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S.I.: NEUROSCIENCE AND ITS PHILOSOPHY

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,

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and providing an explanatory framework and guiding principles that will hopefully ease the integration of research on the quest for plant intelligence.

Keywords Plant neurobiology (philosophy of) · Plant intelligence · Cognitive science

1 Introduction: the study of plant intelligence

Speaking about plant intelligence is not taboo any longer. *Plant behaviour and intelligence* by Anthony Trewavas, *Brilliant green: The surprising history and science of plant intelligence* by Stefano Mancuso and Alessandro Viola (2015), or Michael Marder's (2013) *Plant-thinking: A philosophy of vegetal life*, are but a sample of the ever-increasing number of publications devoted in the last decade to the scientific and philosophical study of plant intelligence.[1] As the debate over plant intelligence gathers pace, a common thread that brings together different aspects that bear upon the discussion begins to emerge. Intelligent, non-hardwired, strategies appear to underlie the capacity of plants to integrate diverse sources of information into flexible overt responses; to make decisions as to how to change phenotypically; and to perform predictive modeling for the sake of fitness improvement (Trewavas 2005a), to name but a few (see below). It is the degree of flexibility that can be observed in the behavioral repertoire of plants as they assess, say, potential conditions under pressure (Trewavas 2014) that grants the ascription of intelligence to plants.

Think of plant tropic (directional) and nastic (non-directional) responses (Gilroy 2008), such as the well known phototropic, gravitropic, photonastic, and gravinastic patterns of growth and movement documented throughout the plant kingdom. According to a mechanistic understanding of such responses (a view that can be traced back to Julius von Sachs and Jacques Loeb—see Greenspan and Baars 2005), a non-cognitive ("reactive") interpretation is the default stance. Plants would react to sources of stimulation, such as light or gravity, instinctively. Reactive behavior can be accounted for in hardwired terms, so the story goes, and being hardwired, the ascription of intelligence is seriously undermined.

But there is a body of literature that calls into question this received view (see Calvo and Keijzer 2011, and references therein). Intelligence, as approached in this manifesto, has to do with "sets of biological functions … that exhibit a degree of flexibility against contingencies in their environment-induced behavioral repertoire" (Calvo and Baluška 2015). Plants eke out a living in highly complex environments with many vectors other than light or gravity to be appropriately navigated. Their survival depends on reliably sampling many other vectors whose integration and subsequent anticipation to contingent future outcomes is critical and accounts for the variety in the types of growth and movement adaptive responses observed. With the need to sample and integrate a wide array of environmental signals to flourish in a dynamic environ-

[1] Trewavas' seminal "Aspects of plant intelligence," an article that appeared in *Annals of Botany* in 2003 with 246 citations as of Fall 2015—total downloads of over 50,000 (full-text), and a number of downloads for 2014 that quadruples the average annual download of the 10 years since its publication in 2003—bears witness to the growing attention being paid to the topic.

ment, a hardwired set of responses does not appear to have the plasticity required for such sampling and integration. Bluntly, hardwiredness does not work under complex conditions.

The investigation of plant intelligence is a matter of interest in emerging disciplines such as cognitive biology. Bechtel (2014), for instance, considers model organisms, prokaryote and eukaryote alike (other than animals), in the quest for cognitive processing. Put in terms of common ancestry, and considering a 'principle of evolutionary conservation' (Bickle 2003)—'evolution does not start from scratch', so the dictum goes—, it makes sense to approach intelligence in an incremental and comprehensive manner. As a matter of fact, that minimal forms of intelligence exist across Eukaryota (Calvo and Baluška 2015) is not breaking news anymore (see Lyon 2007 for *E. coli* and other prokaryotic forms of intelligence).

Plant intelligence furnishes us with an opportunity to unearth underlying general principles. Is there a mark of intelligence? Probably not. Sensory-motor and perceptual capacities, goal-oriented behavior, basic forms of learning and memory, communication, and even decision-making and problem solving, all seem to fit the bill in our quest and are subject to scrutiny with the toolkit of the cognitive sciences.

