



Why studying plant cognition is valuable, even if plants aren't cognitive

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Abstract

Philosophers and scientists propose the idea that plants are cognitive, which has been met with criticisms. These criticisms focus on the fact that plants do not possess the properties traditionally associated with cognition. By contrast, several proponents introduce novel ways to conceptualize cognition. How should we make sense of this debate? In this paper, I argue that the plant cognition debate is not about whether plants meet a set of well-delineated and agreed-upon criteria according to which they count as cognitive. Rather, many proponents are *hypothesizing about cognition*. They construe COGNITION not as an expression of what cognition is, but rather as a conjecture about what cognition might be. These conjectures orient research that can uncover novel similarities amongst the phenomena to which these concepts extend. In defending this view, I argue that investigating plant cognition is valuable, even if the results of these investigations lead us to reject the claim that plants are cognitive.

Keywords Plant cognition · Concepts · Cognitive kinds · Hypotheses

1 Introduction

Several philosophers and scientists propose the idea that plants are cognitive, drawing from both provocative empirical studies and novel approaches to conceptualizing cognition.¹ These proposals, perhaps unsurprisingly, have been met with criticisms. These criticisms include the following: plant cognition involves non-literal uses

¹For examples, see Trewavas 2003; Calvo Garzón, 2007; Calvo, 2016; Segundo-Ortín & Calvo, 2019; 2022; Keijzer, 2021.

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of the term ‘cognition’ (Firn, 2004; Adams, 2018), plant behavior is adequately explained in non-cognitive terms (Adams & Garrison, 2013), and proposals of plant cognition equivocate between cognition and mere information processing (Adams, 2018). For these reasons and others, critics argue that plants do not bear the mark of the cognitive, suggesting that proposals of plant ‘cognition’ are metaphorical, or perhaps prudential moves that make research sound more exciting than it otherwise might be perceived.

In this paper, I argue that plants are valuable to the study of cognition, even if it turns out that, from what we learn from this study, we end up rejecting the claim that plants are cognitive.² Despite my thesis seeming like a contradiction, I argue that investigating plant cognition is valuable because these investigations test novel concepts of cognition, allowing us to refine the content and extensions of these concepts via these tests. Investigating this “border case” of cognition (Akagi, 2018) can supply us the evidence necessary for us to settle independent debates about what cognition is and where it can be found.

My thesis reflects that this debate is not about whether plants meet well-delineated and agreed-upon criteria for cognition. Rather, several proponents are *hypothesizing about cognition*.³ They construe COGNITION not as an expression of what cognition is, but rather as a conjecture about what cognition might be. To test this conjecture, researchers compare phenomena in plants to paradigmatic cognitive phenomena in humans and other animals, uncovering similarities and differences between these phenomena and the relevance of these similarities and differences for scientific aims.

In *Sect. 2*, I briefly review the plant cognition debate. In *Sect. 3*, I characterize what this debate is about and address how conceptualizations of cognition have changed over time. Because of our growing knowledge of phenomena in both paradigmatic and controversial cognitive systems, I propose that plant cognition is a productive research program when understood as hypothesizing about cognition. In *Sect. 4*, I support my account by showing how hypothesized concepts guide new and productive empirical practices. By reshaping our understanding of this debate, I recast criticisms in *Sect. 5*. My assessment of the plant cognition debate gives us insight into how concepts like COGNITION inform and are informed by research.

2 The plant cognition debate

While claims about plant sentience can be found throughout history, many of the recent proposals of plant cognition stem from research on plant signaling. Electrical signaling in plants has been investigated since at least Alexander von Humboldt (Brenner et al., 2006, p. 414), and researchers have measured plant “action potentials” with spike frequencies like electrical activity in animals (Pickard, 1973). Since

² I discuss whether plants are cognitive rather than whether they (say) possess cognition, as my thesis does not commit to whether cognition is better construed as a property or an activity. I thank an anonymous reviewer for pointing out this potential worry.

³ For clarity, I adopt the philosophical practice of using COGNITION to refer to the concept, ‘cognition’ to refer to the term, and cognition to refer to the phenomenon itself (Akagi, 2021).

then, plant scientists have studied the mechanisms that underwrite plant signaling and their similarities to those thought to underwrite cognition. Based on the fruits of these findings, several researchers have adopted the controversial title of “plant neurobiology” for their nascent subdiscipline (Brenner et al., 2006; Calvo Garzón, 2007).

Additionally, studies on plant intelligence putatively show plant growth and movement is not merely reflexive; rather, it expresses learning-informed choice adapted to environmental conditions (Trewavas, 2003). For instance, dodders putatively anticipate reward when this parasitic plant accepts or rejects hosts (Kelly, 1992). Likewise, arguments for plant cognition address how postulating internal processes can help us to “understand their highly sophisticated adaptive responses” in the same way these processes explain human behavior (Calvo Garzón, 2007, p. 209). For instance, leaf reorientation in *Lavatera cretica* can occur without direct sunlight (Schwartz & Koller, 1986). This nocturnal reorientation seems to model the environment, leading proponents to argue that “leaf laminae of *Lavatera cretica* can, not only anticipate the direction of the sunrise, but also allow for this anticipatory behavior to be retained for a number of days in the absence of solar-tracking” (Calvo Garzón, 2007, p. 210). This conclusion suggests that the plant’s behavior can be explained via cognition just as productively as many human behaviors can be explained via cognition (Garcia Rodriguez & Calvo Garzon, 0102).

Other examples have made waves. Peas purportedly associate stimuli. This claim is based on a study where a cue was paired with a light source, resulting in plant growth directed through a maze based on this cue’s position (Gagliano et al., 2016). Tomatoes purportedly communicate. This claim is based on a study of tomatoes that have connections between plant roots (Song et al., 2010). A pathogen was introduced to one connected member, and disease resistance and defense mechanisms of other members activated, though these members had no direct exposure to the pathogen. French beans purportedly have goal-directed behavior. This claim is based on a study of differences in plant bending movements between contexts in which there was and was not support for the plant to climb (Raja et al., 2020). Together, these findings suggest that plants demonstrate hallmarks of cognition.

