THE PHILOSOPHY OF PLANT NEUROBIOLOGY: A MANIFESTO

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Abstract: 'Plant neurobiology' has emerged in recent years as a multidisciplinary endeavor carried out mainly by steady collaboration within the plant sciences. The field proposes a particular approach to the study of plant intelligence by putting forward an integrated view of plant signaling and adaptive behavior. Its objective is to account for the way plants perceive and act in a purposeful manner. But it is not only the plant sciences that constitute plant neurobiology. Resources from philosophy and cognitive science are central to such an interdisciplinary project, if plant neurobiology is to maintain its target well-focused. This manifesto outlines a road map for the establishment and development of a new subject—the Philosophy of Plant Neurobiology—, a new field of research emerging at the intersection of the philosophy of cognitive science and plant neurobiology. The discipline is herewith presented, introducing challenges and novel lines of engagement with the empirical investigation, and providing an explanatory framework and guiding principles that will hopefully ease the integration of research on the quest for plant intelligence.

Keywords: (Philosophy of) plant neurobiology; cognitive science; plant intelligence.

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1. Why a *Philosophy of plant neurobiology* manifesto?

Plant neurobiology is a child of the 21st century. The last decade witnessed its origins as a new area of inquiry when the Society for Plant Neurobiology was formed, back in 2005, and the journal *Plant Signaling and Behavior* began. The release in 2006 of *Communication in plants: Neuronal aspects of plant life*, a volume edited by František Baluška, Stefano Mancuso and Dieter Volkmann, further served to catalyze the establishment of the field. Plant neurobiology (Baluška et al., 2006; Brenner et al., 2006) focuses on plant signaling and adaptive behavior with an eye to providing an account of plant intelligence that escapes the limits of particular plant science areas, such as plant cellular and molecular biology or plant biochemistry. But the study of plant *intelligence* is dominated by information-processing—representational-cum-computational—assumptions incorporated, more or less tacitly, from cognitive psychology and artificial intelligence. These assumptions, if not made explicit, and contrasted against non-representational/computational ones, run the risk of weakening the potential of the field.

Moreover, despite the existence of a solid body of literature on plant neurobiology (see Brenner et al., 2006; Stahlberg, 2006; Baluška & Mancuso, 2007; Calvo, 2007; Barlow, 2008; Baluška & Mancuso, 2009a; and references therein), discussions still subscribe to particular sub-disciplines with their own focuses and objectives. One of the shortcomings of the interdisciplinary endeavor of plant neurobiology is the lack of insight by researchers into the relevant questions and problems being pursued by researchers from other fields within the discipline. We further seek to highlight potential lines of collaboration across the various sub-disciplines, making explicit the links and the structure of the overall plant neurobiology enterprise as such. In doing so, this manifesto aims to outline a road map for the establishment and development of a particular area of research with a character of its own. The Philosophy of Plant Neurobiology comes into existence with the aim of providing a set of theoretical and methodological guidelines that can help to frame and propel this young discipline.

2. Plant neurobiology

Plant neurobiology (Brenner et al., 2006) aims to unearth that plants perceive and act in an integrated and purposeful manner, and how they do it. The field proposes an interdisciplinary and integrated view of plant signaling and adaptive behavior in order to study plant intelligence. The rationale that underlies this effort is the idea that intelligent, flexible behavior requires coordination among the diverse plant structures. This calls for the integration of information signaling across the root and shoot systems to achieve the plants' overall goals via phenotypic, morphological and physiological plasticity (Trewavas, 2005). Intercellular signal integration is implemented at the electrical, chemical and molecular levels courtesy, in part, of long-distance electrical signaling, the production of certain neurotransmitter-like chemicals, and the transport of auxin as well as other phytohormones (Brenner et al, 2006). A number of disciplines are thus called for. These constitute the foundation of plant neurobiology. The list of integral disciplines includes, among others, plant cell and molecular biology, (electro)physiology, biochemistry, evolutionary and developmental biology, and plant ecology.

Before further ado, why 'plant *neuro*biology'? The Online Etymology Dictionary traces the origin of the prefix 'neuro-' back to the Ancient Greek term νευρο-: "sinew, tendon, cord, bowstring," also "strength, vigor," from PIE *(s)neu- "tendon, sinew" <http://www.etymonline.com>. Although someone may thus, technically speaking, conclude that any tissue made of fiber "counts" as neural, there has been heated discussion as to the usage of the term by the plant neurobiology community (Alpi et al., 2007; Brenner et al., 2007; Trewavas, 2007). Animal neurobiology covers the nervous system and brain of animals at the level of their morphology, physiology and biochemistry. Plants, by contrast, lack a nervous system or a brain; they even lack their very building blocks: neurons and synapses. It is for this reason that 'plant neurobiology' may not be the best of labels. And yet plant and animal cells and tissues share a number of 'neural' similarities. To name some of them, glutamate, dopamine, serotonin, and other neurotransmitters are found in plants, although their function still needs to be clarified (auxin can be identified as the plant-specific neurotransmitter for the purpose of signaling—Baluška & Mancuso, 2009b). Also, both types of cells exhibit polarity or have an endocytosis-driven vesicle recycling apparatus that permits the secretion of signaling molecules (Baluška & Mancuso, 2009b). Further similarities include "non-centrosomal microtubules, motile post-Golgi organelles, …, and cell-cell adhesion domains based on the actin/myosin cytoskeleton which serve for cell-cell communication." (Baluška, 2010, p. 1).

Moreover, as has been observed elsewhere (Calvo and Keijzer, 2011), 'neuroid conduction' (Mackie, 1970), that is "the propagation of electrical events in the membranes of non-nervous, nonmuscular cells" (p. 319), takes place not only in animals, but also in protists (e.g., *Noctiluca*) and plants (*Dionaea muscipula* and *Mimosa pudica*, being the examples that first come to mind). Neuroid conduction is thus a basic and widespread form of signaling. Animal nervous systems only organize signaling systems, ion channels or synapses in new, more complex, ways, but the basic components are already present in precursor organisms (Ryan & Grant, 2009; Ovsepian & Vesselkin, 2014).

