category of indices. The emission of methyl salicylate or ethylene gas does not symbolically represent herbivore attack but stands in a direct causal relation to it. These chemical emissions serve as ecological indices, signaling the presence of stress or damage through their causal connection, not through encoded semantic content.

Importantly, the "meaning" of these signals arises not within the plant itself but within the ecological context of other organisms' evolved or learned sensitivities. For example, predatory wasps use plant-emitted VOCs to locate caterpillars feeding on leaves (Dicke & Baldwin, 2010).[124] Similarly, neighboring plants can detect root exudates or airborne signals to prime their own defensive mechanisms (Heil & Karban, 2009).[125] In these cases, the interpretive and responsive acts are performed entirely by receivers; plants are not sending intentional messages but rather releasing environmental cues. This ecological interdependence exemplifies structural coupling (Maturana & Varela, 1980)[126] - that is, organisms become mutually responsive to each other's

123 Peirce, C. (1932). *Collected Papers of Charles Sanders Peirce, Volumes I and II: Principles of Philosophy and Elements of Logic*. Harvard University Press.

124 Dicke, M., & Baldwin, I. T. (2010). The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help.' *Trends in Plant Science, 15*(3), 167-175. https://doi.org/10.1016/j.tplants.2009.12.002

125 Heil, M., & Karban, R. (2009). Explaining evolution of plant communication by airborne signals. *Trends in Ecology & Evolution, 25*(3), 137-144. https://doi.org/10.1016/j.tree.2009.09.010

126 Maturana, H. R., & Varela, F. J. (1992). *Tree of knowledge: The Biological Roots of Human Understanding*. Shambhala.

physiological states through causal interaction without requiring shared intentionality or representation.

To further delineate the boundary between signaling and communication, we may consider the conceptual criteria for genuine communication. Communication generally involves several interrelated features: first, the directedness of signals, whereby a sender produces them specifically to affect a receiver's behavior or mental state; second, audience contingency, meaning that signal production varies depending on the presence or identity of potential receivers; third, the existence of an interpretive process on the receiver's side, involving some level of internal representation, inference, or context-sensitive decoding; and fourth, feedback sensitivity, where the sender adapts signaling strategies based on the receiver's responses.

Many animal communication systems exhibit these features, at least in part. For example, vervet monkeys produce distinct alarm calls for different predators, modulating calls depending on who is nearby (Cheney & Seyfarth, 1990).[127] Honeybees perform waggle dances that encode distance and direction to food sources, which are actively interpreted by nestmates who respond accordingly (von Frisch, 1993).[128] These interactions are embedded within dynamic, reciprocal exchanges that allow for flexible, adaptive communication. By contrast, plant signaling is typically invariant with respect to social context. The emission of VOCs or electrical signals does not change when potential receivers are present or absent, and there is no evidence of feedback loops whereby plants adjust signaling based on the responses of neighbors. Receivers respond through biochemical pathways or behavioral changes, but without cognitive inference or representational mediation.

Therefore, while plant signals can profoundly influence ecological interactions and contribute to community-level dynamics, they do not satisfy the conceptual standards for communication as intentional or representational acts. Instead, plant signaling should be understood as a form of ecological indexicality - causally grounded signals that function as environmental cues rather than communicative messages. This perspective avoids anthropomorphic projections of cognition or intentionality onto plant processes while preserving an appreciation for the rich and adaptive ways plants participate in their ecosystems. Ultimately, the structural coupling of plants and their environment exemplifies a distributed, non-representational responsiveness that, although functionally sophisticated, differs fundamentally from the communicative phenomena observed in animals.

5.3 Structural Coupling Without Representation: The Ecology of Plant Signaling

This section explores the concept of "structural coupling" in plant signaling, examining how plant interactions with their environment and other organisms are shaped by reciprocal modulation rather than communication in the traditional sense. Drawing from enactivist perspectives, it

127 Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the Mind of Another Species*. University of Chicago Press.
128 Von Frisch, K. (1993). *The dance language and orientation of bees*. Belknap Press.

emphasizes that plant signaling functions within a system of ecological responsiveness, where signals trigger endogenous changes without representing or conveying information. By focusing on examples like VOC-mediated signaling and root-based communication, the section argues that plant signaling should be understood as a dynamic process of ecological coordination, not as a form of cognitive or semiotic communication. This approach highlights the need for a relational ontology that respects the unique forms of plant interaction within their ecological contexts.

5.3.1 Structural Coupling

Having distinguished plant signaling from genuine communication and established its fundamentally indexical nature, we turn now to the ecological and systemic context within which such signals function. Plant signaling unfolds within a web of structural couplings between organisms and their environments. From an enactivist perspective, these couplings do not require internal representations or information-processing architectures. Rather, they emerge from the reciprocal modulation of organismal and environmental states over time. In this view, plant signaling is best understood not as a communicative exchange between cognitively individuated agents, but as an ongoing pattern of environmentally mediated responsiveness distributed across living systems.

Structural coupling, a central concept in the work of Maturana and Varela (1980),[129] refers to the recursive co-regulation of systems that maintain their own organizational closure while remaining in operational contact with each other. In this sense, an organism and its environment become mutually specified over the course of their interaction history. Signals do not function here as instructions or representations to be decoded, but as perturbations that trigger endogenous changes in the receiver. For plants, such perturbations include changes in chemical gradients, light intensity, soil nutrient distribution, or biotic signals like volatile organic compounds and microbial exudates. These inputs do not bear representational content but act as triggers that modulate internal dynamics - gene expression, ion fluxes, growth patterns - according to the plant's evolved sensitivities.

Consider the example of VOC-mediated signaling among sagebrush plants. When one plant is damaged by herbivores, it emits a complex bouquet of volatiles including terpenes and green leaf volatiles. Nearby conspecifics, upon detecting these compounds, upregulate their own defensive genes even before being attacked (Karban, 2008).[130] This cascade appears “communicative” in that one plant’s condition affects another’s physiology, but from the enactivist standpoint, the process is better understood as reciprocal modulation within a shared ecological niche. The “sender” plant does not emit volatiles in order to warn others; the emission is an artifact of its damaged tissue and ensuing metabolic response. The “receiver” does not interpret a message but reacts in accordance with its own structural dispositions - membrane-bound receptors, transcriptional machinery, and biochemical pathways tuned by evolutionary pressures.

129 Maturana, H., & Varela, F. J. (1980). *Autopoiesis and cognition: The Realization of the Living*. Springer.

130 Karban, R. (2008). Plant behaviour and communication. *Ecology Letters, 11*(7), 727-739. https://doi.org/10.1111/j.1461-0248.2008.01183.x

5.3.2 Structural Coupling and the Plant *Umwelt*

This interaction resembles what Jakob von Uexküll (1957)[131] called an *Umwelt* – a species-specific perceptual world structured by the organism's sensory and motor capacities. A sagebrush's sensitivity to airborne volatiles and ability to modify its metabolic state in response does not imply symbolic reference but indicates a co-evolved responsiveness to patterns in its environment. Importantly, this responsiveness is neither passive nor reactive in a mechanistic sense. It is an active maintenance of viability within a fluctuating world – a central enactivist tenet. Still, it does not entail the mediation of representational states.

Similarly, in root-based signaling, plants release a range of soluble compounds – amino acids, phenolics, flavonoids – into the rhizosphere, which influence microbial communities and neighbor root systems. Legumes, for example, secrete flavonoids that activate Nod factor production in rhizobia, initiating symbiotic nitrogen fixation (Oldroyd, 2013).[132] While this process involves highly specific biochemical recognition and reciprocal morphological transformation, it lacks the representational asymmetry of typical animal communication. Each partner responds according to internal regulatory pathways without constructing a model of the other. Their interaction is scaffolded by biochemical compatibility and environmental contingencies, not by mutual understanding.

What these examples reveal is that plant signals function as part of a distributed system of ecological responsiveness. The plant is not sending or receiving information in the cognitive sense but participating in causal loops that link it to other organisms and environmental variables. In this respect, plant signaling is akin to structural affordance – it makes possible specific patterns of interaction without presupposing informational content. These interactions have evolved to stabilize certain beneficial outcomes – reduced herbivory, improved symbiosis, optimized resource use – but they do so through modulation and co-regulation rather than through encoding and decoding.

5.3.3 A Systems-Based, Relational Ontology of Plant Signaling

In place of the sender-receiver model of communication that dominates animal studies, plant interactions call for a systems-based, relational ontology. Signals in plants are neither subjective messages nor objective signs; they are interfacial events, triggers whose function lies not in what they mean but in what they do. To describe these systems as "communicative" is to impose an anthropomorphic framework that occludes their underlying logic of coupling and response. Enactivism, with its rejection of representationalist accounts and emphasis on embodied, situated cognition, offers a compelling way to interpret plant signaling without inflating its cognitive or semiotic status.

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131 von Uexküll, J. (1957). A stroll through the worlds of animals and men. In C. H. Schiller (Ed.), *Instinctive behavior: The development of a modern concept* (pp. 319-391). International Universities Press.

132 Oldroyd, G. E. D. (2013). Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nature Reviews Microbiology, 11*(4), 252-263. https://doi.org/10.1038/nrmicro2990

We thus arrive at a crucial distinction: whereas animal communication frequently involves representational content mediated by neural processes, plant signaling consists in non-representational, environmentally entrained coupling. This distinction matters not only for terminological clarity but also for theoretical integrity. If we are to take seriously the intelligence and agency of plants, we must do so on terms appropriate to their form of life - not by stretching categories developed for animals, but by developing conceptual tools that reflect plants' own ecologies of responsiveness.

5.4 Interspecies Signaling and the Ecology of Coordination

This section examines interspecies signaling between plants and other organisms, such as microbes, insects, and fungi. While these interactions can appear coordinated and sophisticated, they are better understood as forms of ecological coordination rather than true communication. By analyzing examples like mycorrhizal symbiosis and pollination, the section highlights how plant signaling is driven by evolved regularities and ecological interactions, without symbolic meaning or cognitive mediation. The distinction between ecological coupling and communication helps clarify the functional role of plant signaling in broader ecological systems.

5.4.1 Interspecies Signaling Without Representation or Intention

The apparent sophistication of plant-involved interspecies signaling - such as that between plants and microbes, insects, or fungi - can easily tempt us to describe these interactions as instances of communication. However, such a description risks misrepresenting their nature. While these exchanges often involve highly specific and coordinated molecular signals, they do not meet the criteria for communication in the intentional, representational, or interpretive sense familiar from animal models. Instead, they are best understood as forms of ecological coordination - dynamically coupled interactions shaped by co-evolution and structural compatibility, not by symbolic meaning or cognitive mediation.

Take, for example, the mycorrhizal symbiosis between plant roots and arbuscular mycorrhizal fungi (AMF). In this relationship, plants secrete strigolactones into the soil, which stimulate hyphal branching in AMF and guide the fungi toward the roots (Akiyama, et al., 2005).[133] In response, AMF produce lipochitooligosaccharides, triggering changes in root membrane potential and the initiation of symbiotic accommodation pathways in the plant (Bonfante & Requena, 2011).[134] On the surface, this reciprocal exchange of molecular signals appears tightly choreographed and responsive, suggesting a form of dialog. However, both parties act through the activation of endogenous signaling cascades, guided by genetically encoded sensitivities. There is no evidence of intentional signaling or representational inference. Each organism acts according to its own structural constraints and metabolic interests, shaped by evolutionary history, without a shared symbolic code or interpretive engagement.