2.1 Approaches to COGNITION in the debate

Proponents of plant cognition do not assert that plants possess what cognitive scientists traditionally consider to be human cognition. Rather, several research groups are dissatisfied with these existing concepts, and they pair their discussion of empirical findings with novel approaches to conceptualizing cognition. I review three approaches to COGNITION that are presented in tandem with the study of plant cognition.

Lyon’s biogenic approach “starts with the facts of biology as the basis for theorizing and works ‘up’ to the human case by asking psychological questions as if they were biological questions,” which contrasts with an “anthropogenic approach,” which assumes “human cognition as the paradigm and work ‘down’ to a more general explanatory concept” (2006, p. 11). Lyon posits ten cognitive principles informed by evolutionary biology, self-organizing complex systems, and autopoiesis. Lyon’s principles, such as “cognition relates to the (more or less) continuous assessment of

system needs relative to prevailing circumstances, the potential for interaction, and whether the current interaction is working” (2006, p. 19), allow for the biological study of cognition. The biogenic approach does not answer “what-it-is and what-it-does questions regarding cognition”; rather, its “aim is to stimulate debate about the correct way to proceed to answers” (Lyon, 2006, pp. 11–12).

Another approach is basal cognition, which “focuses on the phylogenetic origins of learning and goal-directed activity,” drawing a “continuum between the humble origins of information processing in the metabolic homeostatic mechanisms of ancient cells and more complex learning, representation, and goal directed activity” (Levin, 2021, p. 117). Basal cognition addresses the evolution of cognition in terms of metrics for anticipation, decision-making, and learning as well as similarities between neuronal and non-neuronal organisms, which reveal an “insight necessary for broadening our understanding of substrates of cognition” (Levin, 2021, p. 117). This approach implies that cognition is “necessary for any autonomous biological system’s survival, wellbeing and reproduction,” which supporters recognize is “an uncomfortable proposition for many” (Lyon et al., 2021, p. 4). In response, supporters claim that “whether one wishes to concede cognition to prokaryotes (for example) remains a matter of personal choice,” and the more important question is “whether proceeding as though this were the case, in a biologically realistic fashion, is productive” (Lyon et al., 2021, p. 14).

A third approach is cobolism, which “refers to the systematic ways in which each living system encompasses structures, processes and external events that maintain the fundamental metabolic processes that constitute the core of each living system” (Keijzer, 2021, p. S137). Cobolism pinpoints a cognitive toolkit, through which systems “are brought together and held together in a cyclic organization that as a whole systematically maintains the internal and external conditions that enable metabolic processes to continue” (Keijzer, 2021, p. S151). If an organism possesses a toolkit for maintaining this kind of cyclic organization, it should be investigated as a cognitive system. Cobolism is therefore intended to support research by “fitting existing cases and suggesting new research on phenomena that have cognitive characteristics irrespective of whether we are currently willing to call these phenomena cognitive” (Keijzer, 2021, p. S152).

2.2 Criticisms

Several criticisms are levied at plant cognition. Though some of these criticisms directly challenge the empirical research (Markel, 2020; Mallatt et al., 2021), I focus on three criticisms that address conceptual issues with the proposal that plants are cognitive.

The first criticism is that ‘cognition’ when applied to plants does not literally mean the same thing as it does when it is applied to humans. Firm notes that terms like ‘cognition’ apply to individuals, while proponents often apply these terms to parts of plants. He concludes that plant ‘cognition’ at the sub-individual level cannot mean the same thing as human ‘cognition’ (Firm, 2004). Extending this criticism to the biogenic approach, Adams argues that the principle above “doesn’t require the kind of processing of information that rises to the level of cognition,” from which he con-

cludes that “if the term ‘cognition’ is used here, it is being used to talk about something completely different from the term’s use from the anthropogenic perspective” (2018, p. 25).

A second criticism is that COGNITION is not needed to explain plant behavior. Postulating internal processing is valuable when behavior cannot be explained via physical causes alone. Critics argue that these internal states represent the organism’s environment as well as their reasons, intentions, and goals. Cognition adds a representational dimension to the physical causes that underwrite the system, as a complete “explanation of cognitive behavior includes the representational content of the internal states” (Adams & Garrison, 2013, p. 347). Adams and Garrison argue that “the chemical mechanism within the plant that causes it to turn its leaves toward the light doesn’t rise to the level of attributing reasons to the plant itself;” as the “causes aren’t representations of the plant’s goals or strategies for attaining them” (2013, p. 347). In other words, “the plant is not doing things for reasons (not reasons of its own)” (Adams & Garrison, 2013, p. 347). Evolutionary arguments also putatively debunk plants’ need for cognition. Taiz and colleagues argue, “there is no evidence that plants require, and thus have evolved, energy-expensive mental faculties... to survive or to reproduce” (2019, p. 684). Therefore, there is no need to explain plant behavior in terms of cognition.

A third criticism is that even if plants process information, mere information processing is not the mark of the cognitive. For instance, leaf orientation can be understood in terms of information processing, but so can motion detection by a garage door (Adams, 2018, p. 28; though see Segundo-Ortin & Calvo 2019 for concerns with this analogy). Cognition involves information processing, but it is processing that “alters the representational format to a different level—to the level of meaning and not just information” (Adams, 2018, p. 28). Transformations of the representational vehicle, this criticism suggests, are absent from plant ‘cognition.’ Likewise, cognition can misrepresent. I can mistakenly believe I am in the sun. By contrast, if a plant’s sensors are working, its sensing of sunlight cannot be mistaken. This difference, critics argue, reflects the fact that information processing in plants does not have the complexity of cognition. Cognition transforms representations while “los[ing] the tight informational connection with truth that is had by sensors” (Adams, 2018, p. 28).