In any case, degree of similarity aside, coordination is needed, and cellular electrical excitability for the purpose of the transmission of information relies upon the capacity of plant cells to conduct signals from receptor to effector sites. For the purpose of this manifesto, I shall stick to the original label, and make use of ‘neuro-’ in its broader sense in order to lay the stress, regardless of the type of tissue, on the accomplishment by which information is conveyed through an electro-chemical communication system (for a recent reinterpretation of the role of nervous systems, see Keijzer et al., 2013).

Notwithstanding terminological and etymological disputes, what matters is to appraise the role of what eukaryote excitable cells actually *do* share. Cellular electric excitability and response in the form of action potentials underlies the ability of both animals and plants to respond in a fast, and yet coordinated manner, to environmental contingencies. In the case of plants, the reader may probably have *Mimosa pudica* or *Venus flytrap* in mind as classic examples of electrically mediated leaf closure, but all plants depend in one form or another upon electrical signaling. Plant communication obtains partly via action potentials (APs) that propagate multidirectionally along the phloem (for a review of plant APs, see Pickard, 1973; see also Baluška & Mancuso, 2009c; Volkov, 2006). As in the case of animal APs, ion channels mediate the generation of APs in plants. In addition, another type of long-distance signaling exists in plants: slow wave potentials (SWPs) (aka variation potentials, VPs—Trebacz et al., 2006; Stahlberg et al., 2006). Both APs and SWPs (VPs) share the three-fold phase of depolarization-repolarization-hyperpolarization of animal APs. And yet, according to mainstream plant physiology, action potentials (APs) are a nuisance. Plant physiology either ignores APs altogether, or considers APs as some kind of ‘error’ or ‘blind alley’ in plant evolution.[1] By contrast, under the lens of plant neurobiology, APs and other electrical long-distance signals play a central role in integrating the plant body. This is a clear instance of the need for interdisciplinary cooperation under the umbrella of plant neurobiology.

Inspired by the pioneering work of Charles Darwin,[2] considerations of this kind have driven plant neurobiologists to coin the expression of the "root-brain" (Baluška et al., 2004; 2009; Barlow, 2008). The idea was inspired by the discovery of the 'transition zone' (TZ) within the root-apex of maize seedlings; an area where oxygen consumption is maximal, and where electrical synchronization obtains (Masi et al., 2009; Baluška and Mancuso, 2013). According to plant neurobiologists, TZ acts as a 'brain-like' command center for the purpose of the integration of sensorimotor information. In an often-quoted passage, Baluška et al. (2006) claim:

> "Each root apex is proposed to harbor brain-like units of the nervous system of plants. The number of root apices in the plant body is high, and all "brain units" are interconnected via vascular strands (plant neurons) with their polarly-transported auxin (plant neurotransmitter), to form a serial (parallel) neuronal system of plants" (p. 28).

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[1] Despite the fact that the role of calcium, and chloride and potassium as ion components of APs in plants is well known from studies of giant *Characean* cells (see Calvo, 2012, and references therein), there is no single reference to APs in the fifth edition (2010) of Lincoln Taiz and Eduardo Zeiger's companion to *Plant Physiology*. Thanks to Franstišek Baluška for pinpointing this omission to me.

[2] In a memorable passage that puts an end to *The Power of Movement in Plants*, Darwin claims: "It is hardly an exaggeration to say that the tip of the radicle thus endowed [with sensitivity] and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements." (1880, p. 573).

In addition to electrophysiological considerations, a thorough understanding of the chemical processes involved, both within and across plants, of the way information pathways obtain via biochemical signaling, and its relation with metabolic needs, is clearly needed. This is a process that spans all the way from the intracellular molecular level of gene expression to the level of plant communities. Plant neurobiology, furthermore, views evolution and development as central to the study of plant intelligence. The manifest competencies of plants are to be situated in their particular evolutionary contexts. Different needs, different solutions, so to speak. In fact, evolutionary considerations permit us to turn tailor-made arguments upside down, devised by philosophers of cognitive science, meant to deny the ascription of intelligence to plants on the grounds that they lack movement. Patricia Churchland, for instance, observes that:

> “If you root yourself in the ground, you can afford to be stupid. But if you move, you must have mechanisms for moving, and mechanisms to ensure that the movement is not utterly arbitrary and independent of what is going on outside.” (1986, p. 13),

Elsewhere, she insists:

> “… first and foremost, animals are in the moving business; they feed, flee, fight, and reproduce by moving their body parts in accord with bodily needs. This modus vivendi is strikingly different from that of plants, which take life as it comes.” (2002, p. 70)

But evolutionary developmental biology considerations have a simple answer: how intelligent you must be if, *despite* being rooted, you have succeeded in passing down your genes in the face of a wide variety of selective pressures! Furthermore, recent research shows that this is not "merely" a matter of adaptation; plant *learning* does take place during development (Gagliano et al., 2014).

The list of plant competencies has been growing at a considerable pace in recent years. Plants can, not only learn and memorize, but also make decisions and solve complex problems. They can sample and integrate in real time many different biotic and abiotic parameters, such as humidity, light, gravity, temperature, nutrient patches and microorganisms in the soil, and many more, courtesy of a highly sophisticated sensorimotor system (Hodge, 2009; Trewavas, 2009; Baluška and Mancuso, 2013) that includes proprioception (Bastien et al., 2013; Dumais, 2013), with sensory information being transduced via a number of modalities. More distant aspects of their vicinity are also brought in. Plants can anticipate competition for resources, growing differentially depending upon the future acquisition of minerals and water (Novoplansky, 2015). They exhibit self-recognition and territoriality (Schenk et al., 1999), being able to tell apart own from alien, directing their movements towards their targets of interest (Gruntman & Novoplansky, 2004). Plants can communicate aerially (via released volatile organic compounds—VOCs—Dicke et al., 2003; Baldwin et al., 2006) with members of their own kind and with members of other species. They can even communicate bioacoustically, making and perceiving 'clicking' noises (Gagliano et al., 2012). Some plants can tell vibrations caused by predators apart from innocuous ones (wind or the chirps of insects), eliciting chemical defenses selectively (Appel and Cocroft, 2014). In a sense, plants can *see*, *smell*, *hear*, and *feel* (Chamovitz, 2012).