133 Akiyama, K., Matsuzaki, K., & Hayashi, H. (2005). Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature, 435*(7043), 824-827. https://doi.org/10.1038/nature03608

134 Bonfante, P., & Requena, N. (2011). Dating in the dark: how roots respond to fungal signals to establish arbuscular mycorrhizal symbiosis. *Current Opinion in Plant Biology, 14*(4), 451-457. https://doi.org/10.1016/j.pbi.2011.03.014

5.4.2 Plant Signaling and Absence of Meaning

Similar dynamics occur in pollination syndromes. Flowering plants produce volatile organic compounds (VOCs), nectar, pigments, and structural cues that attract specific pollinators. These signals – floral scent bouquets, UV patterns, nectar guides – are often species-specific and finely tuned to the perceptual apparatus of their pollinators (Raguso, 2008).[135] Pollinators, in turn, have evolved preferences and learning mechanisms that enable them to associate particular sensory cues with rewards. While there is mutual benefit and apparent signal-receiver fit, it is critical to distinguish co-evolved coupling from communicative intent. The flower does not "inform" the pollinator of nectar availability; it emits chemical and visual cues that reliably co-occur with a resource. The pollinator does not "understand" the flower; it follows learned or innate behavioral rules that associate cues with action. The interaction functions through mutual exploitation of evolved regularities, not shared meaning.

Even in cases where such interactions exhibit plasticity – e.g., plants altering VOC production depending on pollinator presence or herbivore damage – the modifications arise from physiological feedback loops, not agentive expression. For example, *Nicotiana attenuata* can reduce floral scent emission in response to herbivory, minimizing attraction of herbivore-vectored moths while still attracting diurnal pollinators (Kessler et al., 2008).[136] This context-sensitive modulation is adaptive, but again, not communicative in the cognitive or semiotic sense. It lacks a representational layer through which the plant encodes information about its state or the environment for a receiver to interpret. The "signal" is a byproduct of metabolic regulation and ecological history, not a symbolic gesture.

5.4.3 Plant Signaling as Ententional – But Not Intentional

Plant communication is best understood as ententional rather than intentional, in the sense developed by Deacon (2011).[137] Ententional phenomena display a kind of purposiveness or directedness – they are about something in a minimal, functional sense – but they do not require cognition or representation. In plants, signaling behaviors such as the release of volatile compounds in response to herbivore attack are reliably constrained by specific internal and environmental conditions. These signals play adaptive roles, modulating the behavior of other organisms or priming defenses in nearby tissues. What makes them ententional is that they are embedded in a system of constraints that refer, in a causal and functional sense, to ecologically relevant states of affairs. However, they are not intentional in the stronger, representational sense.

On Deacon's account, intentionality emerges from ententionality when a system is capable of recursively modeling its own ententional dynamics – when it can not only generate signals, but

135 Raguso, R. A. (2008). Wake up and smell the roses: The ecology and evolution of floral scent. *Annual Review of Ecology Evolution and Systematics, 39*(1), 549-569. https://doi.org/10.1146/annurev.ecolsys.38.091206.095601

136 Kessler, D., Gase, K., & Baldwin, I. T. (2008). Field Experiments with Transformed Plants Reveal the Sense of Floral Scents. *Science, 321*(5893), 1200-1202. https://doi.org/10.1126/science.1160072

137 Deacon, T. W. (2011). *Incomplete Nature: How Mind Emerged from Matter*. W. W. Norton & Company.

represent those signals as symbols that stand for something in a way that can be flexibly interpreted, evaluated, and manipulated. This emergent symbolic capacity requires recursive operations on constraints, such as modeling the relation between a sign and its referent, and evaluating whether that relation holds. There is no evidence that plants engage in such operations. These recursive, meta-ententional processes appear to require the kinds of dynamic, integrative architectures characteristic of nervous systems - especially their capacity for metastable coupling and layered constraint hierarchies. While plant communication is richly functional and environmentally responsive, it does not cross the threshold into the domain of intentionality because it lacks the organizational means to represent its own signals as symbols.

5.4.4 An Ecological and Systemic View of Plant Signaling

From the perspective of enactivist and ecological models, these interspecies signaling systems represent structural coupling across species boundaries. The plant, fungus, insect, or bacterium modulates its behavior in relation to the perturbations introduced by others in its ecological niche. These perturbations - molecular, electrical, or mechanical - act not as carriers of semantic content but as catalysts of internal regulation. There is no semantic asymmetry, no internal representation of another's state, and no interpretive act. Instead, each participant remains operationally closed while remaining structurally open to co-modulation. In this sense, interspecies signaling involving plants exhibits reciprocal functional entrainment, not communication proper.

This distinction is essential if we are to avoid anthropomorphizing ecologically complex but cognitively minimal phenomena. Genuine communication, particularly in the animal context, entails at least three ingredients: (1) a sender capable of selecting or modulating a signal with some autonomy; (2) a receiver capable of interpreting that signal in relation to its inferred meaning or referent; and (3) a semiotic asymmetry in which the signal stands for something beyond itself. In interspecies signaling involving plants, none of these criteria are robustly met. Signal production is environmentally and physiologically constrained; signal reception is based on evolved sensitivities, not interpretation; and the signal lacks referentiality.

The temptation to describe these interactions as communicative arises from the elegance of their coordination and the strategic benefits they confer. Yet functionally successful coordination does not entail communication. Ants and aphids, for instance, form intricate mutualisms involving chemical cues and behavioral feedback loops, but even in these cognitively richer cases, much of the coordination can be explained without invoking symbolic reference or communicative intent (Hölldobler & Wilson, 1990).[138] In the case of plants, where cognitive capacities are minimal or absent, it is even more crucial to adopt an ecological and systemic view.

In conclusion, interspecies signaling involving plants constitutes a powerful example of distributed ecological coupling. These systems display functional specificity, dynamic plasticity, and mutual influence, but they do so without representational content or interpretive engagement. They are better understood as patterns of interaction that have evolved to stabilize mutually beneficial

138 Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. Harvard University Press.

outcomes under environmental constraints - not as instances of communication in any rich or intentional sense. By reserving the term “communication” for interactions that involve symbolic mediation or cognitive agency, we gain a clearer view of the genuinely alien form of intelligence exhibited by plants: one rooted not in messages and meanings, but in morphogenic plasticity, recursive responsiveness, and ecological attunement.

5.5 Conclusion

This section concludes the discussion of plant communication by highlighting the inappropriateness of applying the concept of communication to plant signaling. It emphasizes the importance of avoiding the conflation of animal communication with plant signaling, stressing that plant interactions should be understood in terms of ecological coordination rather than symbolic or intentional exchange.

5.5.1 Communication as an Inappropriate Notion for Plant Signaling

The notion of communication has long carried significant cognitive and philosophical weight. To say that an organism communicates is often to imply that it has something to say - that it operates with internal states, representations, or intentions that it seeks to share with others. When applied to animals, this assumption can be appropriate, given their behavioral flexibility, symbolic reasoning, and the centrality of nervous systems in mediating social interaction. However, when applied to plants, such language risks obscuring rather than clarifying. The evidence reviewed in this paper suggests that while plants engage in rich, structured, and ecologically effective signaling interactions - both intra- and inter-species - these do not amount to communication in the robust sense familiar from animal behavior.

What distinguishes plant signaling from genuine communication is the absence of symbolic reference, interpretive cognition, and expressive agency. Plant signals - whether airborne volatiles, hydraulic pressure waves, root exudates, or electrical potentials - are contingently modulated outputs of physiological and environmental states, not autonomous acts of expression. They are causally linked to internal conditions and external stimuli, making them indexical in a strict semiotic sense: like smoke to fire, they reliably correlate with the plant’s condition without conveying information about that condition in a representational mode. Receivers - be they other plants, insects, fungi, or bacteria - do not interpret these signals through a process of inference or decoding; rather, they respond in ways shaped by evolutionarily tuned sensitivities and structural affordances.

5.5.2 Avoiding Conflation of Animal Communication and Plant Signaling

This ecological embeddedness points toward a more appropriate conceptual model for plant signaling: not communication, but structural coupling. Enactivist frameworks offer a compelling vocabulary here. From this perspective, plants do not construct internal models of their environments or exchange messages across a semantic interface. Instead, they participate in

dynamically reciprocal perturbation loops that enable them to remain viable within an ever-shifting ecological context. These loops - composed of chemical emissions, growth pattern adjustments, microbial feedback, and environmental modulation - function not through shared symbols but through co-determined responsiveness. What results is not a dialogue, but an emergent coordination of behavior distributed across species boundaries and mediated by ecological constraints.

This view does not deny the complexity or adaptive significance of plant signaling systems. On the contrary, the forms of sensitivity, modulation, and responsiveness that plants exhibit are central to what might be called a plant-specific mode of intelligence - an intelligence without a nervous system, without movement, without a centralized processing organ, but with a remarkable capacity for distributed sensing and morphogenetic plasticity. Recognizing the distinctness of this form of intelligence requires resisting the pull of analogy when it tempts us to flatten ontological differences. It also demands conceptual tools that are not tethered to the animal paradigm of cognition and communication.

Indeed, the repeated temptation to describe plant signaling as communicative reflects not just an empirical question, but a philosophical one: what does it mean to communicate, and what kinds of beings can be said to do so? If communication requires the capacity to mean - to express and interpret, to symbolize and respond interpretively - then plants do not qualify. But if communication merely means the reliable transmission of causally informative signals, then the door opens not only to plants, but to rocks, rivers, and thermostats. Such broad usage drains the concept of its explanatory power. A scientifically and philosophically robust account of plant behavior must preserve distinctions that track relevant cognitive, semiotic, and agentive differences.

The question is not whether plants communicate like animals. They do not. Nor is it whether they are capable of remarkable forms of environmental responsiveness. They are. The real challenge is to understand plant signaling on its own terms - neither reducing it to mechanistic output, nor elevating it to proto-conscious expression. It is a form of ecological sense-making: The dynamic enactment of viability through structural coupling with the environment and other organisms. This framing avoids both the anthropomorphic trap and the reductive dismissal of plant life as passive. It allows us to take seriously the agency of plants without overstating their similarity to us.

In conclusion, by refusing to conflate plant signaling with communication, we avoid universalizing animal models, instead acknowledging the diversity of life's strategies for coping with complexity. Plant signaling is not communication but modulated responsiveness, and is rooted not in representation but in embodied coupling, and trades not in meaning but in structure-driven adaptation. This is not a deficiency - it is a different form of life.

6 Sense Perception

6.1 Introduction: Plant Sensitivities and Claims for Plant Sense Perception

This section explores the sophisticated environmental sensitivities exhibited by plants, demonstrating their ability to respond adaptively to a wide range of sensory inputs, from light and mechanical touch to chemical cues and gravity. It highlights how plants integrate these sensory signals to guide context-sensitive behaviors that optimize survival, reproduction, and growth. The section also introduces the debate surrounding plant sensitivity, emphasizing the need for a balanced perspective that avoids both anthropomorphizing plant behaviors and dismissing their complex responsiveness. The following discussion delves into whether this environmental sensitivity can be accurately described as sense perception, drawing on both empirical evidence and conceptual clarity.

6.1.1 Plant Environmental Sensitivities and Context-Sensitive Behaviors

Plants, despite lacking nervous systems, exhibit a rich array of environmental sensitivities across multiple sensory modalities, revealing a sophisticated capacity to perceive and respond to their surroundings. Research has shown that plants detect light not only in terms of intensity but also direction, wavelength, and duration, via an array of photoreceptors including phytochromes, cryptochromes, and phototropins (Galvão & Fankhauser, 2015; Chen et al., 2004; Franklin & Quail, 2009).[139] Mechanoreception enables plants to sense touch and mechanical stress, as in the thigmonastic responses of *Mimosa pudica* or the tendril movements of climbing species (Braam 2004).[140] Plants also respond to a wide range of chemical cues, both airborne and soil-borne, which they use for detecting herbivores, pathogens, and neighboring plants (Karban, 2008; Baluška & Mancuso, 2008).[141] Additionally, root systems exhibit gravitropism and hydrotropism, allowing plants to orient growth in relation to gravity and water availability (Wexler et al., 2024).[142] These modalities collectively constitute a complex sensory ecology, challenging traditional assumptions that sensory perception is exclusive to animal systems.