3 How and why we conceptualize cognition

The disagreement between proponents and critics makes salient a difference in outlook in the plant cognition debate. Proponents highlight that their approaches might facilitate productive scientific research and make sense of novel phenomena. Critics seem to assume a concept, if not a full theory, of cognition, which they show plants do not meet. The differences between proponents’ and critics’ responses raises a question: how should we understand this debate?

3.1 What the debate is about

The approaches to COGNITION presented by proponents show that the plant cognition debate should not be understood as one about whether plants meet well-delineated and agreed-upon criteria that count an organism as cognitive. In other words, interlocutors in this debate do not share commitments about the mark of the cognitive. Rather, whether plants are cognitive is linked to a debate about what cognition is.

This debate exemplifies the fact that how we conceptualize cognition is not inert. Akagi notes, “the norms for using the concept COGNITION have changed since the cognitive revolution” (2018, p. 3554). For instance, cognitive scientists have used ‘cognition’ more inclusively over the years, providing a defense to the idea that COGNITION no longer extends only to “highfalutin” rational thought but also to affective psychology and motor control (Akagi, 2018, p. 3553), though this idea is controversial. Not only has COGNITION debatably changed, but these changes “are motivated in substantial part by efforts to respond to evidence” (Akagi, 2018, p. 3554). One source of evidence is “border” cases of cognition, including plant cognition. As Akagi argues, debates like plant cognition are “about how scientists should understand and ascribe the concept COGNITION” (2018, p. 3555).

If evidence can motivate a change in how we conceptualize cognition, how should we proceed? Answers to this question are present in the literature. Allen proposes “working definitions” of cognition that are “suitable... for orienting newcomers to phenomena of potential interest” instead of focusing solely on what concept we might formulate following the study of these phenomena (2017, p. 4239). Akagi proposes an ecumenical characterization, which categorizes “phenomena not only as cognitive or non-cognitive, but as phenomena that are generally agreed to be cognitive... and phenomena that engender disagreement” (2018, p. 3560). This characterization reflects the debate instead of picking sides in it. Keijzer suggests a world-to-concept fit with his cobolism, where a system’s organization “is dominant and the concept must be adapted to accommodate the features of the investigated organization” (2021, p. S145). Thus, a world-to-concept fit “provides a testing ground for these concepts... often leading to conceptual changes” (Keijzer, 2021, p. S145). By testing COGNITION, researchers can inform this concept’s content and its extension.

These answers show that a concept of cognition may be proposed for reasons that are not in efforts to express what cognition is. Rather, COGNITION can orient research by demarcating phenomena whose properties inform how we should conceptualize them. I argue that proponents of plant cognition, specifically those who propose the approaches in *Sect. 2.1.*, are hypothesizing about cognition.

3.2 Hypothesizing about cognition

At its core, a hypothesis is a content-bearing conjecture. In virtue of its content, it extends to some set of phenomena, the measures of which serve as data that confirm or disconfirm it. Hypothesis-testing involves collecting these data and confirming or disconfirming this hypothesis, following which it may be accepted, modified, or rejected.

While we tend to think of hypotheses as scientific claims—or perhaps something else with representational content like a model—the same idea can be applied to other content-bearing items. This idea builds on and extends my earlier work, in which I address circumstances in which definitions are hypotheses (Colaço, 2022). Rather than these definitions expressing researchers’ commitments, “the content of the definition orients researchers to its test, and researchers adopt it because its content demarcates phenomena on which they test,” allowing researchers to “investigate phenomena to which the definition applies, which they may not do if it did not apply to these phenomena” (Colaço, 2022, p. 93). My account of definitions-as-hypotheses captures the idea that proposing definitions does not automatically entail that the proposer’s stance towards this definition is one of expression. Instead, the proposer can be making a conjecture. When making a conjecture, there is no commitment that the claim or other content-bearing item is correct. Rather, the aim is to test the conjecture against data and determine what epistemic attitude we ought to adopt to its content. To adopt this stance towards a content-bearing item like a definition or, as I argue, a concept is to hypothesize about the item in question.

Thus, to hypothesize about cognition is to put forward a concept of cognition as a conjecture that demarcates a set of phenomena against which it can be tested. In virtue of the content of this concept, researchers orient themselves towards a set of phenomena upon which tests are performed. In this case, this set includes phenomena that occur in plants. Because the tests are performed on a set that is based on the conjecture, researchers might not orient themselves to this set of phenomena were they not to make this conjecture.

My account of hypothesizing about cognition matches the approaches that I presented in *Sect. 2.1*. The three approaches each consist in a concept that demarcates a set of phenomena. Not just anything counts as cognition on any of the approaches, even if many more things count as cognition than critics might want. These concepts extend to all phenomena that fit how philosophers and cognitive scientists traditionally have conceptualized cognition, as each novel approach extends to both paradigmatic and controversial cognitive systems. Further, these approaches do not “supplant definitions for a well-specified and supported category that researchers investigate” (Colaço, 2022, p. 96). In contrast to earlier “cognition=life” accounts (Stewart, 1995), these approaches differ, at least in terms of their content, from existing concepts. Together, this overlap between concepts’ extensions provide a rationale for why we should consider them concepts of cognition.

These approaches are better thought of as conjectures than expressions. Lyon emphasizes that the biogenic approach examines a way of approaching questions rather than expressing what cognition is. Supporters of basal cognition emphasize the productivity of this approach for research rather than whether we should assert that this view is correct or that it is correct to say that plants are cognitive. Keijzer emphasizes that the value of cobolism lies not in us accepting that cobolistic organisms are cognitive; rather, its value lies in us productively researching phenomena that count as cognitive according to this approach. For each approach, expressing what cognition is and what phenomena are cognitive are not the aims. Instead, their aims converge on examining the set of phenomena to which their concepts extend. In essence, their conceptualizing is hypothesizing.