In order to study this set of competencies (for a survey, see Calvo & Keijzer, 2011), plant neurobiology relies on pressing questions from plant electrophysiology, cell and molecular biology, biochemistry, evolutionary and developmental biology, ecology, and related disciplines. But insofar as the target is cognitive phenomena (learning, memory, attention, decision-making, etc.) plant neurobiology transcends the individual scope of the constituent disciplines. In this way, it is not only the plant sciences that constitute plant neurobiology; resources from cognitive science and philosophy are central to such interdisciplinary project, if plant neurobiology is to maintain the study of plant intelligence well-focused.

3. The place of philosophy within plant neurobiology

Departing from traditional philosophical reflection, the philosophy of plant neurobiology is to be found at the junction of the philosophy of cognitive science and plant neurobiology. The philosophy of plant neurobiology is not *itself* in the business of providing the empirical evidence with regard to the phenomena of interest allegedly worth deserving the label ‘intelligent’; it rather concerns foundational issues within the plant sciences. But, on the other hand, its basic toolkit is not armchair conceptual analysis or *a priori* reasoning (Fumerton, 1999). Bluntly, plant intelligence cannot be proved or disproved by the hand of ingenious thought-experiments designed to identify necessary conceptual links, or counter-examples (Wheatherson, 2003), nor by *reductio ad absurdum* argumentation. We should not rely on these when it comes to analyzing the concept of intelligence, a concept that ought not to be fixed by our intuitions regarding animal intelligence. We would otherwise run the risk of not understanding correctly the role that philosophy has to play in the collaborative effort that plant neurobiology represents.

Instead, a naturalistic philosophy of plant neurobiology has a crucial role to play *within* an interdisciplinary plant neurobiology, similar to the role it has traditionally played within a representational cognitive science (Bechtel, 2009a; 2010), or the role it is nowadays playing within a more pluralistic, embodied and/or ecological cognitive science (Chemero, 2009; Dale, Dietrich and Chemero, 2009). Discussion of the alleged representational nature of the discipline is pivotal, and a naturalistic undertake may ease integration of theoretical reflection more fully into plant neurobiology. Endorsing an embodied approach would permit to lay the stress upon the sensorimotor grounding of plant intelligence, suggesting new, non-computational, ways to understand the relationship between plants and their local environments.

Although a naturalistic philosophy of science can team up with plant neurobiology by contributing with its distinctive theoretical and methodological toolkit, the philosophy of plant neurobiology can likewise contribute to the analysis, for instance, of the nature of the underlying theories under empirical scrutiny or by spelling out how the different plant science fields relate to each other. The payoff of such collaborative effort among philosophers, cognitive scientists and plant neurobiologists in the study of plant intelligence is twofold: first, the establishment of theoretical hypotheses, and the generation of testable predictions that render more specific empirical hypotheses subject to confirmation; and second, the design of experimental procedures and interpretation of experimental results in narrow collaboration with plant neurobiologists. The conclusions drawn from within a naturalistic setting can have a direct bearing upon plant neurobiology.

Consider, for illustration's sake, the role of philosophy in cognitive science in the last few decades. When the *Report of The State of the Art Committee to The Advisors of The Alfred P. Sloan Foundation* (hereafter, the *Sloan Report*) was first published in 1978, the only well-established roles to be ascribed to philosophy reduced to the philosophy of psychology and the philosophy of language. As depicted in the "cognitive hexagon" (figure 1), the connection of philosophy with computer science, anthropology and neuroscience (represented by dashed lines indicating weak ties in between the disciplines) was almost non-existent. Nowadays, the philosophy of cognitive science has substantially increased the range of research topics that fall under its umbrella. The philosophy of neuroscience, to take the clearest instance, could be barely envisioned in the days when the *Sloan Report* saw the light (see figure 1, legend). Today it is a well-established area of research, with the flourishing of journals, conferences, etc., devoted to the field.

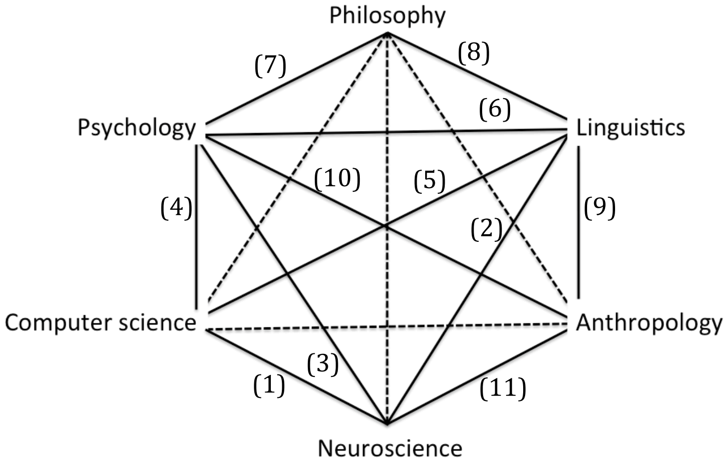

Figure 1: The "Cognitive Science hexagon" in 1978. Vertices represent contributing disciplines. Lines joining vertices represent the following interdisciplinary collaborations: (1) Cybernetics; (2) Neurolinguistics; (3) Neuropsychology; (4) Simulation of cognitive processes; (5) Computational linguistics; (6) Psycholinguistics; (7) Philosophy of psychology; (8) Philosophy of language; (9) Anthropological linguistics; (10) Cognitive anthropology; and (11) Evolution of brain. Continuous lines represent consolidated collaborations; unnumbered dotted lines, in-progress ties between philosophy and computer science, neuroscience and anthropology as of 1978. (Adapted from the *Sloan Report*, pp. 3-ff.).