The integration of diverse sensory inputs enables plants to enact context-sensitive behaviors that optimize growth, reproduction, and survival. For instance, light detection not only drives

139 Galvão, V. C., & Fankhauser, C. (2015). Sensing the light environment in plants: photoreceptors and early signaling steps. *Current Opinion in Neurobiology, 34*, 46-53. https://doi.org/10.1016/j.conb.2015.01.013
Chen, M., Chory, J., & Fankhauser, C. (2004). Light signal transduction in higher plants. *Annual Review of Genetics, 38*(1), 87-117. https://doi.org/10.1146/annurev.genet.38.072902.092259
Franklin, K. A., & Quail, P. H. (2009). Phytochrome functions in Arabidopsis development. *Journal of Experimental Botany, 61*(1), 11-24. https://doi.org/10.1093/jxb/erp304

140 Braam, J. (2004). In touch: plant responses to mechanical stimuli. *New Phytologist, 165*(2), 373-389. https://doi.org/10.1111/j.1469-8137.2004.01263.x

141 Karban, R. (2008). Plant behaviour and communication. *Ecology Letters, 11*(7), 727-739. https://doi.org/10.1111/j.1461-0248.2008.01183.x
Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6

142 Wexler, Y., Schroeder, J. I., & Shkolnik, D. (2024). Hydrotropism mechanisms and their interplay with gravitropism. *The Plant Journal, 118*(6), 1732-1746. https://doi.org/10.1111/tpj.16683

phototropic curvature but modulates shade-avoidance responses, altering stem elongation and leaf morphology based on competitive light environments (Ballaré, 2014).[143] Mechanical stimuli can influence developmental trajectories, as persistent touch reduces internode elongation – a phenomenon termed thigmomorphogenesis (Braam, 2004).[144] Chemical signaling facilitates both defense and cooperation: Plants exposed to volatile organic compounds from damaged neighbors preemptively activate defense genes (Heil & Karban, 2009),[145] while root exudates modulate allelopathic interactions and kin recognition (Biedrzycki et al., 2010).[146] Even gravitational and hydric cues guide root foraging patterns in heterogeneous soils, optimizing resource acquisition (Freschet et al., 2021).[147] These responses underscore the functional role of plant sensory systems in modulating behavioral strategies, aligning with emerging frameworks that conceive of plant behavior as a product of decentralized, adaptive information processing (Trewavas, 2003; Garzón & Keijzer, 2009).[148]

6.1.2 A Balanced View of Plant Sensitivity

The capacity of plants to exhibit a sophisticated sensitivity to their environments – one that guides their growth and behavior in ways that are clearly adaptive – has led proponents of plant intelligence and agency to draw analogies between animal sense perception and plant environmental attunement.

In their 2014 paper, "Role of plant sensory perception in plant–animal interactions," Mark Mescher and Conseulo De Moraes[149] argue that the human tendency to interpret non-human life through an anthropocentric lens has long obscured the study of plant sensory capacities. They note that this bias manifests in two divergent yet equally misleading forms – the denial of plant perception based on their immobility and physiological invisibility to the human eye, and the uncritical projection of animal-like agency onto plants when they exhibit conspicuous behaviors, such as rapid movement. This bifurcation, they write, has led to both the neglect of subtle but adaptive plant responses and the proliferation of pseudoscientific claims – most notably in popular works of the 1970s that posited plants could feel emotions, respond to music, or possess extrasensory perception. The scientific backlash against such claims, though necessary, had the unintended consequence of casting a pall over legitimate inquiries into the perceptual sophistication of plants.

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143 Ballaré, C. L. (2014). Light regulation of plant defense. *Annual Review of Plant Biology, 65*(1), 335-363. https://doi.org/10.1146/annurev-arplant-050213-040145

144 Braam, J. (2004). In touch: plant responses to mechanical stimuli. *New Phytologist, 165*(2), 373-389. https://doi.org/10.1111/j.1469-8137.2004.01263.x

145 Heil, M., & Karban, R. (2009). Explaining evolution of plant communication by airborne signals. *Trends in Ecology & Evolution, 25*(3), 137-144. https://doi.org/10.1016/j.tree.2009.09.010

146 Biedrzycki, M. L., Jilany, T. A., Dudley, S. A., & Bais, H. P. (2010). Root exudates mediate kin recognition in plants. *Communicative & Integrative Biology, 3*(1), 28-35. https://doi.org/10.4161/cib.3.1.10118

147 Freschet, G. T., Pagès, L., Iversen, C. M., Comas, L. H., Rewald, B., Roumet, C., Klimešová, J., Zadworny, M., Poorter, H., Postma, J. A., Adams, T. S., Bagniewska-zadworna, A., Bengough, A. G., Blancaflor, E. B., Brunner, I., Cornelissen, J. H. C., Garnier, E., Gessler, A., Hobbie, S. E., . . . Mccormack, M. L. (2021). A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist, 232*(3), 973-1122. https://doi.org/10.1111/nph.17572

148 Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1-20. https://doi.org/10.1093/aob/mcg101
Garzón, P., Keijzer, F. (2009). Cognition in Plants. In: Baluška, F. (eds) *Plant-Environment Interactions. Signaling and Communication in Plants*. Springer. https://doi.org/10.1007/978-3-540-89230-4_13

149 Mescher, M. C., & De Moraes, C. M. (2014). Role of plant sensory perception in plant-animal interactions. *Journal of Experimental Botany, 66*(2), 425-433. https://doi.org/10.1093/jxb/eru414

Yet, as the authors emphasize, plants occupy a unique ecological niche in which sessility necessitates a high degree of physiological plasticity and environmental responsiveness. Lacking the capacity for locomotion, plants must instead adapt in situ to fluctuating conditions over extended timescales. This requires nuanced sensory mechanisms that guide morphological and biochemical changes. Contemporary research increasingly affirms the complexity of these perceptual processes, though debates persist – often more semantic than empirical – about whether terms like "intelligence" or "consciousness" are appropriate. Mescher and De Moraes suggest that a balanced approach is needed: one that avoids both reductive dismissal and sensational overreach, and that recognizes the distinctive modes of environmental engagement characteristic of plant life.

This thesis takes up Mescher and De Moraes' call to develop nuanced positions that avoid both the anthropomorphic projection of human or animal capacities onto plants and the undue dismissal of plants' sophisticated environmental responsiveness. The following discussion embraces the value of high-level comparative frameworks that illuminate shared features among living systems – particularly their embodied engagement with dynamic environments – while remaining attuned to the crucial distinctions between animal sense perception and the distinctive modalities of plant responsiveness. That plants exhibit sensitivity to a wide range of environmental cues is now uncontroversial; the more contentious and philosophically significant issue concerns whether such sensitivity warrants characterization in terms of sensing – or even perception. The following section addresses this question with close attention to both conceptual clarity and empirical grounding.

6.2 Dynamic Information Processing and Analogy to Animal Perception

This section examines how plants function as dynamic information-processing systems, integrating a wide array of environmental signals to regulate their growth and behavior. It explores how plants continuously monitor multiple variables – such as light, gravity, humidity, and nutrient levels – to coordinate complex behaviors like root foraging and shade avoidance. The section also discusses the analogy between plant and animal perception, highlighting the similarities and differences in how both systems process information, and emphasizes the unique, decentralized nature of plant information processing compared to animal systems.

6.2.1 Plants as Dynamic Information-Processing Systems

To begin, it is essential to recognize that plants operate as dynamic information-processing systems, capable of integrating heterogeneous environmental signals across multiple modalities to regulate growth and behavior. Far from responding reflexively to isolated stimuli, plants continuously monitor and integrate a range of environmental variables – including light, gravity, humidity, nutrient concentration, mechanical stimuli, and even the presence of neighboring

organisms (Trewavas, 2003; Calvo and Baluška, 2015).[150] This multi-modal integration enables plants to coordinate complex behaviors such as directional root foraging, phototropism, shade avoidance, and competitive or cooperative growth patterns.

Crucially, no single environmental cue is typically sufficient to predict plant behavior in isolation. For instance, the direction of root growth is not determined solely by nutrient availability but also by moisture gradients, mechanical impedance, and the plant's internal nutrient status (Gruntman & Novoplansky, 2004; Pierik & Testerink, 2014).[151] Likewise, shoot architecture is shaped not only by light direction and intensity but also by spectral composition, neighboring vegetation, and past growth history (Ballaré & Pierik, 2017).[152] These behaviors require plants to weigh multiple – and often conflicting – informational inputs, reflecting a form of decision-making that entails trade-offs between competing environmental demands.

6.2.2 Analogy to Animal Perception

At first glance, this capacity for integrative environmental assessment may appear analogous to the kind of centralized information processing found in animals, where sensory data from diverse modalities are coalesced to guide behavior in a coordinated manner. This analogy has prompted some researchers to suggest that plants possess a decentralized analogue of neural processing (Calvo et al., 2017),[153] or that they engage in forms of non-neural computation that functionally resemble aspects of animal cognition (Trewavas, 2005; Gagliano, 2017).[154]

As compelling as this analogy may seem, it risks obscuring important architectural and organizational differences between plant and animal systems. Unlike animals, plants lack a centralized nervous system or a functionally equivalent coordinating center. Their information processing is distributed across tissues and meristems, often occurring via slow-moving biochemical and electrical signals rather than rapid neural transmission (Baluška and Mancuso, 2008).[155] While plants do integrate information in adaptive and often – in a certain sense – anticipatory ways, the mechanisms by which they do so are radically different from those found in animal sensorimotor systems.

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150 Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany, 92*(1), 1-20. https://doi.org/10.1093/aob/mcg101
Calvo, P., & Baluška, F. (2015). Conditions for minimal intelligence across eukaryota: A cognitive science perspective. *Frontiers in Psychology, 6*, 1329. https://doi.org/10.3389/fpsyg.2015.01329

151 Gruntman, M., & Novoplansky, A. (2004). Physiologically mediated self/non-self discrimination in roots. *Proceedings of the National Academy of Sciences, 101*(11), 3863-3867. https://doi.org/10.1073/pnas.0306604101
Pierik, R., & Testerink, C. (2014). The Art of Being Flexible: How to Escape from Shade, Salt, and Drought. *Plant Physiology, 166*(1), 5-22. https://doi.org/10.1104/pp.114.239160

152 Ballaré, C. L., & Pierik, R. (2017). The shade-avoidance syndrome: multiple signals and ecological consequences. *Plant Cell & Environment, 40*(11), 2530-2543. https://doi.org/10.1111/pce.12914

153 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065

154 Trewavas, A. (2005). Plant intelligence. *The Science of Nature, 92*(9), 401-413. https://doi.org/10.1007/s00114-005-0014-9
Gagliano, M. (2017). The mind of plants: Thinking the unthinkable. *Communicative & Integrative Biology, 10*(2), e1288333. https://doi.org/10.1080/19420889.2017.1288333

155 Baluška, F., & Mancuso, S. (2008). Plant neurobiology: from sensory biology, via plant communication, to social plant behavior. *Cognitive Processing, 10*(S1), 3-7. https://doi.org/10.1007/s10339-008-0239-6

6.3 Distinguishing Plant Sensitivity from Animal Sense Perception

This section explores the architectural differences between plant and animal sensory systems, focusing on the structural distinctions that affect whether plant responsiveness can be considered true sense perception. It highlights the absence of specialized sensory organs in plants and contrasts this with the more complex, structured sensory systems in animals. The section also examines arguments for and against functional equivalence, considering whether plants' sophisticated environmental responsiveness can be equated with animal sense perception. Through these discussions, it clarifies the critical role of signal-processing architecture in defining what qualifies as sense perception.