While the reader might accept that hypothesizing about cognition is a fair diagnosis of the proposals of plant cognition proponents, they might question its value. In response to this potential question, the extensions of these concepts group together novel sets of phenomena, which likely would not be grouped together without these concepts. These concepts extend to phenomena in plants, but they also extend to paradigmatic phenomena in humans and other organisms. If concepts of cognition have different contents, we can examine the degree to which their extensions overlap. Examining this overlap as a “non-classical extension” amongst these concepts clarifies points of disagreement (Akagi, 2018, p. 3560), which in turn elucidates critics’ commitments. At minimum, hypothesizing about cognition demands that all interlocutors in the debate are precise about what they take cognition to be.

The value of hypothesizing about cognition is not merely that it clarifies interlocutors’ concepts. Researchers who hypothesize about cognition can test for what properties cluster amongst these phenomena, beyond what is specified by the concept itself. The content of COGNITION specifies a set of properties that facilitate the test of the concept, and “researchers may determine additional similarities” amongst these phenomena (Colaço, 2022, p. 93). By uncovering similarities amongst members of the set of phenomena in a concept’s extension, researchers can make projectable claims about members of this set of phenomena.

The idea that concepts underscore projection and induction is the basis of hypothesizing about cognition. The addition my account makes is that hypothesizing about cognition is a means of assessing these concepts’ potential for supporting projection and induction by offering them as conjectures. Thus, the aim of hypothesizing about cognition is to uncover novel, non-superficial similarities amongst the phenomena to which these concepts extend. Novelty is achieved if researchers uncover similarities following testing that they did not have prior to testing. Non-superficiality is achieved if these similarities inform researchers’ ability to characterize, explain, or control phenomena in line with their research aims (Colaço, 2022, p. 95). If novel, non-superficial similarities are uncovered amongst the members of the set of phenomena to which a hypothesized concept of cognition extends, then this concept is confirmed.

Hypothesizing about cognition therefore consists in investigating projectable claims that can be made about phenomena. If the hypothesis is confirmed, the researchers can unify our conceptualization of seemingly unrelated phenomena. Because the concepts are conjectures, “there is no assumption or commitment that there are relevant similarities” beyond what is known prior to testing (Colaço, 2022, p. 93). Rather, the hypothesis is more akin to a question: if phenomena have the properties specified by the concept, what (if any) other properties cluster amongst them (Colaço, 2022, p. 94)? The nature of hypothesis testing leaves open the possibility that researchers might not uncover any similarities in the process, and if they find similarities, they might not be relevant to scientific aims. Nonetheless, proponents of plant cognition aim to do the research that will determine whether there are novel similarities, following which we will be in a better position to determine what a concept of cognition ought to capture.

Further supplying a rationale for hypothesizing about cognition is the fact that, independent of the plant cognition debate, there are disagreements about what cogni-

tion is. Regardless of where the reader's sympathies lie, no one can deny that there are debates over whether we can or should formulate a clear account of cognition (Allen, 2018), whether cognition is representational (van Gelder 1998), whether cognition is distinct from perception (Burnston, 2017), whether cognition is embodied, embedded, enactive, or extended (Menary, 2010), and which systems are cognitive (Levin et al., 2021). Given these disagreements, researchers can find value in orienting themselves towards investigations that can address these debates. Proponents' claims support this outlook: "there are no empirical or theoretical reasons to discard beforehand that certain patterns of plant behavior call for some form of cognitive agency," except criticisms that plant phenomena do not fit existing concepts of cognition (Segundo-Ortin & Calvo, 2019, p. 70). However, how cognition should be conceptualized is the locus of debate. Making conjectures about cognition respects this fact, while ignoring debates about COGNITION might perfunctorily perpetuate these debates.

Hypothesizing about cognition comes with requirements that are unlike those that we typically associate with conceptualizing. Proponents who make these conjectures must try to uncover similarities amongst the set of phenomena that fit the extension of the hypothesized concept. If they do not do this research, or they do this research and do not uncover these similarities, then they should abandon or at least modify the concept. The concept should be considered disconfirmed, as is the case for any hypothesis. Otherwise, the research program degenerates. Because of the need to do research and inform one's stance towards the concept based on this research, we should not expect a hypothesized concept of cognition to endure in its existing form. Once the results arrive, the concept might be accepted, at which time researchers can commit to it. However, it is likely that the hypothesized concept will be modified or rejected.

However, modifications or rejections of hypotheses are not valueless. When researchers test a hypothesis, both confirmation and disconfirmation are at least potentially valuable. While confirmation's value might be obvious, we should not overlook the value of disconfirmation in scientific investigations. Going back to a basic point from Karl Popper, refuting a conjecture is a means by which we can grow our scientific knowledge.

The value of disconfirmation is evident in cases of rival empirical hypotheses. Consider Camillo Golgi's reticular theory, or the theory that the nervous system is a continuous network through which electrical signals are propagated. This theory was a viable candidate for decades but was ultimately refuted by several sources of evidence, the last and definitive piece coming from measurements of synapses via electron microscopy. Though ultimately refuted, the decades of tests of this theory were valuable for analyzing brain anatomy, not the least of which being how the disconfirmation of the reticular theory also supplied evidence for its rival, Santiago Ramon y Cajal's neuron doctrine, which predicted synaptic gaps (Raviola & Mazerello, 2011). The reticular theory was proposed at a time when the evidence did not call for a judgment of which of the rivals was better supported. Had it not been proposed and tested, these endeavors would have taken a different shape, and we might not have discovered several important features about neuronal connectivity and neurotransmission.