In addition, the role of the philosophy of cognitive science is not simply to undertake a methodological or an epistemological analysis of some object of study. From a naturalistic perspective, the philosophy of cognitive science has made an effort to understand the phenomena of interest and to enrich empirical research by offering an integral framework, at a higher, more abstract, level of analysis. By paying close attention to the methodologies and practices of plant scientists, the philosophy of plant neurobiology can play a role equivalent to the one that philosophy is now playing within cognitive science.[3] Because plant neurobiology is becoming increasingly inclusive, encompassing a broad range of disciplines, from molecular biology to population ecology and ecosystems, the philosophy of plant neurobiology can help rephrase problems and unify approaches that cut across the plant sciences. An aim of the philosophy of plant neurobiology is thus to systematize research with an eye to putting forward an explanatory framework that integrates work on plant signaling and adaptive behavior that spans many different disciplines and levels of description. The philosophy of plant neurobiology can further play a leading role in making plant scientists aware of the variety of cognitive science paradigms, their pitfalls and virtues, in order to adopt them in the quest for plant intelligence (see the two guiding principles, below).

By drawing an analogy with the "cognitive hexagon" of the cognitive sciences, the structure of plant neurobiology may be represented by a "plant neurobiology hexagon" whose vertices are the aforementioned plant neurobiology disciplines. Figure 2 illustrates the existing connections among disciplines that operate at different levels of discourse, where connecting lines reflect the ties between them, as well as between plant neurobiology and philosophy itself (it is hoped that philosophers of plant

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[3] Echoing the distinction between a philosophy *of* cognitive science and a philosophy *in* cognitive science made explicit in cognitive science research (Brook, 2009), we may say that the discipline comprehends a philosophy of plant neurobiology and a philosophy in plant neurobiology. Dennett's (2009) and Thagard's (2009) respective ways of approaching the relation between philosophy and cognitive science is also congenial with the one herewith defended in the domain of plant neurobiology.

neurobiology establish contact with as many vertices of the plant neurobiology hexagon as possible).

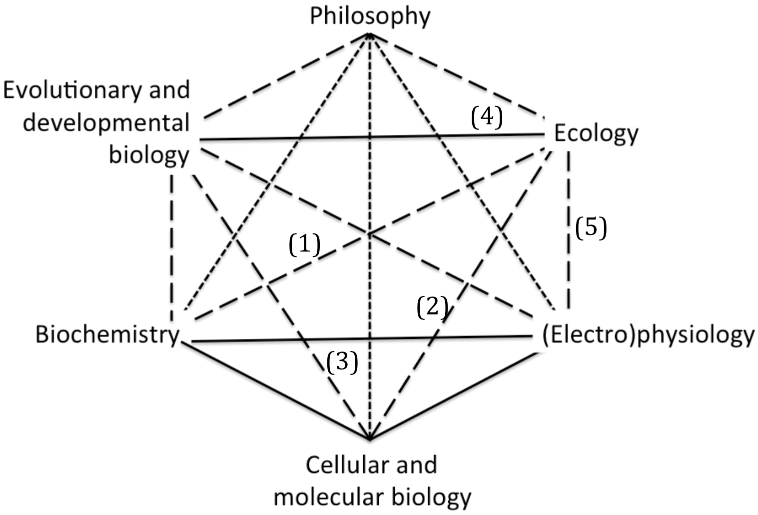

Figure 2. The hexagon of Plant Neurobiology in 2014. Vertices represent contributing disciplines. Lines joining vertices represent the following interdisciplinary collaborations (only a few are drawn): (1) Biochemical ecology; (2) Molecular ecology and ecological genetics; (3) Evolutionary genetics; (4) Evolutionary ecology; and (5) Ecophysiology. Continuous lines represent consolidated collaborations; dashed lines, in-progress ties; unnumbered dotted lines, areas necessitating more stable collaboration.

It goes without saying that not all interdisciplinary plant neurobiology collaborations at present are shown in figure 2. For simplicity, I have illustrated existing links with regard to chemically-mediated interactions between plants and their local environment; the electrophysiological basis for ecological adaptation; ecology and evolution, and molecular genetics; and between evolution and ecology. But the take-home message is that the plant neurobiology hexagon can furnish a graphical road map for the exploration of potential lines of collaboration in plant neurobiology. Certainly, both the number of vertices and the patterns of connectivity, representing disciplines and sub-disciplines, can be broadened and further articulated, providing a much more complex landscape. 'Evo-devo' (Vergara-Silva, 2003) and plant inspired bio-robotics (Mazzolai et al., 2010) constitute an illustration of somewhat recent flourishing ties. The cognitive sciences themselves, and not just the philosophy of cognitive science, are particularly welcome as well, as it should be clear by now.[4]

The tools and methodologies of the respective disciplines are put to the service of addressing the phenomena of interest, in our case, plant intelligence. To this end, contributing disciplines must coordinate with each other, as has been the case in the emergence of modern cell biology (Bechtel, 1993), or in the history of cognitive science (Bechtel and Herschbach, 2010). Understanding plant intelligence requires the integration of research obtained in a variety of domains. The whole network of disciplines and connections should be considered, in their interaction and integrity, the field of Plant Neurobiology. As to the philosophy of plant neurobiology itself, dotted lines in figure 2 have not yet become the focus of academic undertaking, and that is one of the reasons for this manifesto.