6.3.1 Architectural Differences

Although both plants and animals exhibit sensitivity to their environments, the structural basis of this sensitivity differs in a way that bears directly on whether such responsiveness should count as sense perception in a biologically meaningful sense. The difference is not one of complexity or mere speed, but of architectural form: Animals typically process environmental inputs through specialized sensory organs, while plants rely on distributed, non-specialized receptors embedded across their tissues. This architectural distinction carries important information-theoretic implications that help clarify the boundary between genuine sense perception and more diffuse environmental responsiveness.

In animals, sense perception begins with organs that are selectively tuned to specific types of environmental energy - light, sound, pressure, or chemicals. These organs do more than passively detect stimuli; they actively filter, amplify, and encode those stimuli into structured informational signals. For instance, the retina decomposes light into spatiotemporal patterns, while cochlear hair cells translate sound waves into frequency maps. Even in sensory systems that are likely non-representational - like olfaction - this front-end processing imposes a form of signal structuring that temporally separates detection from response. As a result, the organism gains access to a manipulable internal variable that can be modulated, compared, or integrated before action occurs. Sensory information becomes portable within the system: it can be weighted, suppressed, routed, or stored depending on context, internal state, or behavioral goals.

Plants, by contrast, lack sensory organs. Their receptors - light-sensitive phytochromes, mechanoreceptors, or ion channels - are not localized in specialized tissues but are dispersed throughout the plant body. These receptors do transduce environmental inputs into internal changes, such as calcium waves, membrane depolarization, or hormonal fluxes. But the resulting signals are locally embedded in ongoing metabolic and morphogenetic processes. They are not encoded in a way that permits temporary abstraction or combinatorial manipulation. The signal is not lifted out of its substrate to serve as an informational token; rather, it is the physiological change. There is no distinct signal-processing layer that mediates between input and output. The transduction event and the organismal response are biochemically entangled - constituting a single, indivisible process of internal modulation.

6.3.2 Argument for Functional Equivalence

One might object that the absence of specialized sensory organs in plants does not entail a categorical difference in kind, but rather reflects an alternative biological implementation of the same functional role. From this perspective, both plants and animals transduce environmental energy into internal state changes that guide behavior. If the core function of sense perception is to extract and use information from the environment to modulate action, then plants appear to qualify, albeit through distributed and non-neural means.

Indeed, plants exhibit a wide range of stimulus-specific signaling phenomena: light detection via phytochromes and cryptochromes, mechanotransduction in tendrils and root tips, and long-distance electrical or calcium signaling following wounding or herbivory. These processes often show non-trivial integration - cross-talk between signaling pathways, modulation by internal states, and context-sensitive thresholds. Advocates of plant neurobiology argue that such features resemble basic information processing, or even computation.

Moreover, plants do exhibit functionally differentiated tissues with modality-specific responsiveness - root caps sensitive to gravity and touch, stomata responsive to CO_2 and humidity, pulvini that drive movement in response to light or mechanical stimulation. While these structures may not rise to the level of discrete organs, they arguably serve a similar purpose in filtering and responding to distinct environmental cues.

Finally, comparisons to simple animals like sponges, jellyfish, or sea stars suggest that centralized nervous systems and formal sensory organs are not prerequisites for sense perception. These animals often operate with nerve nets or diffusely organized receptors, and yet we commonly attribute to them some form of sentience or at least minimal sense perception. If animal sense perception can exist in such unstructured or low-bandwidth systems, why exclude plants?

In short, the objection holds that the relevant criteria for sense perception - stimulus specificity, internal signal modulation, and behavioral coordination - are all present in plant systems, just instantiated in a slower, biochemically mediated format. From this view, the distinction between animal and plant responsiveness is architectural but not fundamental.

6.3.3 Argument Against Functional Equivalence

This objection deserves to be taken seriously, particularly because it challenges us to identify what makes an information-processing system count as sensory in the biologically robust sense. However, the key response is that plant responsiveness lacks the architectural features that make sense perception possible, even in its non-representational forms. The absence of specialized sensory organs is not merely a surface-level difference; it reflects the absence of an intermediate signal-processing layer that is critical to sense perception as such.

In animals, even in the most basic reflex loops, sensory input is temporally decoupled from behavioral output via structured signal transformation. A stimulus is not immediately identical to the response; it is encoded, modulated, and passed through internal filters or gates. This makes it possible to compare sensory inputs across time, to prioritize one stimulus over another, or to integrate information from different modalities. These operations require that the system instantiate what we might call an informational surface: a layer within the organism where environmental input is handled as a manipulable signal.

Plant systems lack this layer. While plants do modulate signals – e.g., via hormonal thresholds or ion-channel gating – the signals remain chemically and spatially bound to their site of origin and immediate physiological role. There is no evidence that such signals are abstracted into a reusable or combinable format that supports behavioral arbitration or sensory comparison. The biochemical signal is not lifted out of its context in the way neural signals are. It cannot be stored, buffered, inhibited, or rerouted in a domain-general format.

Moreover, the plant's modality-specific responses remain locally embedded rather than centrally integrated. Although root caps and stomata may be functionally specialized, they do not feed into a common decision structure where inputs are weighted against one another. Animal sense perception, even in the absence of a brain, relies on such coordination – whether via nerve nets, ganglia, or distributed feedback loops. What plants lack is not speed or complexity per se, but the integrative signal architecture required to structure environmental information across space, time, and modality.

In this light, the comparison to simple animals is instructive. Sponges and jellyfish may lack centralized control, but they possess structured signal hierarchies – networks that allow even minimal abstraction, temporal delay, or sensory arbitration. Plant signaling systems, by contrast, remain bound to the dynamics of growth, hydration, and morphogenesis. The signal is not decoupled from its effect; it is the effect. That is the crucial difference.

Thus, the distinction between animal sense perception and plant responsiveness is not merely about the presence or absence of neurons, or about the timescale of response. It is about whether the organism has a signal-processing architecture capable of informational abstraction – however minimal. Without this, there is no sense perception, only complex reactivity. This is not a dismissal of plant sophistication, but a clarification of the constraints on sensory systems and the kinds of information structures they can sustain.

6.4 Triangulating Sense Perception: Functional Architectures of Responsiveness in Plants and Animals

This section introduces three theoretical frameworks to examine whether plant responsiveness can be considered sense perception in a biologically meaningful sense. It explores sensorimotor integration, affective learning, and structural integration, arguing that while plants exhibit complex environmental sensitivity, they lack the key organizational features required for even minimal

sense perception. The section concludes that plant responsiveness should be understood as pre-sensory information registration rather than true sense perception, highlighting the structural and functional distinctions between plant and animal systems.

6.4.1 Theoretical Frameworks

The question of whether plants possess anything like sense perception – understood in minimal, non-representational terms – has been increasingly pressed by recent advances in plant electrophysiology, signaling, and adaptive responsiveness. Yet a careful examination of the functional architectures underlying sense perception in animals, even in its most rudimentary forms, reveals systematic and principled differences between plant environmental sensitivity and animal sensory processing. Three distinct theoretical frameworks – based on sensorimotor coupling, affective learning, and information-structural integration – converge on a shared conclusion: Plant responsiveness lacks the organizational properties required for even non-representational forms of sense perception.

6.4.1.1 Sensorimotor Integration and Loop Closure

On an enactive or dynamical systems account of sense perception, elaborated by figures such as Peter Godfrey-Smith (2016, 2020),[156] sense perception is rooted not in representational content per se, but in the establishment of temporally closed sensorimotor loops. These are systems in which sensory input modulates motor output in real time, and that output, in turn, alters the sensory input – a feedback architecture that enables the system to modulate its interactions with the environment in a self-referential way.

In such systems, the organism is not merely acted upon by stimuli but participates actively in the structuring of its own sensory field. This looped interaction is central to the emergence of minimal subjectivity – the organism's tracking of changes as they pertain to itself, rather than merely altering in response. In contrast, plants exhibit open-loop reactivity: their growth-based responses to light, gravity, touch, or predation (e.g., via phytohormonal cascades or action potentials) are uncoupled from immediate sensorimotor feedback. These responses are temporally extended and developmentally entangled, lacking the dynamical closure required for the kind of self-involving interaction that grounds minimal phenomenal presence.

To appreciate the distinction, it is helpful to draw a contrast between animals with rudimentary nervous systems and plants. Many species of jellyfish, such as the box jellyfish, display phototaxis – they actively orient and swim toward or away from light sources using eyes and jet propulsion-based locomotion (Petie et al., 2011).[157] These eyespots register changes in ambient light, which are transduced by neural structures into fine-tuned motor responses. Critically, these

156 Godfrey-Smith, P. (2016). *Other minds: The Octopus, the Sea, and the Deep Origins of Consciousness*. Macmillan.
Godfrey-Smith, P. (2020). *Metazoa: Animal Life and the Birth of the Mind*. Farrar, Straus and Giroux.

157 Petie, R., Garm, A., & Nilsson, D. (2011). Visual control of steering in the box jellyfishTripedalia cystophora. *Journal of Experimental Biology, 214*(17), 2809-2815. https://doi.org/10.1242/jeb.057190

animals modulate their movement in real-time based on sensory feedback, thus satisfying the minimal criterion of a sensorimotor loop.

By contrast, plant phototropism, such as that observed in *Arabidopsis thaliana*, is mediated by phototropin receptors and asymmetric auxin redistribution, which causes differential cell elongation and directional growth over hours or days (Christie et al., 2014; Friml et al., 2002).[158] There is no ongoing feedback modulation, and the response is developmentally embedded and irreversible on behavioral timescales - hence open-loop in structure.

6.4.1.2 Affective Evaluation and Associative Capacity

A second axis of analysis is offered by Simona Ginsburg and Eva Jablonka (2019),[159] who propose that the evolutionary origin of consciousness correlates with the emergence of unlimited associative learning (UAL). UAL is characterized by the capacity to form novel associations across arbitrary sensory modalities, retain these associations over time, modulate them based on reinforcement, and integrate them into flexible behavioral repertoires. Crucially, this capacity presupposes the existence of an affective-evaluative layer - a system that assigns valence (positive or negative significance) to sensory stimuli in a manner decoupled from immediate motor output.

On this model, sense perception is not just the detection of environmental regularities, but the embedding of such detection within a valuation architecture that confers relevance. While plants certainly register and respond to environmental stimuli, there is no empirical evidence that their responses are organized by a central integrative system capable of affective modulation. Their "decision-making" is emergent from local signaling networks and bioelectric or hormonal gradients, without any analog to a valuation-based reinforcement system. The absence of this modulatory architecture forecloses the possibility of sense perception as Ginsburg and Jablonka define it: There is no evidence of affect-laden learning or behavioral plasticity in plants beyond domain-specific, hardwired responsiveness.

Consider the sea slug *Aplysia californica.* In *Aplysia californica*, classical conditioning can be demonstrated when a neutral tactile stimulus is paired with an aversive shock, leading to gill withdrawal in response to the previously neutral cue. This associative learning is underwritten by synaptic plasticity mechanisms in identified neural circuits (Carew et al., 1981; Kandel, 2001).[160] Critically, reinforcement valence modulates future behavior, meeting the threshold for affective learning.