Given that this example involves empirical hypotheses, it could be settled with something like a crucial experiment. This is unlike how hypothesizing about cognition is assessed. Nonetheless, this example shows that tests of a theory that is now considered to be obsolete were not without value. This is akin to hypothesizing about cognition, as the disconfirmation of a hypothesized concept of cognition does not automatically mean that the research done in testing this concept is valueless. Instead, value is measured in terms of the character of the similarities and differences that are uncovered during the testing process. This is my rationale behind the title of this paper. Even if it turns out in the end that, based on our tests, we reject the claim that plants are cognitive, there is still potential value in investigating whether plants are cognitive.

There is an added benefit to hypothesizing about cognition that is related to the value of disconfirmation. I have introduced three approaches to COGNITION in this paper. These, in tandem with more traditional concepts, make for a varied set that we may assess. Construing them as conjectures allows us to treat them as rival hypotheses rather than a potential case of incommensurability. These rivals can be tested against one another via a body of evidence, akin to the example of the reticular theory versus the neuron doctrine. Thus, any tests that produce data about phenomena and their similarities will be relevant to other proposed concepts of cognition. This means of comparing the concepts to one another supplies us a method for deciding between these concepts.

4 What might hypothesizing about cognition uncover?

Plant cognition proponents, directed by their concepts of cognition, investigate similarities between plants and humans. However, it is worth being clear about what fits the criteria for uncovering a similarity in this kind of research. Confirmation of a hypothesized concept of cognition is achieved when novel, non-superficial similarities are uncovered amongst the members of the set of phenomena to which this concept extends. Thus, merely using cognitive terms as labels for plant phenomena is not the same as uncovering similarities, as these terms can be construed in multiple ways (Akagi, 2021). For instance, proponents of the biogenic approach, basal cognition, and cobolism claim that data collected from the study of plants “show that the cognitive operations we usually ascribe to brains—sensing, information processing, memory, valence, decision making, learning, anticipation, problem solving, generalization and goal directedness—are all observed” (Levin et al., 2021, p. 1). One might critique the use of these terms for the same reasons that they critique uses of ‘cognition,’ which is illustrated by debates over when it is appropriate to call something ‘memory’ (Colaço, 2022).

Likewise, if proponents hypothesize about cognition, it serves them no benefit to appeal only to a handful of older studies that suggest similarities. Critics note that “it is a peculiar trait of this debate that the number of review articles vastly exceeds the number of research papers on this matter,” which highlights that the analysis of examples exceeds the number of empirical studies on plants (Nick, 2021, p. 457). For hypothesizing about cognition to be valuable, proponents of these hypothesized

concepts must put them “to work”: they must devise new studies that might uncover novel similarities (Colaço, 2022, p. 100). This aim of hypothesizing about cognition is further reflected in critics’ claims: “to render this debate more fruitful, it should be fed with real-world experiments” (Nick, 2021, p. 457).

Where is progress being made towards uncovering similarities? Cases of plant memory (Gagliano et al., 2016) and goal-directed behavior (Raja et al., 2020) are entry points. These experiments are novel, and they supply researchers a testing grounds for understanding the functions of phenomena, or what these phenomena contribute to the systems in which they occur (Cummins, 1975). Despite the distinct environmental conditions plants face when compared to humans and other animals, plants’ ability to retain and use information that guides behavior informs novel models of behavioral motivation (Raja et al., 2020), which apply to both plants and humans. These models might not have been developed had these studies not been performed.

Another avenue for studying functional similarities amongst phenomena is the set of studies that compare how these phenomena can be similarly manipulated. For instance, recent tests of anesthesia and pain reception are ongoing and informed by hypothesizing about cognition. Studies putatively show that “the induction of immobility by anaesthetics has the same biological basis in humans, animals and plants” (Baluška & Yokawa, 2021, p. 450). These studies show that plants can be immobilized via the same set of anesthetic agents as humans can be, and these agents affect molecular systems that plants share with animals. These studies interest pain researchers because there is no unifying theory for why dissimilar chemicals function as anesthetics. For this reason, plant cognition proponents argue that the “use of anaesthetics promises to be an excellent tool for probing not only the possibility of cognition, and other (awareness) functions in plants, but also the elusive molecular targets of substances producing analgesic and anaesthetic effects in humans” (Baluška & Yokawa, 2021, p. 451).

While proponents and critics agree on these advances on plant anesthesia, whether these advances support plant cognition is a topic of disagreement. Critics argue that plants lack the receptors and neuronal structures that underwrite human pain sensing, though humans and plants share many of the underlying chemical components (Draguhn et al., 2021). For this reason, critics deny that anesthesia supplies us insight into plant cognition. Nonetheless, this debate highlights the value of hypothesizing about cognition. This disagreement engenders the development of new empirical studies about the relation between human and plant sensing, spurred on by conjectures that come with the consequence that plants experience pain due to them being cognitive agents.

The debate about plant anesthetics shows that tests for phenomena with similar functions pair with investigations of the substrates of these phenomena. Proponents and critics agree that plant and human anatomy are importantly dissimilar. Plants do not have structures as complex as brains, and plant signaling mechanisms are not identical to neuronal signaling (Levin et al., 2021; Baluška & Yokawa, 2021). However, these differences bely the similarities that researchers who hypothesize about cognition have uncovered. Beyond the plant signaling phenomena that both resemble action potentials and can be inhibited by anesthetic agents, recent discover-

ies on long-distance signaling propagated by phloem suggest that cellular communication can spread through the whole body of the plant (Baluška & Mancuso, 2021). In response, critics argue that the speed, efficiency, and complexity of these signaling networks do not match those found in the brain, and they further argue that plant cell connectivity more resembles the outdated reticular theory than a system based on synaptic transmission (Robinson & Draguhn, 2021). Proponents counter that these critics operate with a myopic view of what a nervous system is (Miguel-Tomé & Llinás, 2021).