It is noteworthy that interactions among levels might furnish plant neurobiology with a non-reductionist approach to the study of plant intelligence (the study of plant intelligence may not reduce to the study of, say, cellular and molecular biology or biochemistry, whenever that tie is firmly established). If plant neurobiology focuses on intelligence, the detail provided by cellular and molecular biology or biochemistry cannot be the whole story. Plant neurobiology needs to abstract from those details, and bring the resources of subdisciplines ranging at different levels of description to bear on the over-arching phenomena of interest. Older analytic or mechanistic models can now be superseded in plant neurobiology by an organic, non-reductionist explanatory framework, a research program that aims to combine decomposition techniques with an integrated, system-level, ecological perspective. The plant neurobiology hexagon

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[4] To list but a few more diverse areas of research, plant neurobiology would benefit from interaction with the forestry sciences; bio-computing; edaphology; or paleoecology.

represents such an emergent rationale, and the philosophy of plant neurobiology, as part of this joint effort, aspires to ease integration.[5]

Once the role that methodologies and theoretical discussions play among the plant sciences is put in perspective, the role of philosophy and cognitive science vis-à-vis plant neurobiology may be better appreciated. Among many others, topics include plant perception, learning, memory, attention, decision-making, and problem solving. Just consider for the sake of illustration domain-generality vs. domain-specificity: are "plant minds"[6] domain-general or domain-specific devices? The former option is congenial with an empiricist understanding of the structuring of the plant relevant cognitive architecture, and opposed to a rationalist/nativist approach. Spelling out oppositions like this one ought to allow us to draw a number of working hypotheses.

For one thing, if the principles that govern the inner doings of plants are domain-general and not innate, plant *learning* (that is, not only adaptation at the evolutionary scale, but also individual learning throughout ontogeny) must be taking place, and a number of possibilities open up with regard to the form that such learning might take. In fact, if learning, under the standards of psychology, applies to eukaryotes there is no reason not to pursue plant learning, as opposed to mere plant sensory adaptation. Whether non-associative forms of learning (habituation and dishabituation, and sensitization) or associative forms (either classical or operant conditioning) take place is thus open to empirical scrutiny. Non-associative learning would be consistent with a degraded ascription of competencies to plants insofar as such learning is congruent with

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[5] It is anything but clear that everyone will be convinced that the project is inherently emergentist. The situation is exactly parallel to that found in the cognitive sciences where different communities understand, or not, the discipline from a reductionist or from an emergentist stance. Dual and hybrid positions, of course, also find room to disagree with both the reductionist and the emergentist extremes, but this is not the place to elaborate further on this issue (thanks to Tony Chemero for bringing this point to my attention).

[6] Carruthers (2004), for instance, has argued somewhat convincingly that ants and bees have minds. Being an open empirical question, we cannot deny on *a priori* grounds that plants equally possess "minimal minds" (Calvo et al., 2014) in the relevant cognitive sense.

an instinctual reading of plant behavior. By contrast, associative learning would beef-up the ascription of intelligence to plants since conditioning evidences the fact that a new competency or the improvement of an existing one is acquired.

If plants are capable of learning (Trewavas, 2003), the philosophy of plant neurobiology can ask whether it is information-processing in between sensing and acting that delivers the goods. Do plants represent and process information computationally? Some of the foundational issues whose discussion the philosophy of plant neurobiology can promote would include this as well as other core topics in debates about the architecture of cognition (Calvo et al., 2014). In fact, from the standpoint of the philosophy of plant neurobiology, and considering the idiosyncrasies and constraints from plant anatomy and physiology, an embodied and situated framework akin to that being developed for the cognitive sciences (Calvo & Gomila, 2008; Robbins and Aydede, 2009) seems to be the arena in which an integrated plant neurobiology is to be founded and critically assessed.

Taking issue with the architecture of cognition, the philosophy of plant neurobiology may supersede the representational-computational approach to the study of intelligence inherited from cognitive psychology and artificial intelligence. According to the *Sloan Report*, the overall objective of cognitive science was “to discover the representational and computational capacities of the mind and their structural and functional representation in the brain.” (p. 6). Four decades later, it would be unwise to endorse such a view uncritically, and try to uncover the representational and computational capacities of plants together with their non-neural correlates. The reason is two-fold: it is not clear anymore, first, that cognitive science ought to account for cognitive capacities computationally-representationally; and second, that the material correlates of intelligence reside within the organism, and not in the organisms-environment, constituted as a coupled system.

If an embodied or situated cognitive science targets neural, body and environmental factors in their reciprocal interaction, plant neurobiology can likewise lay stress upon real-world situations as the context in which plant intelligence naturally emerges. In fact, the very notion of an "extended individual" applies directly to plant-coupled ecosystems. Plant intelligence decentralizes, and is to be understood as an emergent and extended self-organizing phenomenon. Being coupled with their environment, the target is the scientific understanding of the continuous interplay of plants in relation to the environmental contingencies that impinge upon them. Moreover, I may add, the scientific study of plant intelligence may well first require that we erase the border between sensing and perceiving, on the one hand, and cognizing, on the other. Bluntly, perception and cognition belong to the same kind. This allows us to frame plant cognitive processing, not in information-processing terms, but in the very same terms that the processes that constitute perception are studied.

As already mentioned, one key role of the philosophy of plant neurobiology is to help in sharpening empirical hypotheses for the sake of confirmation/refutation. By approaching plant neurobiology, not from the stance of mainstream cognitive psychology and artificial intelligence, but rather from an embodied cognitive science, different possibilities open up for empirical investigation. Two examples of how the philosophy of plant neurobiology can present challenges and direct novel lines of engagement with empirical investigation are presented next.

4. Two guiding principles

How does the philosophy of plant neurobiology connect with the lab? We may consider two guiding studies currently underway for a taste of what the discipline has to offer.

4.1 Perception and the guiding role of ecological psychology

A mark of intelligence is the capacity to select actions that allow an organism to achieve its goals. Plants' interaction with their surroundings appears to be *meaningful* to them in this sense. This may be better appraised by the hand of a number of principles imported from ecological psychology (Gibson, 1966; 1979). First, the proper unit of ecological analysis is the organism-environment system as a whole, and not the detached organism in itself. On the other hand, we should be paying attention to the ecological scale that the interaction takes place at. Furthermore, adaptive behavior is to be understood in terms of emergence and self-organization. And last, what an organism perceives are *affordances*,[7] opportunities for behavioral interaction with its surroundings (see Richardson et al., 2008, for elaboration of this set of principles).