In order to study plant intelligence, we have at our disposal a number of models and frameworks. Traditionally, the emphasis has been laid on studying plant intelligence from a computational point of view. Cognitive biology, among other disciples, urges us to consider intelligence by looking at processes other than computational ones alone. Thus, we may try to figure out how plants are able to cope with the demands of their environment by unearthing how they process information, or we may consider that their flexible behavior gets structured as a result of the way internal and environmental factors couple together. Put in more familiar jargon, we may endorse the view that intelligence is (cognitivist) information-processing as conceived by the representational-computational view of the mind, or we may consider a number of post-cognitivist alternatives (see Calvo and Gomila 2008) that include ecological psychology (Gibson 1979), behavior-based AI (Pfeifer and Scheier 1999), embodied cognition (Varela et al. 1991), and dynamicism (Port and Van Gelder 1995).

As of today, the study of plant intelligence is dominated by information-processing assumptions incorporated, more or less tacitly, from cognitive psychology and artificial intelligence. These assumptions, if not made fully explicit, and contrasted against post-cognitivist ones, run the risk of weakening the potential of the field. An objective of this manifesto is to make explicit those assumptions, and to explore ways to decide among them.

On the other hand, and despite the existence of a solid body of literature (see Brenner et al. 2007; Stahlberg 2006; Baluška and Mancuso 2007; Calvo 2007; Barlow 2008; Baluška and Mancuso 2009a; and references therein), discussions still subscribe to particular sub-disciplines with their own focuses and objectives. One of the shortcomings 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 pursuit of plant intelligence. In doing so, this manifesto aims to promote an approach to the study of plant intelligence through the integration of plant research; encourage collaboration among scholars

across the various disciplines that can potentially contribute; identify the competing working hypotheses that underlie the notion of plant intelligence; and provide theoretical and methodological guidelines for the development of a philosophy of plant neurobiology.

2 Plant neurobiology

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 in 2005, and initiated the journal *Plant Signaling and Behavior*. 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. 2007) 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.

Overall, plant neurobiology (Brenner et al. 2007) aims to unearth that plants perceive and act in an integrated and purposeful manner, and how they do it. 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 2005b). 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. 2007). 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.

As we shall see below, the field proposes an interdisciplinary and integrated view of plant signaling and adaptive behavior in order to study plant intelligence. But a preliminary caveat regarding the very name of the discipline is in order first. 'Plant neurobiology' is anything but uncontroversial. In fact, it is my personal experience, and the experience of many fellow plant neurobiologists, to find audiences perplexed by the very idea of 'plant *neuro*biology,' a reaction that in turn makes academic discussion often deviate into terminological blind alleys, bewildering everyone. So, before further ado, and to dissipate doubts, 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 and Mancuso 2009b). Consider g-aminobutyric acid (GABA), an amino acid present in plant and animals alike. In plants, unlike in the animal literature where its role in neurotransmission is the focus of attention, GABA has been studied primarily for its metabolic role (protection against oxidative stress, cytosolic pH regulation, etc.) But the non-metabolic role of GABA in *signaling* is generating increasing interest (Bouché et al. 2003). In fact, with the identification of GABA receptors in plants, its role as a signaling molecule, including the triggering of defenses against insects is beginning to be understood (Bouché and Fromm 2004).

In addition, plant cells, like animal ones, exhibit polarity and have an endocytosis-driven vesicle recycling apparatus that permits the secretion of signaling molecules (Baluška and 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). Recent work on circadian rhythm synchronization neatly illustrates the signaling and communication role performed by plant and animal cellular circadian clocks. As Takahashi et al. (2015) report, the capacity of the suprachiasmatic nucleus neurons in mammals to put distal circadian clocks in synchrony is paralleled by circadian clocks located in plant shoot apex cells; clocks that can entrain distal root cells courtesy of the plant vasculature signaling pathways.