The debate over signaling substrates is valuable because it mirrors broader debates about the adequacy of synaptic models for explaining cognition. For instance, most neuroscientists at least implicitly endorse the idea that synaptic plasticity adequately explains cognitive phenomena like the storage and recall of memory. However, a growing minority express doubts that a synaptic network, even one of great complexity, can play this explanatory role alone (Gershman et al., 2021). These skeptics argue that molecular mechanisms, which also are present in plants, are needed to explain the timing and longevity of memory retention in humans. While independent of the plant cognition debate, plant signaling mechanisms supply us an avenue for exploring how signaling draws upon both connections between cells and intracellular molecular activities. Thus, while critics argue that comparing plant signaling to the nervous system is “worthless to pursue [sic]” (Robinson & Draguhn, 2021, p. 8), plant signaling supplies us a testing ground for the relation between molecular activity and cell connectivity.

The signaling substrate debate is also valuable because it relates to debates on the cognitive relevance of signaling mechanisms in the human brain. Philosophers (Hauéis, 2018) and scientists (Laumann & Snyder, 2021) argue that some brain activity does not underwrite cognitive phenomena. The brain is an organ, and it must support homeostatic and metabolic functions. These functions are necessary for the brain to work, but they are necessary in the same way that the heart pumping blood is necessary for the brain to acquire oxygen. Supporters of basal cognition, for instance, emphasize that learning how signaling activities occur in organisms like plants can uncover the differences between cognitive mechanisms and noncognitive mechanisms. Here, we see the value of confirming or disconfirming a hypothesized concept: if similarities are not uncovered between mechanisms in plants and cognitive mechanisms in humans, similarities between mechanisms in plants and noncognitive mechanisms in humans can help us to understand the sense in which these mechanisms are necessary for cognition.

Lastly, similarities that might be uncovered via hypothesizing about cognition are those related to evolutionary considerations. It is uncontroversial to say that there is yet to be a clear answer to what the evolutionary precursor of cognition is. Hypothesizing about cognition via the biogenic approach, basal cognition, or cobolism allows researchers to investigate whether these precursors stem from before the split between the animal and plant kingdoms rather than these precursors coming along much later in the history of the animal kingdom. By making a conjecture that allows researchers to investigate plants and animals as evolutionary relatives that both evolved from organisms with cognition or its precursor, they can uncover similarities and “shed light on how cognitive abilities could have evolved, perhaps differently,

across phyla” (Segundo-Ortin & Calvo, 2019, p. 70). Investigations into the etiologies of plant signaling and human cognition substrates have occurred. For instance, philosophers explore cognition grounded in terms of conserved control mechanisms (Bechtel & Bich, 2021), and scientists explore how resource extraction and energy acquisition demand the need for behavior to be adaptive within the organism’s lifespan (Lyon, 2006).

Confirmation or disconfirmation of one’s concept of cognition can address the evolutionary origins of cognition. Research on the ancestors and relatives of human cognition can supply us the evidence that will aid in determining whether we can demarcate cognition from its precursors and, if we can, when about this demarcation occurred. Perhaps the biogenic approach, basal cognition, and cobolism will not withstand these tests, but, as with the reticular theory, their disconfirmation is valuable if they orient researchers to phenomena that aid in the determination of cognition’s evolutionary history.

To sum up, hypothesizing about cognition might uncover similarities amongst function, substrate, and etiology of phenomena in plants and humans. The inclusion of human phenomena in this debate is critical, as novel approaches to COGNITION reflect a general dissatisfaction with existing concepts. This dissatisfaction is not about these concepts not applying to plants. Rather, it extends to applying these concepts to humans and other animals. This dissatisfaction stems in part from the content of traditional concepts of cognition that appeal to notions like representation, reasons, and intentions, given that discussions of these notions themselves are fraught with controversy (Lyon, 2006; Akagi, 2021). Proponents want to use their concepts to drive their empirical research, build a better understanding of cognition, and resolve debates that are independent of whether plants are cognitive. These aims reflect why they present their concepts as conjectures rather than expressions.

5 Recasting the criticisms of plant cognition

How does my account of hypothesizing about cognition address the criticisms I presented in *Sect. 2*? Here, I recast these criticisms. My responses do not entail that the heart of the criticisms is fundamentally flawed. Rather, their target and weight in the plant cognition debate must be reconsidered because of how proponents construe COGNITION. Thus, my responses are not intended to settle the debate. They are instead intended to keep proponents and critics in this debate from speaking past one another. What will settle the debate, I argue, are empirical studies like the examples I addressed in *Sect. 4*.

The first criticism is that ‘cognition’ when applied to plants is not literally the same meaning as when it is applied to humans. This criticism presupposes that uses of the term ‘cognition’ are intended to express what cognition is. However, this presupposition does not consider the difference between expression and conjecture. Plant cognition proponents use the term ‘cognition’ literally (Figdor, 2018), but their use of this term is a conjecture about cognition instead of an expression of their commitments about cognition.

The fact that proponents literally mean something unlike what critics mean when they use ‘cognition’ is a feature of this debate. Because proponents hypothesize about cognition in the light of their dissatisfaction with traditional variants of this concept, the use of the same term with different meanings is not a problem for understanding the debates between proponents and critics. Rather, it is a consequence of treating different concepts of cognition, which are the bases for these unlike uses, as rival hypotheses. While the critic can argue that one of these rivals is better supported by existing and forthcoming evidence, the mere fact that the interlocutors in this debate do not literally mean the same thing when they use ‘cognition’ is not in itself a criticism of the positions put forward by proponents. There is merit to debating which use of the term is best, but critics should not assume that all interlocutors want to use ‘cognition’ to refer to what they have in mind when critics use the term, even when applied to humans.