Once these principles are adopted, we may say that plants, like animals, perceive what is available in terms of biologically relevant interactions. In Gibsonian parlance, plants perceive opportunities for behavioral interaction in the form of affordances. Although Gibson would not have agreed that plants *perceive*, on the grounds that they remain rooted (see Gibson, 1979, chapters 1 and 2; but see also Calvo et al., 2014; Carello et al., 2014), there is ample room to argue that plants do so. Plant neurobiology has taught us that plants have an internal system for organizing sets of behaviors that is functionally similar to the animal nervous system. We can, therefore, approach plant

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[7] Gibson (1979) explains affordances as follows: "The affordances of the environment are what it offers the animal, what it provides or furnishes, either for good or ill. The verb to afford is found in the dictionary, but the noun affordance is not. I have made it up. I mean by it something that refers to both the environment and the animal in a way that no existing term does. It implies the complementarity of the animal and the environment." (p. 127)

behavior and neurobiology from the point of view of ecological psychology, and analyze the plant-environment system as a whole whose behavior emerges and self-organizes at a particular scale of interaction, the one mandated by ecology. (This may be one reason why plant intelligence has been neglected for so long, but time-lapse photography has evidenced the contrary.) Consistent with this approach, plants may well perceive opportunities for behavioral interaction in the form of affordances.

Two further principles of ecological psychology will serve to drive the point home: Perception and action form a continuous and cyclic loop; and environmental information *specifies* ways to interact with the environment (ecological psychologists say that environmental information is *specificational*).

Plant perception may thus be understood in terms of their response to specificational information. A climbing plant and its support, for example, constitute an ecological coupled system. In this way, a vine, say, may perceive the possibility to interact with a support that affords climbing. Environmental affordances, properties of objects like a support, specify ways to interact, and guide the climbing vine in a continuous and cyclic loop of perception-and-action.

Research in plant neurobiology can benefit by endorsing an ecological attitude towards its object of study. If information in the environment guides interactions, perception can be seen as cognitively unmediated, or ‘direct’ (Michaels and Carello, 1981). Direct perception means that once the information has been picked up by the plant, the solution emerges, and thus a computational explanation of an organism’s capacity to select actions in order to achieve its goals need not be invoked. Solutions, perceptually speaking, emerge out of the very interaction between the organism and its local environment. Energy arrays, higher-order information that comes in the form of the invariant properties of objects, furnish the organism with the information needed.

According to ecological psychology, we ‘pick up’ the invariant structure of an ever-changing environment. This is why, despite things being in constant flux, some relations among them remain unchanged (higher-order invariants), and organisms can directly pick these up.

For the sake of concreteness, consider tau theory (Lee & Reddish, 1981; Lee, 1998). Tau theory is an ecological theory of the skilled control of goal-directed behavior. Skilled control obtains by closing ‘motion gaps’. How does a vine control its movements as it interacts with a climbing support? How does it manage to close the gap with respect to its potential support? Perceiving an affordance such as *climbability* requires controlling the gap between the current state of the vine-support system and the desired goal state of reaching the support. The working hypothesis is that tau underlies goal-directed behavior and the control of motion-gaps, as in the case of a climbing plant. Tau is an ecological informational variable given by the equation,

$$\tau(X) = X / \dot{X}$$

where X is the current magnitude of a gap, and X-dot is the current rate of change of X. The tau of a gap is then the time it will take the gap to close at the current closure rate (Lee, 2009). Tau is an invariant that specifies time-to-contact between an organism and its target.

The ecological psychologist’s working hypothesis is that the flow field that obtains in the changing ambient energy arrays during movement permits organisms to grasp the rate at which action-gaps are closing. Although tau theory was initially thought of to account for guided movement in animals, general tau theory (Lee, 2009) has the potential to apply to plants too. Ecological psychology principles are not modality specific. In fact, they are substrate-neutral (Calvo et al., 2014). In this way, it is an open question whether tau information guides climbing. Plant neurobiology may well show that the type of activity that underlies sensorimotor coordination across the plant is tau based. This is a working hypothesis we are testing at the moment (Lee, Mancuso & Calvo, in preparation). By testing whether plants pick up specificational information from the environment or not we may be able to tell for or against non-computational models of plant intelligence.

4.2 Anticipation and the guiding role of non-model-based coordination

A mark of intelligence is anticipatory behavior. If plants exhibit anticipatory behavior (Novoplansky, 2009; forthcoming), this is something that in principle we should be able to test. The underlying working hypothesis is that plant adaptive behavior can only take place by a mechanism that predicts environmental sources of stimulation (Calvo & Baluška, forthcoming). The notion of anticipation, however, may come in a variety of forms, with weaker and stronger readings being possible. Anticipatory behavior may rely upon the capacity of the system to model internally the environmental sources themselves. But stronger forms of anticipation that do not depend on internal modeling cannot be discarded beforehand (Stepp and Turvey, 2010). In this way, we may test for anticipation in plants experimentally by contrasting the following empirical hypotheses, listed in decreasing order of commitment with representational and/or computational principles: ‘feature detection’; ‘predictive coding’; and ‘strong anticipation’. According to ‘feature detection’, plants behave *reactively* by detecting environmental features, and responding adaptively to them—in the limit case, under feature detection, no anticipation whatsoever takes place. ‘Predictive coding’, by contrast, interprets plants’ behavior *pro-actively*, thanks to a process of probabilistic inference akin to that found in animals (Kok et al. 2013) that allows them to scan their surroundings. Plants, under a predictive coding reading, would estimate the likelihood that one particular state of affairs, and not another, is the source of energy. Finally, ‘strong anticipation’ maintains that predictive success does not involve modeling the future at any stage, but is rather a function of actual past behavior (Stepp & Turvey 2010; Stepp, Chemero & Turvey, 2011).[8]

Feature detection has been well studied in visual cognition (Hubel and Wiesel, 1965). The feature detection model interprets neuronal activity in terms of specialized bottom-up feature detectors that respond selectively to angles, lines, movement, edges, etc., with information flowing upwards all the way from V1 into deeper layers (V2, V4, IT). By contrast, predictive coding (Rao and Ballard, 1999; Friston 2005) takes predictions (conditional probabilities of features being the cause of stimulation) to flow firstly top-down; then, mismatches between predictions and the incoming input signals are propagated bottom-up. In this model, perception is the end result of a process of anticipation whereby top-down predictions match the environmental input (Clark, 2015).