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158 Christie, J. M., Blackwood, L., Petersen, J., & Sullivan, S. (2014). Plant flavoprotein photoreceptors. *Plant and Cell Physiology, 56*(3), 401-413. https://doi.org/10.1093/pcp/pcu196
Friml, J., Wiśniewska, J., Benková, E., Mendgen, K., & Palme, K. (2002). Lateral relocation of auxin efflux regulator PIN3 mediates tropism in Arabidopsis. *Nature, 415*(6873), 806-809. https://doi.org/10.1038/415806a

159 Ginsburg, S., & Jablonka, E. (2019). *The evolution of the sensitive soul: Learning and the Origins of Consciousness*. MIT Press.

160 Carew, T., Walters, E., & Kandel, E. (1981). Classical conditioning in a simple withdrawal reflex in Aplysia californica. *Journal of Neuroscience, 1*(12), 1426-1437. https://doi.org/10.1523/jneurosci.01-12-01426.1981
Kandel, E. R. (2001). The Molecular Biology of Memory Storage: A dialogue between genes and synapses. *Science, 294*(5544), 1030-1038. https://doi.org/10.1126/science.1067020

By contrast, *Mimosa pudica* can habituate to repeated mechanical stimulation, such as being dropped, eventually ceasing to close its leaves (Gagliano et al., 2014).[161] While this suggests a form of memory, it is stimulus-specific and does not generalize. Moreover, no reinforcement signal is involved, and there is no cross-modal association. The response is best understood as non-associative desensitization, lacking affective or motivational valuation.

6.4.1.3 Structural Integration and Perceptual Architecture

Finally, Tyler Burge (2022)[162] draws a sharp conceptual line between information registration and perceptual representation, the former being a phylogenetically widespread biological capacity, the latter a rare and cognitively potent specialization. Information registration occurs whenever a system detects and adaptively uses environmental features to regulate its internal states - precisely the kind of reactivity observed in plants. However, Burge argues that genuine perception requires the formation of objective, particularized, accuracy-assessable representations of distal conditions.

Even if one sets aside Burge's representationalist commitments, his analysis underscores a broader point: Perception involves the decoupling of sensory input from metabolic implementation, such that the input is processed through specialized, hierarchically organized structures that allow for modal integration, comparison, and cross-contextual generalization. Animal perceptual systems instantiate these properties through differentiated sensory organs, modality-specific neural pathways, and central integrative hubs. In contrast, plant responsiveness remains entirely embedded within metabolic and morphological pathways, without the kind of modularization or decoupling that would allow information to be processed as such. Their informational economy is radically local, distributed, and physiologically entangled.

By way of illustration, consider the example of the Venus flytrap (*Dionaea muscipula*), which closes its trap when two hairs are stimulated within a ~20-second window, generating an electrical signal that triggers rapid cellular changes in turgor pressure (Böhm et al., 2016).[163] This behavior is localized, threshold-based, and coupled to immediate motor execution, without intermediate evaluation, comparison, or central integration.

In contrast, insect compound eyes, such as those of *Drosophila melanogaster*, feed photoreceptor data to optic lobes where motion, contrast, and direction are extracted and integrated before behavioral output is generated (Borst & Euler, 2011; Bahl et al., 2013).[164] The separation between

161 Gagliano, M., Renton, M., Depczynski, M., & Mancuso, S. (2014). Experience teaches plants to learn faster and forget slower in environments where it matters. *Oecologia, 175*(1), 63-72. https://doi.org/10.1007/s00442-013-2873-7

162 Burge, T. (2022). *Perception: First Form of Mind*. Oxford University Press.

163 Böhm, J., Scherzer, S., Krol, E., Kreuzer, I., Von Meyer, K., Lorey, C., Mueller, T. D., Shabala, L., Monte, I., Solano, R., Al-Rasheid, K. A., Rennenberg, H., Shabala, S., Neher, E., & Hedrich, R. (2016). The Venus Flytrap Dionaea muscipula Counts Prey-Induced Action Potentials to Induce Sodium Uptake. *Current Biology, 26*(3), 286-295. https://doi.org/10.1016/j.cub.2015.11.057

164 Borst, A., & Euler, T. (2011). Seeing things in motion: models, circuits, and mechanisms. *Neuron, 71*(6), 974-994. https://doi.org/10.1016/j.neuron.2011.08.031
Bahl, A., Ammer, G., Schilling, T., & Borst, A. (2013). Object tracking in motion-blind flies. *Nature Neuroscience, 16*(6), 730-738. https://doi.org/10.1038/nn.3386

input and response allows multi-layered processing, enabling flexible orientation behaviors and centralized perceptual computation.

6.4.2 Synthesis: The Architectures of Sense Perception

Across these three models, a consistent distinction emerges: Sense perception presupposes a form of informational decoupling and internal integration that plant responsiveness does not instantiate. Whether framed in terms of closed-loop sensorimotor dynamics (Godfrey-Smith), affectively guided learning architectures (Ginsburg & Jablonka), or structural representationality (Burge), the threshold for sense perception involves cross-modal comparison, evaluative processing, and self-world differentiation.

Plants do not instantiate any of these features. Their sensitivity is real, complex, and functionally integrated - but it remains non-evaluative, open-loop, and metabolically embedded. As such, it is best characterized as pre-sensory information registration, rather than minimal sense perception. To conflate the two would be to erase the functionally significant thresholds that underlie the emergence of sentience.

6.5 Historical Conceptions of Sense Perception and Contemporary Criteria for Sense Perception

This section examines the historical evolution of the concept of sense perception, from classical to contemporary theories, to assess whether plant responsiveness can be considered sense perception. It argues that while plants show complex environmental responses, they lack the internal structures required for sense perception, highlighting the need for conceptual clarity in distinguishing plant behavior from animal sense perception.

6.5.1 A Classical Conception of Sense Perception

The concept of sense perception has historically occupied a liminal space between physiology and philosophy, serving as both a biological function and an epistemic threshold. In classical thought, sense perception (aisthēsis) was typically understood as the faculty that enables organisms to be aware of their environment. Aristotle, for instance, distinguished sense perception from mere nutrition or locomotion, identifying it as the defining feature of animals: beings with the capacity to experience the world through the five senses (Aristotle, 1984).[165] For Aristotle, sense perception involved not only passive reception but also a form of internal actuality, a process by which the sense organ becomes like its object without being identical to it.

6.5.2 Early Modern Conceptions of Sense Perception

Early modern philosophy preserved this dual character. Locke treated sense perception as the primary conduit of ideas, asserting that the mind's first encounter with the world comes through

165 Aristotle. (1984). *The Complete Works of Aristotle, Volume One: The Revised Oxford Translation*. Princeton University Press.

the senses, which furnish it with simple ideas of color, taste, solidity, and motion (Locke, 1998).[166] Hume extended this empiricist project by emphasizing the passivity and immediacy of sensory impressions, contrasting them with the fainter, derivative ideas of memory and imagination (Hume, 2000).[167] Despite their differences, both thinkers agreed on sense perception's foundational epistemological role. Yet they rarely scrutinized its biological underpinnings, treating it largely as a metaphysical primitive.

6.5.3 19th and 20th Century Conceptions of Sense Perception

The scientific turn in the study of the nervous system in the 19th and early 20th centuries introduced a new level of mechanistic specificity to the concept of sense perception. Charles Sherrington's pioneering work on reflex arcs showed that even the simplest behavioral responses presuppose a temporally and spatially structured transformation of input into output (Levine, 2007).[168] Sensory neurons do not merely transduce physical stimuli but serve as the input nodes of a multi-stage signal-processing network. These insights paved the way for mid-century neurophysiological models in which sense perception was not an atomic event but a system-level function involving encoding, filtering, and gating mechanisms.

Concurrently, behavioral paradigms in psychology added a functional dimension to the concept. Pavlovian conditioning demonstrated that stimuli could acquire significance not simply through their physical properties but through their learned associations and reinforcement contingencies (Pavlov, 2010).[169] This research framed sense perception as embedded in a broader context of valuation and learning, anticipating later theoretical frameworks that would link sensory input to affective and motivational processes.

6.5.4 Recent Philosophical Conceptions of Sense Perception

More recent work in the philosophy of mind and cognitive science has moved away from classical representationalism to embrace embodied and enactive models of sense perception. As discussed above, Godfrey-Smith has argued that minimal forms of experience emerge from closed-loop sensorimotor interactions, in which an organism's movements influence the sensory input it receives. This dynamical view foregrounds temporally extended interaction as the substrate of sense perception, decentering the notion of sense perception as passive reception.

Contemporary mechanistic accounts of cognitive functions, such as those advanced by Craver (2009)[170] and others, reinforce this point by emphasizing the multi-level organization of biological systems. Sensory functions are not reducible to inputs or outputs but are distributed across component operations, often nested in feedback loops, inhibitory controls, and cross-modal

166 Locke, J. (1998). *An essay concerning human understanding*. Penguin Classics.
167 Hume, D. (2000). *A Treatise of Human Nature*. Oxford University Press.
168 Levine, D. N. (2007). Sherrington's "The Integrative action of the nervous system": A centennial appraisal. *Journal of the Neurological Sciences, 253*(1-2), 1-6. https://doi.org/10.1016/j.jns.2006.12.002
169 Pavlov P. I. (2010). Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex. *Annals of neurosciences, 17*(3), 136-141. https://doi.org/10.5214/ans.0972-7531.1017309
170 Craver, C. F. (2009). *Explaining the Brain*. OUP Oxford.

processing architectures. These features are what allow sensory systems to perform transformations that go beyond mere stimulus-response pairings.

6.5.5 Historical Trajectories and Contemporary Criteria

These historical and theoretical trajectories suggest that sense perception, even in its most minimal or non-representational forms, presupposes a set of architectural features: temporal decoupling between input and output, modality-specific signal encoding, central integration, and some form of evaluative modulation. Any attempt to attribute sense perception to an organism must therefore attend not only to its responsiveness but to the internal organization of that responsiveness. This conceptual scaffolding background the present evaluation of whether plant systems, despite their undeniable complexity and adaptiveness, instantiate the requisite conditions for sense perception in any robust sense.

6.5.6 Applying Historical and Contemporary Criteria for Sense Perception to Plants

The foregoing comparative analysis has argued that plants, while exquisitely sensitive to their environments, do not meet the functional criteria for minimal sense perception as defined across enactive, associative, and representational frameworks. But these criteria are not merely contemporary inventions – they reflect a lineage of philosophical and scientific reflection on what it means for an organism to sense its world. In this light, the gap between plant responsiveness and sense perception is not only a matter of empirical detail but also one of conceptual inheritance.

As the historical discussion showed, early modern thinkers drew a sharp ontological line between automaton-like reactivity and genuine sentience, a distinction that presaged contemporary concerns with feedback, evaluation, and internalization. While that dualism has largely been set aside, the intuition that not all reactivity constitutes sense perception remains instructive. The very notion of "sense perception" evolved in opposition to models of passive stimulus-response – first in the mechanistic biology of the 17th and 18th centuries, then in 19th-century physiology and psychology, which increasingly tied sense perception to centralized processing, qualitative experience, and subject-involving awareness.

Today's models of animal sense perception, such as those discussed in the preceding section – Godfrey-Smith's sensorimotor enactivism, Ginsburg and Jablonka's affective learning theory, and Burge's theory of perception – reframe this historical arc without erasing its core insight, namely that sense perception is a structured mode of organism-world relation with distinctive information-theoretic and epistemological criteria. These frameworks retain, in different keys, the idea that sense perception requires an inward turn – an ability to integrate, modulate, or evaluate input in ways that decouple proximate stimulation from behavioral response by transducing the environmental signal into packaged information that the organism can use in context-sensitive ways to serve its biological imperatives.