The second criticism is that COGNITION is not needed to explain plant behavior. This criticism presupposes the explanans and the explanandum of COGNITION. For the former, these criticisms assume that cognition explains behavior via a computational framework, such as the framework inherited by cognitive science from computer science. By contrast, the three approaches I mentioned show mixed evaluation of cognition in terms of computation: basal cognition does involve computational explanation, but the biogenic approach and cobolism appear to be more amenable to non-representational dynamical explanations (see van Gelder 1998 for more on dynamical explanations). Further, hypothesizing about cognition does not take as its aim the explanation of phenomena. Instead, its aim is to uncover similarities, including similarities related to the explanatory underpinnings of phenomena that count as cognition according to one of these concepts. This fact means that critics should not be surprised that proponents’ uses of COGNITION do not explain. This is not the purpose of their concepts; it is the aim to achieve by testing them (Colaço, 2022, p. 101).

Perhaps the critic will stand by the idea that physical causes alone explain plant behavior, so there is no need to postulate anything above these causes, regardless of what cognition is taken to be. This potential response relates to an assumption about what proponents want to explain. For cases like adaptive behavior within an organism’s lifetime, based on what appears to be the retention and recall of information from the past, it is far from clear that researchers would not benefit from the postulation of internal states or dynamical processes akin to those put forward in debates about human cognition. This criticism is not without merit if taken as an assessment of whether any plant behavioral phenomenon really has these properties, but the mere assertion that plants do not exhibit these kinds of behaviors without an investigation of these phenomena is an unwarranted preemptive assumption of the research. What cognition is and what phenomena count as cognitive are up for debate, and the value of hypothesizing about cognition lies in part in the uncovering of novel phenomena in plants and other organisms.

The third criticism is that even if plants process information, information processing is not the mark of the cognitive. I agree that information processing likely is not the mark of the cognitive, given that this formalism and conceptual schema can be used to account for most systems depending on how liberally one applies it

(Shannon, 1956). However, this criticism presupposes what, over and above information processing, counts as cognition. None of the three hypothesized concepts I have discussed have bare information processing as their content. Likewise, only one of these hypothesized concepts, basal cognition, appeals to representationality, so merely arguing that plant information processing does not involve the transformations of representations is insufficient for arguing that they are not cognitive. The debate is over what cognition is, so a critic of plant cognition should not assume a particular representational account as the basis for their criticisms, unless they want to beg the question.

One aspect of this criticism that has merit is the concern about misrepresentation and its alleged nonoccurrence in plants. Cashing out this concern in terms of ‘representation’ is not ideal, given disagreements over representationality that I addressed in the last paragraph. Nonetheless, the idea that cognitive processing involves predictable kinds of errors is one type of phenomenon for which proponents must find similarities in plants. This criticism can be understood in terms of hypothesizing about cognition. If researchers cannot discover novel phenomena in plants that share properties with this type of phenomenon in humans, its relevance for characterizing and explaining human behavior might lead to the disconfirmation of novel concepts of cognition. Thus, this criticism can be recast as a challenge to plant cognition proponents: find similarities between plant phenomena and this type of phenomenon in humans. If these similarities are not uncovered, then the concepts should be modified or abandoned.

My reappraisals of these criticisms do not dismiss the concerns that lie at the heart of them. Rather, they are best understood when recast as challenges to the empirical findings when one hypothesizes about cognition. This fact supports my claim that investigating plant cognition is valuable, even if it turns out that plants are not cognitive. Let the proponents test their concepts by doing research on novel phenomena in plants and attempting to uncover similarities between these phenomena and those that are associated with cognition in humans and other animals. At best, they might revolutionize our understanding of cognition. At worst, the evidence they acquire will provide a better impression of the distinctiveness of cognition from other capacities of biological systems.

6 Conclusion

In this paper, I have addressed why investigating plant cognition is valuable, even if plants are not cognitive. In explaining that my thesis is not a contradiction, I argue that several proponents of plant cognition introduce novel approaches to COGNITION. These approaches are best construed as conjectures, which orient empirical research that tests these concepts. This idea, which I call ‘hypothesizing about cognition,’ is valuable because the research needed to confirm or disconfirm these concepts will supply us the evidence of similarities and differences between the set of phenomena to which these concepts extend.

As it stands, whether cognition is a natural kind, let alone what the mark of the cognitive is, is an ongoing debate in cognitive science. I recommend that critics do

not assume that these issues are resolved, though there is much to remain critical of when researchers hypothesize about cognition. Understanding how proponents test their concepts is what is needed for us to assess them, and given the nature of hypothesis-testing, the research these proponents should do might vindicate critics' positions. Thus, even if one is not particularly optimistic about the future of plant cognition research—I include myself in this group—the best reasons for accepting or rejecting the position that plants are cognitive will be found by hypothesizing about cognition.

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References

- Adams, F. (2018). Cognition wars. *Studies in History and Philosophy of Science Part A*, 68, 20–30
- Adams, F., & Garrison, R. (2013). The mark of the cognitive. *Minds and Machines*, 23(3), 339–352
- Akagi, M. (2018). Rethinking the problem of cognition. *Synthese*, 195(8), 3547–3570
- Akagi, M. (2021). Cognition as the sensitive management of an agent's behavior. *Philosophical Psychology*, 1–24
- Allen, C. (2017). On (not) defining cognition. *Synthese*, 194(11), 4233–4249
- Baluška, F., & Mancuso, S. (2021). Individuality, self and sociality of vascular plants. *Philosophical Transactions of the Royal Society B*, 376(1821), 20190760
- Baluška, F., & Yokawa, K. (2021). Anaesthetics and plants: from sensory systems to cognition-based adaptive behaviour. *Protoplasma*, 258(2), 449–454
- Bechtel, W., & Bich, L. (2021). Grounding cognition: heterarchical control mechanisms in biology. *Philosophical Transactions of the Royal Society B*, 376(1820), 20190751
- 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
- Burnston, D. C. (2017). Cognitive penetration and the cognition–perception interface. *Synthese*, 194(9), 3645–3668
- Calvo, P. (2016). The philosophy of plant neurobiology: a manifesto. *Synthese*, 193(5), 1323–1343
- Calvo Garzón, F. (2007). The quest for cognition in plant neurobiology. *Plant signaling & behavior*, 2(4), 208–211