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 and Grant 2009; Ovsepian and Vesselkin 2014).

In any case, degree of similarity aside between the body plans of plants and animals, 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, and plants' usage of many of the same resources that animals use in their nervous systems partly undergirds the concept of plant intelligence. 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,[2] but all plants depend in one form or another upon electrical signaling. Plant communication takes place partly via action potentials (APs) that propagate multidirectionally along the phloem (for a review of plant APs, see Pickard 1973; see also Baluška and 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.[3] By contrast, under the lens of plant neurobiology, APs and other electrical long-distance signals play a central role in integrating the plant body.

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 upside down arguments devised for the purpose of denying 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 must you be if, *despite* being rooted, you have succeeded in passing down

[2] Almost a century ago, Bose (1926) demonstrated that action potentials connect the petiole and the pulvinus of *Mimosa pudica*, triggering leave droop by loss of turgor (for a review, see Trewavas 2014).

[3] 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.

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. Furthermore, plants can anticipate competition for resources, growing differentially depending upon the future acquisition of minerals and water (Novoplansky 2016). Plants also 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 and 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 and 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

What is the potential role that philosophy can play in the field of plant neurobiology? Philosophy could play a constructive role; bluntly put, pretty much the same role that it has played in the cognitive sciences. 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. In this way, 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.

There is thus room for the skills of philosophers in the study of plants. But the basic toolkit of philosophy is not armchair conceptual analysis or *a priori* reasoning (Fumerton 1999). Plant intelligence is not meant to 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, I contend, 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. A naturalistic philosophy of plant neurobiology therefore has a crucial role to play *within* an interdisciplinary plant neurobiology, similar to the role it has traditionally played in cognitive science.[4] Discussion for instance, of the representational or nonrepresentational nature of the discipline is pivotal insofar as their theoretical commitments would lead to different empirical approaches, and a naturalistic undertaking may ease integration of theoretical reflection more fully into plant neurobiology.

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 close 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" (Fig. 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 Fig. 1, legend). Today it is a well-established area of research, with the flourishing of journals, conferences, etc., devoted to the field.

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

[4] Either within a representational cognitive science (Bechtel 2009; 2010), or within an embodied and/or ecological cognitive science (Chemero 2009; Dale et al. 2009)—see Sect. 4, below.

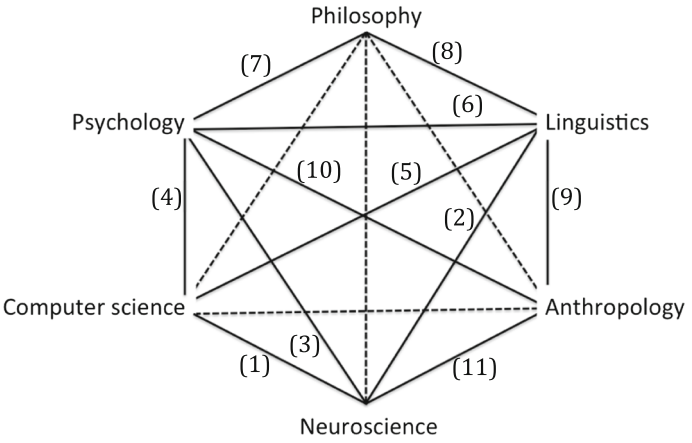

Fig. 1 The "Cognitive Science hexagon" in 1978. Vertices represent contributing disciplines. Lines joining vertices represent the following interdisciplinary collaborations: *1* cybernetics; *2* neurolinguistics; *3* neuropsychology; *4* simulation of cognitive processes; *5* computational linguistics; *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)

plant neurobiology can play a role equivalent to the one that philosophy is now playing within cognitive science.[5] 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 explanatory frameworks that integrate 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.

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

[5] 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.