In the animal literature, it has been possible to test between ‘feature detection’ and ‘predictive coding’. Egner et al. (2010) considered the fusiform face area (FFA), and reasoned that if ‘feature detection’ were correct, the FFA area would respond to facial features *per se*. But if ‘predictive coding’ were correct, the FFA area should respond to the addition of top-down predictions (the expectation to see a face) and bottom-up surprise (the degree of expectation violation). In this way, faces and non-faces may elicit similar FFA responses when subjects have a high face expectation, and maximally differing FFA responses when subjects have a low face expectation (see

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[8] Thanks to Tony Chemero for bringing this third possibility to my attention.

Egner et al., 2010, for the details). These predictions would contrast sharply with those of the feature detection model: FFA responses need not be affected by the expectations involved. The results of Egner et al. (2010) appear to back up the predictive coding hypothesis.

Now, could we possibly test if plants are likewise able to generate expectancies in line with the interpretation of Egner et al. (2010). As Calvo & Baluška (forthcoming) argue, plant neurobiology may well provide the means to explore this possibility: If predictive processing stands, plant excitable cells will respond to the summation of expectation and its violation. If feature detection is correct, cells will respond exclusively to the particular vector of stimulation. In order to make these two hypotheses testable, we may consider a number of stimuli: gravity, light, moisture, oxygen, touch, etc., and we may generate expectations in several ways: electrically, chemically, mechanically, etc. Also, plant neurobiology has a variety of measurement techniques at its disposal, among them behavioral measurements, single-cell recordings as well as non-invasive neuroimaging techniques (Calvo & Baluška, forthcoming).[9]

Predictive coding in plants is an empirical working hypothesis subject to empirical investigation. But predictive coding is not the one and only alternative to feature detection. Strong anticipation may also fit the bill with respect to a number of cognitive processes and phenomena. A classic example is the outfielder problem (how does an outfielder in a game of baseball get to the ball at the right time and place?) Unlike predictive coding-based strategies, an ecological, non-model-based approach will exploit information available at the level of the coupling itself between organism and environment; in this case, between outfielder and ball-in-flight. There are a number

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[9] A survey of techniques in plant neurobiology, among them Multi-electrode array (MEA) technology, the Vibrating Probe Technique or Electrical Impedance Spectroscopy (EIS), is available at the *International Laboratory of Plant Neurobiology* (LINV) site: http://www.linv.org.

of ecological solutions in the market, but just consider for present purposes McBeath et al.’s (1995) Linear Optical Trajectory (LOT) model. According to LOT, in many occasions the outfielder’s trick is simply to follow a path that keeps the optical trajectory projection angle constant. As McBeath remarked, “if you're running along a path that doesn't allow the ball to curve down, then in a sense you are guaranteed to catch it.” For the LOT strategy, solving the outfielder problem boils down to continuously coupling perception and action. Such coupling remains cognitively unmediated, and thus need not rely upon the top-down flow of representational predictions that operate in predictive-coding.

Of course, plants don’t catch baseballs, but the problem of (strongly) anticipating future states of the world remains. Consider biological time-keeping, an ability that confers organisms physiological, metabolic and developmental fitness. Stepp and Turvey (2010)—see also Stepp, Chemero and Turvey, 2011—have recently elaborated on a strong anticipatory model of circadian time-keeping. Circadian mechanisms control many processes, among them the anticipation of day/night cycles. Light onset, dawn or temperature furnish plants with cues that permit synchronization in terms of period, phase, and amplitude with respect to the planetary cycles. This may in part explain the origins of anticipatory behavior more generally speaking. An illustration is offline nocturnal reorientation of *Lavatera cretica* (Schwartz and Koller 1986). Leaf laminas of *Lavatera cretica* can anticipate the direction of sunrise, and allow for this anticipatory behavior to be retained for a number of days in the absence of sunrise stimulation (see Calvo, 2012, and references therein).

Although circadian oscillatory behavior may at first sight be read as more congenial with a model-based approach (Bechtel, 2009), it need not be so (García and Calvo, 2010; Stepp et al., 2011). Circadian rhythms are generated endogenously, and regular resetting is needed in order to maintain synchronization with external cycles. *Zeitgebers* (time givers) serve to entrain plants. A model-based reading of circadian anticipatory systems relies upon an understanding of time-keeping where oscillation and entrainment come apart. Such decoupling is what would allegedly explain "free-running": the capacity to rely upon an internal model. But oscillation simply makes no sense in the absence of entrainment. As Roenneberg, Dann, and Merrow (2003) point out:

> "The circadian clock is not entrained because its free-running period deviates from 24 h, but it is able to free run because of how it evolved to work optimally when entrained. This is supported by the fact that there is no exact circadian period because it depends on the nature of the constant conditions. . . Thus, the correct statement should be the following: The circadian clock has evolved to fine tune biological functions to specific times within the day or night, and, when put into constant conditions, it free runs close to 24 h! To fully appreciate the function of the circadian system, we have to understand how clocks entrain to the environment.'' (p. 183).

