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Plants: Adaptive behavior, root-brains, and minimal cognition

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Abstract

Plant intelligence has gone largely unnoticed within the field of animal and human adaptive behavior. In this context, we will introduce current work on plant intelligence as a new set of relevant phenomena that deserves attention and also discuss its potential relevance for the study of adaptive behavior more generally. More specifically, we first give a short overview of adaptive behavior in plants to give some body to the notion of plants as acting creatures. Second, we focus on “plant neurobiology” and introduce the resurfacing of Darwin’s idea that plants have a control center for behavior dispersed across the root tips (a root-brain). We then discuss minimal forms of cognition, and consider motility and having a dedicated sensorimotor organization as key features for designating the domain of minimal cognition. We conclude that plants are minimally cognitive, and close by discussing some of the implications and challenges that plant intelligence provide for the study of adaptive behavior and embodied cognitive science more generally.

Keywords

Plant intelligence, minimal cognition, adaptive behavior, plant neurobiology

I Introduction

In recent years, the topic of plant intelligence has triggered ample discussion among plant scientists, especially when cast under the label of *plant neurobiology* (e.g., Alpi et al., 2007; Baluška, Mancuso, & Volkmann, 2006; Baluška, Volkmann, & Menzel, 2005; Barlow, 2008; Brenner et al., 2006; Firn, 2004; Trewavas, 2003, 2005a, 2007; see also Calvo Garzón, 2007, and references therein). According to plant neurobiology, it is both claimed (and challenged in turn) that plants exhibit intelligent behavior, and that they possess internal control structures in many ways functionally similar to neuron-based control structures.

So far, this debate has gone largely unnoticed within the field of (animal) adaptive behavior and embodied cognition. However, we hope it becomes clear in the foregoing why this work is highly relevant for research on adaptive behavior and embodied cognition more generally. For one thing, it furnishes researches with a whole new set of relevant phenomena that deserve attention. In addition, by departing from textbook examples of intelligence and adaptive behavior, its theoretical importance in helping disentangle essential characteristics of intelligence and behavior from merely parochial ones is manifested. Thus, the purpose

of this article is to introduce the cognitive science community to current work on plant intelligence, and discuss its potential relevance for the study of adaptive behavior, as formerly limited to the animal kingdom.

A note of caution may be needed at this point. Discussing plants as behavioral and cognitively interesting systems does not imply that we underestimate or neglect the many differences between plants and animals, including humans. We stress that despite these differences there are also important behavioral commonalities. In fact, as one referee notes, there is an analogy with the discussion between “lumpers” and “splitters” in work on phylogenetic systematics or cladistics (Hennig, 1966). Here, different camps may classify species of organisms into coarser (lumpers) or finer grained (splitters) *clades*, either highlighting similarities

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or differences between groups of species. Both are valid tendencies and in fact it is important to seriously discuss where to place the boundaries of such classifications. When it comes to behavior and even cognition in plants, we are clearly acting as lumpers in our stress on commonalities between plants and animals. We think there is a lot to learn from plants interpreted as behaving organisms. However, it goes without saying that for other purposes the emphasis may be rightly placed upon the specifics of some forms of behavior as opposed to others. With this caveat in mind, confronting embodied cognitive science with the “plant question” is sure to raise important new issues in the field of embodied cognition itself.

First, current work on plant intelligence has important repercussions for our understanding of behavior. Behavior is usually understood as involving some form of motor action aimed at achieving some goal. Animals, but also bacteria and robotic devices, provide examples that trigger an intuitive human judgment of behaving as being animate: entities that move about as a unit in a way that remains coordinated to an external object such as “following” or “fleeing” (Scholl & Tremoulet, 2000). Plants, by contrast, do not trigger such intuitive judgments and are usually not considered as animate, behaving organisms. As we will discuss, recent work—that actually goes back a long time—makes this attitude seriously outdated. Plants do behave in ways that are unquestioningly intelligent and thus force researchers of adaptive behavior to clarify their domain further in order to account for the adaptive behavior of plants. Second, one of the most controversial as well as interesting developments in the field of plant intelligence is the already mentioned notion of plant neurobiology:

The goal of plant neurobiology is to illuminate the structure of the information network that exists within plants. Hence, much of the emphasis in plant neurobiology is directed towards discovering and understanding the action of unknown and known systemic signals. (Brenner et al., 2006, p. 413)

Although the very employment of the “brand name” *plant neurobiology* has met with a lot of resistance (Alpi et al., 2007)—the Society for Plant Neurobiology, constituted in 2005 at the *First International Symposium on Plant Neurobiology*, even changed its original name for the less controversial Society of Plant Signaling and Behavior—the aim of understanding plant signaling networks and how plants distribute information, physiologically and (neuro)biologically, is not disputed. Plant neurobiology integrates results from areas of research such as plant electrophysiology, cell biology, molecular biology, and ecology (Baluška et al., 2006; Barlow, 2008; Brenner et al., 2006). One of the upshots

here is that a lot of plant decision-making takes place underground and can be ascribed to a so-called “root-brain” (Baluška, Mancuso, Volkmann, & Barlow, 2004, 2009). Irrespective then of whether one approves of the terminology here, the discussion on root-brains is highly significant for a better understanding of brains and what they do, either by extending the neural domain or by forcing one to be more explicit about the differences between “real” brains and root-brains.