- Colaço, D. (2022). What counts as a memory? Definitions, hypotheses, and “kinding in progress”. *Philosophy of Science*, 89(1), 89–106
- Cummins, R. (1975). Functional analysis. *Journal of Philosophy*, 72(20), 741–765
- Draguhn, A., Mallatt, J. M., & Robinson, D. G. (2021). Anesthetics and plants: no pain, no brain, and therefore no consciousness. *Protoplasma*, 258(2), 239–248
- Figdor, C. (2018). *Pieces of mind: The proper domain of psychological predicates*. Oxford University Press
- Firn, R. (2004). Plant intelligence: an alternative point of view. *Annals of Botany*, 93(4), 345–351
- Gagliano, M., Vyazovskiy, V. V., Borbély, A. A., Grimonprez, M., & Depczynski, M. (2016). Learning by association in plants. *Scientific reports*, 6(1), 1–9
- García Rodríguez, A., & Calvo Garzon, P. (2010). Is cognition a matter of representations? Emulation, teleology, and time-keeping in biological systems. *Adaptive Behavior*, 18(5), 400–415
- Gershman, S. J., Balbi, P. E., Gallistel, C. R., & Gunawardena, J. (2021). Reconsidering the evidence for learning in single cells. *Elife*, 10, e61907
- Hauéis, P. (2018). Beyond cognitive myopia: a patchwork approach to the concept of neural function. *Synthese*, 195(12), 5373–5402
- Keijzer, F. (2021). Demarcating cognition: the cognitive life sciences. *Synthese*, 198(1), 137–157
- Kelly, C. K. (1992). Resource choice in *Cuscuta europaea*. *Proceedings of the National Academy of Sciences*, 89(24), 12194–12197
- Laumann, T. O., & Snyder, A. Z. (2021). Brain activity is not only for thinking. *Current Opinion in Behavioral Sciences*, 40, 130–136
- Levin, M. (2021). Life, death, and self: fundamental questions of primitive cognition viewed through the lens of body plasticity and synthetic organisms. *Biochemical and Biophysical Research Communications*, 564, 114–133
- Levin, M., Keijzer, F., Lyon, P., & Arendt, D. (2021). Uncovering cognitive similarities and differences, conservation and innovation. *Philosophical Transactions of the Royal Society B*, 376(1821), 20200458
- Lyon, P. (2006). The biogenic approach to cognition. *Cognitive Processing*, 7(1), 11–29
- Lyon, P., Keijzer, F., Arendt, D., & Levin, M. (2021). Reframing cognition: getting down to biological basics. *Philosophical Transactions of the Royal Society B*, 376(1820), 20190750
- Mallatt, J., Blatt, M. R., Draguhn, A., Robinson, D. G., & Taiz, L. (2021). Debunking a myth: plant consciousness. *Protoplasma*, 258(3), 459–476
- Markel, K. (2020). Lack of evidence for associative learning in pea plants. *Elife*, 9, e57614
- Menary, R. (2010). Introduction to the special issue on 4E cognition. *Phenomenology and the Cognitive Sciences*, 9(4), 459–463
- Miguel-Tomé, S., & Llinás, R. R. (2021). Broadening the definition of a nervous system to better understand the evolution of plants and animals. *Plant Signaling & Behavior*, 16(10), 1927562
- Nick, P. (2021). Intelligence without neurons: a Turing Test for plants? *Protoplasma*, 258(3), 455–458
- Pickard, B. G. (1973). Action potentials in higher plants. *Botanical Review*, 39, 172–201
- Raja, V., Silva, P. L., Holghoomi, R., & Calvo, P. (2020). The dynamics of plant nutation. *Scientific reports*, 10(1), 1–13
- Raviola, E., & Mazzarello, P. (2011). The diffuse nervous network of Camillo Golgi: facts and fiction. *Brain research reviews*, 66(1–2), 75–82
- Robinson, D. G., & Draguhn, A. (2021). Plants have neither synapses nor a nervous system. *Journal of Plant Physiology*, 263, 153467
- Schwartz, A., & Koller, D. (1986). Diurnal phototropism in solar tracking leaves of *Lavatera cretica*. *Plant physiology*, 80(3), 778–781
- Segundo-Ortin, M., & Calvo, P. (2019). Are plants cognitive? A reply to Adams. *Studies in History and Philosophy of Science Part A*, 73, 64–71
- Segundo-Ortin, M., & Calvo, P. (2022). Consciousness and cognition in plants. *Wiley Interdisciplinary Reviews: Cognitive Science*, 13(2), e1578
- Shannon, C. E. (1956). The bandwagon. *IRE transactions on Information Theory*, 2(1), 3
- 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
- Stewart, J. (1995). Cognition = life: Implications for higher-level cognition. *Behavioural processes*, 35(1–3), 311–326
- Taiz, L., Alkon, D., Draguhn, A., Murphy, A., Blatt, M., Hawes, C., & Robinson, D. G. (2019). Plants neither possess nor require consciousness. *Trends in Plant Science*, 24(8), 677–687

Trewavas, A. (2003). Aspects of plant intelligence. *Annals of botany*, 92(1), 1–20

Van Gelder, T. (1998). The dynamical hypothesis in cognitive science. *Behavioral and brain sciences*, 21(5), 615–628

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