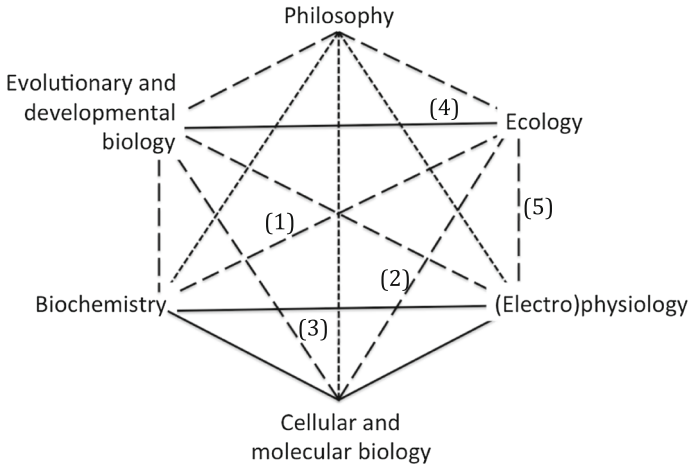

Fig. 2 The hexagon of Plant Neurobiology in 2014. Vertices represent contributing disciplines. Lines joining vertices represent the following interdisciplinary collaborations (only a few are drawn): *1* biochemical ecology; *2* molecular ecology and ecological genetics; *3* evolutionary genetics; *4* 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 Fig. 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 should be clear by now.[6]

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

[6] 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.

lines in Fig. 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. The plant neurobiology hexagon represents such an emergent rationale, and the philosophy of plant neurobiology, as part of this joint effort, aspires to ease integration.[7]

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. Or take domain-generality vs. domain-specificity: are "plant minds"[8] domain-general or domain-specific devices? Spelling out oppositions like this one ought to allow us to draw a number of working hypotheses. Consider the study of fruit flies or honeybees in cognitive science (Dyer and Dickinson 1994; Esch et al. 2001). Presumably, research on invertebrates pays off for human cognition because, in relevant and important respects, they are enough like humans, or vertebrates more generally. The working hypothesis, regardless of whether the outcome is confirmation or refutation, is that the same is true of plants. In this way, acknowledging a number of homologies between plants and animals at the level of the neurochemistry, for example, and by understanding the adaptive behavior of plants as well as by endorsing similar ways of studying such behavior (Calvo et al. submitted), we should be able to put empirical hypotheses in plant neurobiology to the test (Sect. 4).

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 all eukaryotes (Calvo and Baluška 2015) 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

[7] A different issue is whether analytic or mechanistic models will be superseded in plant neurobiology by an organismic, non-reductionist explanatory framework or not. 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).

[8] 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.

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 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 2014), 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 or not? That is an open question. 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 and Gomila 2008; Robbins and Aydede 2009) seems to be the natural contender of information-processing approaches, providing the arena in which an integrated plant neurobiology may be founded and critically assessed. 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).

Taking issue with the architecture of cognition, a philosopher of plant neurobiology may well ask whether the representational-computational approach to the study of intelligence inherited from cognitive psychology and artificial intelligence may be superseded or not. 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. One way or another, this is the focus of our next section, whose objective is to explore the guiding role that different theoretical hypotheses may play in the scientific study of plant intelligence.

4 Putting plant neurobiology research to the test

Does plant neurobiology commit us to endorsing a representationalist framework in the study of plant intelligence? Or could, by contrast, an anti-representationalist framework be employed? We may explore what both options look like, as it is possible that both hold some promise. Ideally, a philosophy of plant neurobiology ought to embrace such diverse methodologies—a representationalist-mechanist understanding (Bechtel 2009), 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 that lays the stress upon the sensorimotor grounding of plant intelligence, suggesting new, non-computational, ways to understand the

relationship between plants and their local environments (e.g., through the maintenance of a coupling between a plant and its local environment under the coordination of tightly closed perception-action loops).[9] 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 representational models are dispensed with altogether.