This historical continuity reveals why attempts to classify plant behavior as "sensory" often rests on a category mistake. Plant responses, as discussed, are metabolically embedded, modularly isolated, and evaluatively flat. Reframing such behaviors in terms of sense perception risks flattening crucial distinctions that have guided philosophical and scientific inquiry for centuries. It would be, in effect, to roll back the conceptual thresholds that the historical tradition has worked to draw and refine.

Yet attending to this tradition does not entail a rejection of plant agency or intelligence. Rather, it urges precision – to recognize that plants operate with sophisticated forms of environmental registration and adaptive response, but without the integrative architectures that underwrite sense perception. The historical perspective thus not only corroborates the functional analysis – it deepens it, by showing how the very concept of sense perception has long served to mark precisely the kind of boundary we observe between plant and animal life.

6.6 Conclusion: Plant Sensitivity vs. Genuine Sense Perception

This section concludes the discussion on plant sense perception, reiterating the argument that while plants exhibit complex responsiveness, they do not meet the conditions for sense perception as defined by contemporary frameworks. It emphasizes the need for conceptual clarity, distinguishing plant sensitivity from genuine sense perception, and stresses that the term "sense perception" should be reserved for phenomena that involve the structural and integrative features found in animal systems.

6.6.1 Argument Against Plant Sense Perception

The preceding analysis has argued that, despite compelling evidence of complex environmental responsiveness in plants, such capacities fall short of constituting sense perception in even its most minimal, biologically grounded sense. While plants detect, transduce, and respond to diverse stimuli through distributed signaling pathways and localized morphological changes, they do so without the structural, temporal, or integrative features that characterize sensory systems in animals.

Drawing on three contemporary frameworks – sensorimotor enactivism (Godfrey-Smith), affectively grounded associative learning (Ginsburg & Jablonka), and the perceptual representationalism of Burge – core conditions for minimal sense perception have been identified: closed-loop feedback between sensory and motor processes; evaluative modulation of stimuli with implications for learning and behavioral plasticity; and hierarchical integration of sensory information across modalities and contexts. None of these are present in the plant kingdom in a form that meets the relevant thresholds. Plant responsiveness remains open-loop, metabolically embedded, and structurally decentralized.

These contemporary analyses resonate with a longer conceptual history of sense perception, from early modern accounts that distinguished passive stimulus-response mechanisms from conscious

perception to 19th-century physiological models that situated sense perception within centralized, nervous-system-based processing. While current theories have moved beyond representationalist or brain-centric assumptions, they have preserved a foundational distinction between mere environmental information registration and sense perception proper.

6.6.2 The Importance of the Distinction Between Plant Sensitivity and Genuine Sense Perception

Reframing plant responsiveness through this lens does not diminish the genuine sophistication of plant life. It does, however, require conceptual discipline in how we categorize biological phenomena. The term “sense perception” has served not merely as a label for complex reactivity, but as a theoretical construct marking the emergence of organismic subjectivity, however minimal. Applying it to plants risks erasing the structural, functional, and historical boundaries that give the concept its scientific and philosophical traction.

To insist on this distinction is not to embrace anthropocentrism or to deny plants their rightful place as adaptive, environmentally-responsive organisms. It is rather to acknowledge the layered architecture of life’s capacities - one that includes but also transcends reactivity, culminating in the fragile but distinctive emergence of sentience. If we are to understand the evolutionary pathways of sense perception, cognition, and consciousness, we must begin with precise criteria, historically informed and biologically grounded. On that basis, we can affirm that plants are sensitive without overreaching theoretically into attributions of sense perception. Plant informational complexity is real, but it does not cross the natural threshold that sense perception demarcates.

7 Consciousness

7.1 Introduction: Do Plants Feel? Sorting Metaphor from Metaphysics

The question of whether plants might be sentient – whether they possess conscious experience – has emerged as a provocative frontier in current debates about plant cognition. As research continues to uncover surprising forms of plant behavior, ranging from intricate environmental responsiveness and inter-plant signaling to phenomena described as learning or memory-like (Trewavas, 2017),[171] some authors have suggested that sentience might form part of the picture. Calvo et al. (2017),[172] for instance, explicitly entertain the possibility of plant sentience, drawing on analogies with animal consciousness and pointing to plant responsiveness to anesthetics and other complex signaling phenomena as suggestive evidence. Such proposals have gained some traction, not only within certain corners of cognitive science but also in the broader cultural imagination, where the boundaries between life, mind, and experience are often loosely drawn.

This section approaches these claims with caution and a measure of skepticism. It does not attempt to deliver a definitive verdict on the matter of plant sentience, for the simple reason that no such verdict is presently available. The science of consciousness – whether under that name or under the more specific heading of sentience – remains deeply incomplete. Moreover, the very term consciousness is ambiguous: it can denote a general state of being awake and responsive, or it can refer to the presence of subjective experience. This section is concerned primarily with the latter sense, that is, with sentience understood as the presence of experience itself. In this sense, sentience is not simply a matter of responsiveness or functional sophistication but of there being something it is like for the organism.

The argument developed here is philosophical in orientation rather than neurobiological. It seeks to sketch the contours of a principled case against attributing sentience to plants, without pretending to settle the matter conclusively. It begins by interrogating the conceptual frameworks that allow claims of plant sentience to appear plausible, noting how responsiveness is often conflated with experience. It then examines the roots of the widespread conviction – present in thinkers as far back as Aristotle, who denied that plants possess perception or experience (Aristotle, 2006)[173] – that plants are not sentient, while also asking whether this conviction rests on prejudice, anthropocentric assumptions, or on well-founded distinctions.

Ultimately, the stance taken here is one of qualified skepticism. There is, at present, no compelling philosophical reason to attribute sentience to plants, though the limits of contemporary science mean that the question cannot be closed once and for all. Nevertheless, caution is warranted: extending the concept of sentience beyond the contexts in which it has explanatory purchase risks obscuring the very phenomena we seek to understand.

171 Trewavas, A. (2017). The foundations of plant intelligence. *Interface Focus, 7*(3), 20160098. https://doi.org/10.1098/rsfs.2016.0098
172 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065
173 Aristotle, (2006). *On the Soul*. Digireads.com Publishing.

7.2 Clarifying Consciousness and Sentience

Any serious discussion of whether plants might possess minds or experience must first disentangle the ambiguity built into the term consciousness. In both scientific and philosophical discourse, consciousness is often used as though it denoted a single, unified phenomenon, but this is misleading. As Ned Block (1995)[174] famously argued, we must distinguish between access consciousness – the availability of information for reasoning, verbal report, and the rational guidance of action – and phenomenal consciousness, which refers to subjective experience itself, to there being something it is like for a system. The former is a functional and cognitive notion; the latter is the felt character of experience.

In this discussion, the focus is on phenomenal consciousness. To avoid the ambiguities attached to the word consciousness, it will be referred to here as sentience. This usage is not idiosyncratic. In his recent book *Sentience*, Nicholas Humphrey (2024)[175] explicitly characterizes sentience as the presence of subjective experience and argues that "sentience" captures the core of phenomenal consciousness more directly than the term consciousness itself. Employing sentience in this way allows the discussion to remain squarely about the presence or absence of phenomenal feel, rather than about informational access or cognitive control. The central question, then, is whether plants have any subjective point of view, however minimal – whether there is anything it is like to be a plant.

It is also important to recognize that consciousness is sometimes used to refer to a particular state rather than a property of experience. In ordinary discourse, to say that an organism is conscious often means simply that it is awake, alert, and oriented toward its surroundings, as opposed to being asleep, anesthetized, or comatose. Consciousness as a state of wakefulness and environmental engagement is indeed an important notion, but it does not exhaust the domain of experience. Humans, for instance, regularly have vivid experiences when they are not in that state – dreaming during REM sleep, undergoing hallucinations, or experiencing dissociative episodes. These are genuine instances of phenomenal consciousness – sentience in the sense described by Humphrey and Block – even though they are not cases of being conscious in the ordinary state-conscious sense.

Moreover, to say that an organism is capable of the state of consciousness is to imply that the organism regularly inhabits other experiential conditions as well. Wakefulness is only one among many modes of subjective experience. An animal capable of consciousness as a state typically alternates between waking, sleeping, dreaming, and other altered states, all of which are instances of phenomenal experience. Recognizing this diversity underscores the importance of distinguishing phenomenal consciousness – sentience – from the narrower notion of being awake

174 Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and Brain Sciences, 18*(2), 227-247. https://doi.org/10.1017/s0140525x00038188

175 Humphrey, N. (2024). *Sentience: The invention of consciousness*. MIT Press.

and oriented. It is this broader and more fundamental sense of sentience that is at issue here, and it is with this sense in mind that the question of whether plants might be sentient is taken up.

7.3 The Argument for the Possibility of Plant Sentience

Calvo, et al. (2017)[176] begin their paper "Are plants sentient?" by drawing attention to a longstanding background assumption in both science and philosophy: that plants, because they lack a nervous system, cannot possibly be sentient. They note that this assumption traces back at least to Aristotle's influential claims in *De Anima* that plants do not have perception, do not sense, and therefore do not have anything like subjective experience. Calvo and colleagues point out that this conviction has persisted largely unexamined through the centuries and has shaped the way modern biology tends to think about the scope of sentience. They argue that such a view may be rooted as much in anthropocentric prejudice as in careful analysis. The mere absence of neurons, they contend, should not be taken as a knock-down reason to exclude plants from consideration in discussions of sentience. What is needed, they suggest, is a re-evaluation of the criteria by which we make attributions of sentience in the first place.

The authors propose that in many areas of animal cognition research, sentience is not treated as something that requires the presence of a human-like brain, but rather as something that can be inferred from certain kinds of behavioral and physiological markers. In animal studies, minimal criteria for sentience often include evidence of flexible responsiveness to the environment, integration of multiple sensory modalities, and the presence of some form of learning or memory. Calvo and colleagues argue that plants, surprisingly, satisfy a number of these criteria. Plants detect and integrate information from light, gravity, humidity, mechanical touch, and chemical gradients. They modify their growth and developmental patterns in light of these inputs in ways that are adaptive and context-sensitive. Moreover, certain plant behaviors show temporal integration that resembles memory; for example, plants can encode past exposure to stressors in ways that influence future responses. While these phenomena are often interpreted purely mechanistically, Calvo et al. argue that the same would be true of many animal systems that are nevertheless taken to be sentient.

One of the most provocative pieces of evidence they discuss involves plant responsiveness to anesthetics. In animals, responsiveness to anesthetic agents such as diethyl ether or halothane is often taken as indirect evidence of a capacity for subjective experience, because anesthetics are understood to disrupt neural activity in ways that abolish consciousness. Calvo and colleagues point out that plants, too, exhibit striking reactions to anesthetics. Under exposure to certain anesthetics, plants lose responsiveness: the rapid leaf movements of *Mimosa pudica* are suppressed, the action potentials that normally accompany wounding are blocked, and growth responses are dramatically altered. These effects are not mere curiosities; they suggest that plant signaling systems share significant biochemical and biophysical mechanisms with those of animals. For Calvo et al., this raises the question of whether we are justified in treating anesthetic responsiveness as an indicator of sentience in animals while dismissing it outright in plants. They

176 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065

do not claim that this responsiveness proves anything about plant experience, but they insist that it should, at a minimum, unsettle our confidence that the line between sentient and non-sentient organisms is straightforwardly drawn at the presence of neurons.