Now, this quote brings a further subtlety, as it is actually not the case that oscillation and entrainment can come apart in the first place. On a weaker reading, we may simply observe that oscillation and entrainment do not come apart while preserving the 'free-running' talk. Or we may hold a stronger version according to which there is simply no such thing as endogenous free-running rhythmicity in the absence of environmental stimulation (this stronger position is congenial with Stepp et al.'s (2011), who illustrate it with examples of the lose of rhythmicity in plants, bacteria and birds as they become decoupled from regular cycles of light and darkness).

Of course, it is a long shot from circadian oscillators to the discussion of ‘predictive coding’ in the animal literature. However, if model-based forms of anticipation can enter the debate at all, there is no reason not to consider stronger forms of anticipation. If non-model based strong anticipation is on the right track, and the rationale of circadian systems can be applied more broadly to higher-level phenomena, this would bear upon our understanding of plant intelligence and adaptive behavior as involving, or not, computational and/or representational resources.[10] The present treatment pretends to stimulate the generation of working hypotheses in the discussion of plant’s anticipatory behavior (Novoplansky, 2015).

Plant neurobiology seeks to understand what adaptive behavior boils down to. Plant cellular and molecular biology can throw light upon the vascular transport of substances throughout the plant body, but only an integrated philosophy of plant neurobiology can shed light on the informational function being served by representations, if a representational-computational model is favored; or on the ecological level of analysis required, if models are dispensed with altogether. Ideally, a philosophy of plant neurobiology ought to embrace such diverse methodologies—a representationalist-mechanist understanding (Bechtel, 2009a), according to which intelligence is defined as information-processing that produces representations that plants can exploit in a purposeful manner; or a nonrepresentational-ecological one, understood in terms of the maintenance of a coupling between a plant and its local

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[10] It is noteworthy from a plant neurobiological perspective that although the actual proteins involved in time-keeping by plant and animal oscillators are different, their role in feedback loops of reciprocal regulation among molecular components is functionally identical.

environment under the coordination of tightly closed perception-action loops, as the nonrepresentational discussion of plant circadian clocks illustrates.

5. Conclusions

The interdisciplinary emphasis of plant neurobiology is expressed by the shared objective of explaining plant signaling and adaptive behavior with an eye to ultimately providing a satisfactory account of plant intelligence; an account that honors the place of plant life in nature. Philosophy should not be alien to this project. In this manifesto I have defended the role of philosophy as integral to plant neurobiology. Plant neurobiology needs to push towards interdisciplinary cooperation more steadily. Philosophy and cognitive science can contribute in a distinctive manner to the establishment and consolidation of plant neurobiology as an interdisciplinary endeavor with a research agenda of its own by providing a theoretical and methodological framework much needed for the guidance of plant research. This manifesto thus seeks to encourage collaboration among scholars across the various disciplines that can potentially contribute to plant neurobiology.[11]

Probably there is not set of necessary and sufficient conditions that trigger the creation and establishment of new scientific disciplines. But it is clear that the development of brand new explanatory models in plant neurobiology transcend the type of questions that could be posed from within each of the constituting plant sciences. The quest for plant intelligence requires the integration of multiple levels of description and explanation. Whether this collaborative effort fructifies in the consolidation of plant neurobiology as a distinct area of enquiry remains to be seen. For one thing, it is not

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[11] In addition to the core issues thus far discussed, philosophical reflection can play a number of subsidiary roles in plant neurobiology that range from questions of plant intentionality, consciousness and phenomenology, to topics in ethics and beyond (see Marder, 2011; 2012a; 2012b, for an overview).

only the interaction between vertices in the plant neurobiology hexagon of figure 2 above what matters. Institutionally speaking, the situation is akin to that found in Cognitive Science four decades ago, prior to the commissioning of the *Sloan Report*, when there were no academic departments as such that would take the lead and help shape the discipline. Professional societies and scientific journals in plant neurobiology have seen the light in the last decade. Incidentally, the *Society for Plant Neurobiology* was renamed *Society of Plant Signaling and Behavior* in 2009. Having changed the very name of the society in recent years is symptomatic of the not-yet-stabilized state of the field. Collateral controversies aside I would like to think that the time is ripe to undertake the study of plant intelligence in an integrated, non-reductionist manner.

Last, but not least, it is noteworthy that no undergraduate majors are being offered in the field of Plant Neurobiology, to the best of my knowledge, in any institution. Considering the structure of plant neurobiology to be represented by the aforementioned "plant neurobiology hexagon", a demanding curriculum in the plant sciences ought to consider the production of a six-course based requirement that covered plant cell and molecular biology, (electro)physiology, biochemistry, evolutionary and developmental biology, plant ecology, and the philosophy of plant neurobiology. In fact, it should ideally include, not only plant neurobiology and its philosophy, but also comparative psychology and behavioral neuroscience.[12] The former in order to help highlight existing commonalities in behavioral repertoires and intelligent responses across eukaryote; the latter, with its emphasis on the connection

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[12] It strikes to the plant neurobiologist that whereas nonhuman animal models are used to know more about humans, the same cannot be the case with plants. Can we draw lessons from *Aplysia*, but not from, say, *Zea mays*? As František Baluška observes (personal communication), maize is one of the most developed plant models. Its primary and lateral root system constitute a highly sophisticated network, with the primary root apex generating a very large transition zone (the maize's 'neocortex', if we may), where the highest rate of consumption of oxygen and of sucrose pumped throughout the phloem has been registered. What is then in a sea slug that cannot be found in a plant?

between intelligence and adaptive behavior at the level of the organism and the underlying neural substrate, which can also help to draw the parallel between the molar-componential correspondence in animals and plants. Cognitive ethology, artificial intelligence and robotics, among other disciplines, are likewise welcome to contribute. In a sense, the full range of methodologies, concepts and theories that would allow a mature plant neurobiology and its philosophy to zoom back and enlarge the picture in the overall quest for plant intelligence is therefore still to come. It is hoped that this manifesto has conveyed a sense of the need for integration and the exciting future that lies ahead in this joint venture.

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