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, both from the stance of mainstream cognitive psychology and 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. The purpose is to furnish the building blocks for empirical investigation of these possibilities by way of exploratory case studies that will hopefully lead to more in-depth research. In particular, we shall consider for the sake of illustration debates on perception and anticipation for a taste of what plant neurobiology has to offer. So, how does the philosophy of plant neurobiology connect with the lab?

4.1 Constructivist versus direct perception models of plant perception

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 contrasting Helmholtzian constructivism (Rock 1983) with ecological psychology (Gibson 1966, 1979). According to a constructivist, information-processing framework, perception is the outcome of a logic-like process of inference. Proponent of this approach hypothesize that perception is mediated or indirect on the grounds that the stimulus is inherently ambiguous and that perception therefore needs to be treated as an inferential process. Under an ecological framework, ecological theories of perception would hypothesize that perception is organized around action. Opportunities for action could in principle be perceived directly as interaction with an unambiguous environment takes place.

Because the general reader is more familiar with information processing than with ecological models,[10] I shall briefly review some of the main tenets of the ecological approach. According to ecological psychology, (i) the proper unit of analysis is the organism-environment system as a whole, and not the detached organism in itself; (ii) we should likewise be paying attention to the ecological scale at which the interaction takes place; (iii) adaptive behavior is to be understood in terms of emergence and

[9] I thank Bill Bechtel for urging me to consider both options in tandem.

[10] Good entry points to the indirect and the direct perception approaches are Rock (1997) and Michaels and Carello (1981), respectively.

self-organization; and last, (iv) what an organism perceives are *affordances*,[11] opportunities for behavioral interaction with its surroundings (see Richardson et al. 2008, for elaboration of this set of principles).

By adopting principles (i)–(iv), the ecological psychologist (Carello et al. 2012) defends the view 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), 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 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.

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 testing these ecological principles in the form of empirical hypotheses subject to experimental scrutiny. 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.

[11] 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).

For the sake of concreteness, consider tau theory (Lee and 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 (Calvo et al. technical report). 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: feature detection versus predictive processing

A mark of intelligence is anticipatory behavior. If plants exhibit anticipatory behavior (Novoplansky 2009, 2016), this is something that in principle we should be able to test. A working hypothesis is that plant adaptive behavior can only take place by a mechanism that predicts environmental sources of stimulation (Calvo et al. submitted). The notion of anticipation, however, may come in a variety of forms, with weaker and stronger readings being possible. With a stronger reading, anticipatory behavior may rely upon the capacity of the system to *model* internally the environmental sources themselves.[12] In this way, we may test for anticipation in plants experimentally by contrasting two working hypotheses: 'feature detection' and 'predictive coding', where

[12] According to yet another approach to the notion of anticipation, predictive success does not involve modeling the future at any stage, but is rather a function of actual past behavior (Stepp and Turvey 2010; Stepp et al. 2011). This form of anticipation does not depend on internal modeling, and although cannot be discarded beforehand we shall ignore those for present purposes. Thanks to Tony Chemero for bringing this third possibility to my attention.

the latter is more committed with full-fledged representational and/or computational principles than the former.

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 proper 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.

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 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 et al. (submitted) elaborate, 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.[13]

[13] 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.

5 Conclusions

The interdisciplinary emphasis of plant neurobiology is expressed by the shared objective of explaining plant signaling and adaptive behavior with an eye ultimately to 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 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.[14]

Probably there is no set of necessary and sufficient conditions that can trigger the creation and establishment of new scientific disciplines. But it is clear that the development of 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 only the interaction between vertices in the plant neurobiology hexagon of Fig. 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. I would like to think that the time is ripe to undertake the study of plant intelligence in an integrated 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. 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 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

[14] 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, b, for an overview).

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, aiming ultimately to outline a road map for the establishment and development of a particular area of research with a character of its own, conveys a sense of the need for integration and the exciting future that lies ahead in this joint venture.

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