Another theme in their paper concerns methodology. Calvo and colleagues are explicit that their purpose is not to offer a conclusive demonstration of plant sentience but to challenge the prevailing frameworks that prevent the question from being taken seriously. They argue that a methodological conservatism dominates current thinking: because plants lack nervous systems, they are assumed to be beyond the scope of consciousness science. But they suggest that this stance risks closing off inquiry prematurely. Instead, they advocate for what might be called a methodological pluralism. Rather than insisting that any attribution of sentience must first identify a neural correlate of consciousness, they propose that we begin with behavioral and physiological evidence, as is often done in the study of non-human animals. In their view, the burden should be on us to articulate why plant phenomena that satisfy minimal criteria for sentience in other taxa must be excluded, rather than on plants to meet criteria that are narrowly tailored to animal nervous systems.

They also point to the fact that our scientific understanding of sentience, even in animals, remains fragmentary and contested. We do not yet have a complete theory of how subjective experience arises from biological processes. Given this epistemic situation, Calvo et al. suggest that it is premature to rule out sentience in organisms simply because their architectures differ from those we know best. If the function of consciousness or sentience is, in part, to integrate information for flexible behavior, then it is not self-evident that only nervous systems can support it. They urge researchers to remain open to the possibility that biological systems other than animals might implement analogous forms of integration.

Throughout their paper, Calvo, et al. repeatedly emphasize that they are not making a final or dogmatic claim. They acknowledge the conceptual and empirical challenges involved in investigating sentience in non-neural organisms. However, they maintain that dismissing the question out of hand is unwarranted, particularly in light of growing evidence of the complexity of plant signaling, plasticity, and responsiveness. Their argument is thus best read as an invitation to broaden the scope of research on sentience, to develop new methodologies suited to organisms without nervous systems, and to remain agnostic but curious in the absence of decisive evidence. In this way, they position plant sentience as a live, though controversial, possibility - one that challenges the boundaries of current theories of mind and calls for deeper investigation.

In addition to the arguments put forward in the article “Are plants sentient,” Calvo - this time writing with Miguel Segundo-Ortin - advances the view that the very way we conceptualize cognition and consciousness needs to be reframed if we are to do justice to plant life. In their article “Consciousness and Cognition in Plants,” (2021)[177] the authors use phenomenology and enactivism as methodological lenses. Whereas the earlier article focused primarily on empirical

177 Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews Cognitive Science, 13*(2). https://doi.org/10.1002/wcs.1578

parallels between plant signaling and animal nervous systems, this later work argues that traditional computational and representational models of mind are too restrictive. Segundo-Ortin and Calvo suggest that cognition is not necessarily something that happens inside a brain but is better understood as an embodied, environmentally embedded process. By appealing to phenomenological perspectives, they emphasize the lived, situated character of experience and argue that even very simple organisms enact a meaningful world through their interactions. This move shifts the debate from asking whether plants replicate animal-like processes to asking how their distinctive organization might realize a form of minimal experience on its own terms.

Another important addition in this paper is the explicit treatment of plants as model organisms for rethinking the boundaries of mind. Segundo-Ortin and Calvo contend that plants challenge deeply entrenched assumptions about the necessity of neuronal structures for cognition, thereby opening new conceptual space for a more pluralistic account of consciousness. They argue that studying plants can force philosophers and cognitive scientists to re-examine what counts as a cognitive system and to develop criteria that are not implicitly tailored to animal physiology. This is not simply a plea for extending animal-based concepts to plants but an invitation to rethink those concepts themselves. In doing so, they propose that plants might exhibit forms of consciousness and cognition that are radically non-neural, profoundly unlike our own, and therefore philosophically significant even if difficult to access or interpret.

7.4 Response to the Argument for the Possibility of Plant Sentience

Before turning to specific points of disagreement, it is useful to outline the central claims Calvo and colleagues have advanced and to consider how they might be met. The following subsections engage directly with key aspects of their reasoning - information integration, plant susceptibility to anesthesia, and broader methodological concerns - while remaining mindful of the limits of current scientific understanding and the need for conceptual discipline in approaching the question of plant sentience.

7.4.1 Information Integration and the Question of Sentience

Calvo et al. (2017)[178] suggest that because plants integrate information from multiple sensory modalities in sophisticated ways - light, gravity, touch, chemical gradients - this integration should lead us to take the possibility of their being sentient seriously. The difficulty with this reasoning is that the kind of information integration found in plants is not only structurally but also functionally unlike the integration that appears to underlie consciousness in animals. Research into neural correlates of consciousness (NCCs) strongly supports global workspace models (Baars, 1993; Dehaene & Naccache, 2001),[179] according to which consciousness arises when information from diverse modules is recurrently broadcast to a global neuronal workspace, enabling competition, attentional selection, and flexible cross-domain use. Plants not only lack the thalamocortical

178 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065

179 Baars, B. J. (1993). *A cognitive theory of consciousness*. Cambridge University Press.
Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition, 79*(1-2), 1-37. https://doi.org/10.1016/s0010-0277(00)00123-2

architectures necessary for such broadcasting, they show no evidence of any functionally equivalent process. Their signaling remains distributed and localized, without the recurrent loops that characterize a workspace.

It is true that this argument is framed in terms of consciousness as a state rather than sentience understood narrowly as phenomenal feel. Yet Calvo et al., in invoking information integration as evidence, appear themselves to be gesturing toward capacities tied to conscious access – wakefulness, orientation, and complex information sharing. In this respect, the argument offered here meets their own reasoning on its own terms.

7.4.2 Plant Susceptibility to Anesthesia

Calvo et al. also note that plants are susceptible to anesthetics, taking this as a reason to pause before ruling out sentience. It is indeed striking that *Mimosa pudica* and other plants lose their characteristic movements under anesthetic exposure. But as argued elsewhere in this thesis, plants do not have neurophysiology; they have electrophysiology. They rely on excitable tissues and ion-channel dynamics for rapid signaling, and anesthetics interfere with those dynamics. Once this is recognized, the phenomenon is no longer puzzling. It shows only that plant electrophysiology can be disrupted by agents that dampen excitability. It does not indicate, even indirectly, that plants support any form of experience.

7.4.3 Intuition, Incompleteness, and Methodological Caution

Calvo et al. frame their discussion against the backdrop of an incomplete science of consciousness and urge openness to possibilities that fall outside conventional categories. That incompleteness must be acknowledged, and it justifies an attitude of humility rather than dogmatism. Yet the long-standing human conviction that plants are not sentient – a conviction that stretches back at least to Aristotle – also deserves consideration. It is likely shaped in part by species-centrism, by our tendency to recognize mindedness only in creatures whose behavior is recognizably like ours. But until the science of sentience advances further, that conviction remains part of our conceptual inheritance and carries some weight in resisting premature extensions of sentience to plant life.

Indeed, there may be good scientific reason to treat skepticism, rather than openness, as the default stance. Allowing the possibility of plant sentience too readily risks encouraging a backward methodology in the science of sentience. If we begin by supposing that sentience is so widespread as even to include plants, we may find ourselves compelled to look for commonalities between plants and animals. Yet given the strong intuition – supported by structural and functional analysis – that plants are not sentient, such a strategy risks focusing on features that may simply reflect traits common to all life (such as the basic form of agency argued elsewhere in this thesis to be universal to all living organisms), rather than features genuinely diagnostic of sentience. A more productive methodology would start with paradigmatic cases: those organisms we universally acknowledge as sentient, such as humans and many animals, and work to understand how sentience emerges from their physiology. Only once we have a principled understanding of

sentience in these clear cases should we turn to more speculative comparisons, rather than allowing speculative cases like plants to distort or distract the inquiry from the outset.

7.4.4 Enactivism and the Prospect of Plant Sentience

Segundo-Ortin and Calvo (2021)[180] go further than the claims made in Calvo et al. (2017)[181] by proposing that enactivism provides a promising theoretical framework for making sense of how plant consciousness might arise. On an enactivist view, cognition is not confined to internal representation or neural computation but emerges from the dynamic coupling of an organism with its environment through sensorimotor engagement (Varela, Thompson, & Rosch, 1993; Di Paolo et al., 2017).[182] This perspective has indeed proven fruitful in rethinking many aspects of cognition. It has helped clarify, for example, how perception, memory, and agency are shaped by embodied interaction rather than being reducible to symbol manipulation inside the head.

However, while enactivism offers powerful tools for understanding cognitive organization and adaptive behavior, it does not, on its own, supply a convincing account of sentience – understood here as phenomenal consciousness, the presence of subjective experience. As others – even enactivists and those sympathetic to enactivism – have noted (e.g., Thompson, 2010; Adams & Aizawa, 2010; Hutto & Myin, 2017),[183] enactivist accounts can explain how an organism achieves situated, flexible action without positing that there is anything it is like to be that organism. The explanatory bridge from dynamical coupling to felt experience remains unbuilt. For this reason, appealing to enactivism does not resolve the central issue at stake in claims about plant sentience. Until a framework – enactivist or otherwise – can provide a principled explanation of how phenomenal consciousness arises, its use to support claims about plant sentience remains suggestive rather than decisive.

7.5 How to Address the Question of Plant Sentience

The following section considers how one might approach the question of plant sentience in a principled way, outlining why the issue is conceptually complex and how a meaningful argument would need to be grounded in an account of how experience arises rather than in surface analogies or purely epistemic inferences.

180 Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews Cognitive Science, 13*(2). https://doi.org/10.1002/wcs.1578

181 Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40*(11), 2858-2869. https://doi.org/10.1111/pce.13065

182 Varela, F. J., Thompson, E.T., Rosch, E. (1993). *The embodied mind: Cognitive Science and Human Experience*. Mit Press.
Di Paolo, E. A., Buhrmann, T., & Barandiaran, X. E. (2017). *Sensorimotor life: An Enactive Proposal*. Oxford University Press.

183 Thompson, E. (2010). *Mind in life: Biology, phenomenology, and the sciences of mind*. Belknap Press/Harvard University Press.
Adams, F., & Aizawa, K. (2010). *The bounds of cognition*. Wiley-Blackwell.
Hutto, D. D., & Myin, E. (2017). *Radicalizing enactivism: Basic Minds without Content*. MIT Press.

7.5.1 Framing the Question

The central question is whether plants have experiences. This deceptively simple inquiry is immediately complicated by the fact that to define experience in a general way is extraordinarily difficult, if not impossible. Human experience ranges from the mundane to the abstract - from the sensation of warmth on the skin to the act of deliberating over whom to vote for in the next election. Plainly, no one seriously proposing plant sentience is suggesting that plants entertain the kinds of richly conceptual, cognitively elaborate experiences that we do. If plants have experiences, they would have to be far more primitive: a form of felt responsiveness stripped of the complexities of deliberation, self-narration, or higher-order reflection.

7.5.2 Pain as a Test Case

One crude kind of experience that often serves as a test case in debates about animal and artificial sentience is pain. Do plants feel pain? There is, of course, no logical requirement that an organism capable of experience must be capable of experiencing pain. But pain is a useful focal point because it is a paradigmatic example of a felt state that we know in ourselves and can, with varying degrees of confidence, attribute to other animals. The challenge is in determining what sort of evidence would count as showing that some other organism feels pain.

The immediate temptation is to turn the question into an epistemic one: how do we know something is in pain? We look at causes and effects. We know that injury is often a cause of pain, and we look for expressive behaviors - vocalizations, grimaces, withdrawal responses - as effects. It may sound facetious to say, “we know plants do not feel pain because when we cut them, they do not yell,” but that remark illustrates something important about how we ordinarily think about pain: we expect there to be an observable effect, some expressive behavior that signals the felt state. However, the felt state itself - the experience of pain - is internal. We infer it from patterns of cause and effect, but those patterns are imperfect. Even in humans there are injuries we do not feel at all, or pains we feel without any observable injury.

Plants clearly can be injured. Their tissues can be cut, burned, or otherwise disturbed in ways that compromise life processes. We also know they react to such injuries, sometimes by sealing wounds, altering growth, or releasing chemical signals. But these reactions, however adaptive, do not by themselves amount to evidence of pain. What is missing is an expression that could only plausibly be interpreted as the manifestation of a felt state, not merely a functional adjustment to damage. And because plants are so radically different from us, it is unlikely that any epistemic argument of this sort - looking for a plant analogue of yelling “ouch” - will succeed. If plants do experience pain, their way of expressing it may be so unlike our own that we would not recognize it as such.

7.5.3 Moving Beyond Epistemic Arguments

For this reason, the better approach is not epistemic but structural and explanatory. We need an argument grounded in an account of how a state like pain arises. Calvo et al. are right to caution that we cannot simply assume the absence of a nervous system entails the absence of experience. To argue that would be to beg the very question at issue. It is true that in humans, all known experiences appear to arise from the nervous system, but that fact alone does not exclude the possibility that radically different biological architectures might also give rise to experience. The task, then, is to reach a level of abstraction in our understanding of nervous systems that reveals what it is about them that generates experience. Only then can we ask whether anything functionally equivalent exists in plants.

At present, the science is nowhere near providing such an account. We do not yet know why, or even exactly how, nervous systems give rise to pain or any other kind of phenomenal experience. Until we have that, we cannot say with confidence that nervous systems are strictly required. Still, this is the kind of argument we need: an argument that shows why certain organizational features – whatever they are – are necessary for experience, and then examines whether plants share those features. Given how differently plants are organized, the likely answer is that they do not. But at this stage, that remains a "probably," not a "definitely."

7.5.4 Is This Asking Too Much of Science?

Some may object that demanding a structural explanation of how sentience arises – one that identifies the organizational features necessary for conscious experience – is asking more than science can deliver. On one view, consciousness is a strongly emergent property, meaning that no scientific account of a system's parts and their interactions will ever suffice to explain why subjective experience arises (Chalmers, 1996).[184] If this is correct, then experience is not merely causally but ontologically irreducible, and the most that science can hope to do is characterize its correlates, not its basis.

Yet this does not mean we must retreat to agnosticism. As Robert Rosen argued in the context of biology, irreducibility does not preclude explanatory traction. Although Rosen denied that life could be reduced to the physics and chemistry of its parts, he nonetheless offered a rigorous account of the organizational properties – such as metabolic closure and impredicative modeling – that characterize living systems (Rosen, 1991).[185] A similar approach may be possible in the case of sentience: even if experience cannot be explained reductively, we may yet identify the kinds of organizational patterns that make it possible. These would not explain why sentience arises, but they could tell us what kinds of systems are capable of supporting it.

A more modest view, widely held among neuroscientists and cognitive theorists who take the hard problem seriously, is that science can map the neural correlates of consciousness (NCCs), construct

184 Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory*. Oxford University Press.
185 Rosen, R. (1991). *Life itself: A Comprehensive Inquiry Into the Nature, Origin, and Fabrication of Life*. Columbia University Press.

predictive models of when consciousness occurs, and identify necessary conditions for its emergence – while acknowledging that this will not explain why those conditions feel like anything (Koch, 2017; Dehaene, 2014; Seth & Bayne, 2022).[186] This approach has already yielded significant results in studies of non-human animals, patients with disorders of consciousness, and artificial systems. Although it does not solve the hard problem, it provides a framework for assessing where consciousness is likely to occur and under what structural conditions.

Applied to plants, this strategy has important implications. If we can identify, even in abstract terms, the organizational features that support sentience in paradigmatic cases – such as recursive signal integration, global information availability, or self-modeling architectures – we will be better positioned to ask whether anything functionally analogous exists in plants. At present, there is little reason to think so, given the absence of central coordination, long-range integrative signaling, or any clear candidate for the kind of unified informational workspace associated with experience. But the value of this approach lies precisely in making these comparisons explicit and principled. Even without solving the metaphysical mystery of consciousness, science can still guide us in determining whether sentience is likely to be present – and in the case of plants, the answer, for now, remains probably not.

7.6 The Possibility of Alien Experience

It is also worth bearing in mind that if plants do have experiences, those experiences are unlikely to resemble anything familiar to us. They would not be richly cognitive but crude and alien, grounded in dynamics and forms of organization that diverge sharply from animal life. If such experiences exist, they might be so unlike ours that we could not interpret or relate to them in any meaningful way. Recognizing this possibility further underscores the need for caution and conceptual discipline in approaching the question of plant sentience. Only by developing a deeper understanding of how experience arises in paradigmatic cases can we hope to address, in a principled way, whether something as different as a plant might also possess it.

This difficulty recalls Wittgenstein's famous remark that "if a lion could speak, we could not understand him" (Wittgenstein, 2010).[187] The idea is not that we would lack the vocabulary to translate lionish thoughts into English, but that the lion's way of being in the world – its form of life – would be so radically different from ours that genuine understanding would be impossible. The same holds, to an even greater degree, for any hypothetical plant experience. If plants were sentient, their experiential world would not merely be unfamiliar – it might be incommensurable with ours, shaped by informational architectures and metabolic dynamics that bear no analogy to pleasure, pain, desire, or suffering. In that case, even if we had principled reason to attribute experience to plants, it is far from clear what ethical stance we should adopt. Our current ethical frameworks are grounded in affective states that motivate action and matter morally – above all,

186 Koch, C. (2017). *Consciousness: Confessions of a Romantic Reductionist*. MIT Press.
Dehaene, S. (2014). *Consciousness and the brain: Deciphering How the Brain Codes Our Thoughts*. Penguin.
Seth, A. K., & Bayne, T. (2022). Theories of consciousness. *Nature Reviews. Neuroscience, 23*(7), 439-452. https://doi.org/10.1038/s41583-022-00587-4

187 Wittgenstein, L. (2010). *Philosophical investigations*. Wiley-Blackwell.

the capacity to suffer. If plant experience lacks any comparable structure, then the moral significance of such experience would remain not only inaccessible but perhaps irreconcilable with our normative intuitions.

7.7 Conclusion

The question of plant sentience remains, for now, an open and deeply challenging one. This section has not sought to close that question but rather to map the conceptual terrain and to highlight why the issue resists simple answers. While plants exhibit remarkable forms of responsiveness, integration, and adaptive behavior, none of these phenomena, taken on their own, establishes the presence of subjective experience. The arguments reviewed - from information integration to anesthetic responsiveness and enactivist reconceptualizations - show that it is possible to draw provocative analogies, but analogies alone do not suffice to demonstrate that there is anything it is like to be a plant.

What emerges instead is a picture that calls for caution and conceptual clarity. The science of consciousness, even in animals, is incomplete, and until we understand how phenomenal experience arises in paradigmatic cases, claims about sentience in radically different systems remain speculative. There is, at present, no positive philosophical reason to ascribe sentience to plants, and doing so risks overextending concepts that have been carefully developed to explain particular forms of biological organization. At the same time, humility is warranted: the limits of current knowledge mean that we cannot rule out the possibility that experience could arise in ways unfamiliar to us. For now, a posture of qualified skepticism - respectful of the complexity of plant life but resistant to premature attribution of sentience - offers the most responsible path forward.

8 Conclusion

8.1 Summary of the Argument

This thesis has argued that, despite increasing claims in recent literature, it is misleading to speak of plant cognition. While plants are capable of remarkable forms of environmental responsiveness, developmental plasticity, and biochemical sensitivity, these do not amount to cognition in any robust scientific or philosophical sense. Instead, it has been maintained that plants possess a basic form of agency - shared with all living systems - that enables goal-directed interaction with the environment through metabolic self-regulation and adaptive responsiveness. They also exhibit a form of intelligence, understood here as flexible problem-solving constrained by internal and external conditions, but this intelligence lacks key hallmarks of animal cognition, including representational processing and associative learning.

It has also been argued that plants do not communicate in any strict sense of the term. Although they engage in elaborate forms of chemical signaling and ecological coupling with other organisms, such interactions lack the intentional, representational, and inferential structure that characterizes genuine communication. Likewise, claims that plants possess neurophysiology or neurobiology have been shown to rest on superficial analogies rather than on structural or functional continuities. What plants possess is a form of electrophysiology - distributed, local, and chemically mediated - which does not fulfill the integrative and computational roles played by nervous systems in animals.

Furthermore, it has been argued that the responsiveness of plants to environmental stimuli, however refined and complex, does not in itself amount to sense perception. With respect to consciousness - here understood in the more specific sense of sentience, the presence of subjective experience - this thesis does not claim to deliver a definitive verdict. Rather, it sketches a principled case for skepticism. Current science offers no clear account of how sentience arises even in paradigmatic cases, and while plants exhibit remarkable signaling and adaptive behavior, there is at present no compelling philosophical reason to ascribe to them a subjective point of view. Until a functional basis for experience is identified and shown to be present in plants, the attribution of sentience remains, at best, an unsubstantiated conjecture.

8.2 Limitations and Open Questions

These conclusions are necessarily provisional, grounded in the current state of empirical knowledge and philosophical theory. As with all scientific inquiry, the possibility remains that future discoveries will reveal unknown dimensions of plant behavior or physiology that compel a revision of our conceptual frameworks. Although it appears unlikely, it is not impossible that plants possess forms of cognition that current methodologies are unable to detect or interpret. The biological substrates of cognition may turn out to be more diverse than is presently assumed.

At the same time, the conceptual foundations of cognition itself remain unsettled. Even in humans and animals, the mechanisms of consciousness, the structure of perception, and the nature of representational states are not fully understood. It is therefore conceivable that future theoretical developments will alter our understanding of cognition in ways that reopen questions currently considered settled. These limitations call not for skepticism but for epistemic humility and a cautious, evidence-driven approach to interdisciplinary research.

8.3 Directions for Future Research

Future empirical research in plant biology should continue to investigate the sophisticated ways in which plants process information, coordinate physiological responses, and interact with their environments. The detailed study of chemical and electrical signaling and systemic coordination in plants remains vital to building a more comprehensive understanding of plant life. The kinds of experiments undertaken by Gagliano and others - designed to probe the extent and limits of learning, memory, and behavioral adaptation in plants - should be refined and extended, even if prior results remain inconclusive or controversial.

Efforts to identify the biological conditions under which capacities such as associative learning emerge are particularly important. Although current evidence suggests that nervous systems are required for such capacities, the possibility that functionally equivalent mechanisms might exist in other biological architectures cannot be ruled out. The investigation of such mechanisms is essential not only for plant science but for the broader project of understanding cognition as a natural phenomenon.

A further and equally important direction for future research concerns the very foundations of the science of sentience itself. As emphasized in this thesis, any meaningful assessment of whether plants might be sentient depends on first clarifying how sentience arises in organisms whose experiential capacities are not in doubt. The task is therefore not merely to look for analogies between plant processes and animal processes, but to deepen our understanding of the biological and organizational features that generate subjective experience in paradigmatic cases such as humans and other animals. Advancing this line of research - uncovering the conditions under which experience emerges, identifying the mechanisms that support it, and explaining why certain architectures give rise to phenomenal consciousness - is essential. Only with that groundwork in place can the question of plant sentience be approached with the conceptual rigor and empirical grounding it requires.

Philosophical analysis must also continue to clarify the boundaries between agency, intelligence, cognition, and consciousness. Distinctions drawn in this thesis - between responsiveness and perception, signal transduction and communication, electrophysiology and neurophysiology - are not merely terminological, but track significant differences in biological organization and function. Keeping these distinctions clear is essential to avoid conceptual conflation and to ensure that scientific interpretations are grounded in coherent explanatory frameworks. In this spirit,

interdisciplinary collaboration between philosophers, biologists, cognitive scientists, and systems theorists will remain essential in mapping the terrain of life and mind.

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