Third, we will discuss the question of whether minimal readings of cognition, such as have been developed within embodied cognition (Beer, 2003; van Duijn, Keijzer, & Franken, 2006), might apply to plants. Within this framework, the notion of cognition is broadened to make sense of a wide range of behaviors exhibited by “simple” animals, such as nematodes or flies. Though simpler than the behavior of humans, these behaviors are nevertheless not simple, and the intricacy of the underlying organizations warrants the use of a cognitive terminology here. The message is clearly that we should avoid generalized dismissive intuitions concerning the capabilities of such “lower” animals and attempt a more empirically informed approach. We believe that this open attitude is also beneficial to the study of possible cognitive phenomena in plants. In fact, we believe that the adaptive behavior of animals and plants alike can be explained by identifying a common set of principles (García Rodríguez & Calvo Garzón, 2010).

The article has the following structure. In Section 2, we give a short overview of adaptive behavior in plants to give some body to the notion of plants as acting creatures. Section 3 focuses on plant neurobiology and introduces the idea, going back to Darwin, that plants have a root-brain: a control center for behavior dispersed across the plants’ root tips. Sections 4 and 5 focus on minimal forms of cognition and provide a more in-depth discussion of the question whether plants can be said to be cognitive given criteria that have been developed in the context of free-living creatures and robots. Motility and having a dedicated sensorimotor organization is a key feature here for designating the domain of minimal cognition. Drawing on previous work (Calvo & Keijzer, 2009), Section 4 develops the question, using the work of Hans Jonas, *why* having sensorimotor organization and free motility is actually important for cognitive phenomena, and whether plants may fulfill some of these functions in other ways. In Section 5, we argue for the similarities between plant growth and animal learning and memory, and deal with plant structures for forms of offline cognition. We conclude that these examples show that plants can be considered to be minimally cognitive and that they constitute an important domain for cognitive studies. In the final section, we

discuss some of the implications and challenges that plant intelligence provide for the study of adaptive behavior and embodied cognitive science more generally.

2 Adaptive Behavior by Plants

Plants are not passive systems that build up photosynthates. Plants do exhibit sophisticated forms of behavior, and are able to assess current data that can lead to an advantage at a later stage. Roots, for instance, exhibit patterns of growth that depend upon future acquisition of minerals and water. Plants are sensitive to a variety of signals, which include not only water, light, minerals, and gravity, but also soil structure, neighbor competition, herbivory, allelopathy, and wind, to name but a few. Likewise, plant roots can, for instance, sense volume, discriminate self from alien roots, and allow for phenotypic root reordering as a function of competition for nutrients. We shall not attempt to provide a full review of all competencies. In fact, the list of signals, both biotic and abiotic, that plants can sense and integrate is ever growing. If 15 different signals had been identified (Trewavas, 2003), the list has now grown to 22 different vectors (Trewavas, 2008), and counting! Thus, rather than giving the apparently exhaustive list, we shall lay the stress upon a number of canonical, as well as less well-known, examples of plant behavior of especial significance for our purposes. Considering that their animal counterparts have uncontroversially been considered cognitive, we shall briefly review: (a) movement in response to a variety of integrated stimuli; (b) root decisions and self-acquaintance; and (c) plant-level communication.

Plant Movement and Signal-Integration Plant tropisms (Stanton & Galen, 1993) involve a number of directional changes by differential cellular elongation in response to an array of environmental stimulations. Tropisms can vary substantially as a function of the type of stimulus that plants are responsive to (e.g., light, touch, or gravity), and the part of the plant that responds to the stimulation, which, somewhat simplifying, is achieved via cellular growth and development (Esmon, Pedmale, & Liscum, 2005). In response to, for example, directional light, moisture, fluctuations in temperature, and physical forces such as gravity and touch, or mechanical stimulations more generally, plant scientists have identified different types of responses such as phototropism, hydrotropism, thermotropism, gravitropism, and thigmotropism, respectively. In addition, many of these tropistic responses can be positive or negative, depending on whether plants respond, directionally speaking, for or against the source of stimulation. This is the case of roots (that respond negatively to blue light), or stems that,

by contrast, react positively. But beyond the “classics,” many other environmental vectors prompt plants to react adaptively. A non-exhaustive list includes oxygen, chemicals, trauma, fluctuations in water flow, geomagnetic fields, electric fluxes, shade, darkness, and parasites. In this way, we may also talk of oxytropic, chemotropic, traumatotropic, rheotropic, magnetotropic, galvanotropic, (shade-avoidance) thigmotropic, skototropic, and parasitic host tropistic responses (Baluška et al. 2009; Barlow, 2010; Trewavas, 2003).

It is noteworthy that plants do not react tropistically to stimuli on a one-by-one basis (one stimulus, one directional response). Consider highly sophisticated responses such as gravitropisms (Baluška, Barlow, Volkmann, & Mancuso, 2007). Roots, for instance, stop developing downwards as they encounter a physical obstacle, and grow horizontally instead. However, they are able to assess the state of affairs, and periodically try to move downwards, remaining horizontal if unable to respond gravitropically (Massa & Gilroy, 2003). Incidentally, this is very similar to the well-known example of a basic wall-following robot that accomplishes wall-following by having a tendency to veer to the right or left and turn left or right when it bumps into the wall. As a result, what we find is anything but simple and linear tropistic responses. Optimal root tip growth requires the integration of gravity and mechanical perturbations, among other vectors such as moisture, whose integration takes place probably in the root cap (Takahashi, Goto, Okada, & Takahashi, 2002). Less familiar, although very illustrative, examples include salt-avoidance behavior (Li & Zhang, 2008). In this case, salinity interacts with the gravitropic response of shoots, and plants are forced to assess the overall integrated signal to optimize shoot growth under abnormal saline conditions. Phenotypic plasticity is the result of overall signal integration, and not of a fixed, say, graviresponse (Barlow, 2010; Trewavas, 2005a).

Complexity increases substantially with the integration of types of signals; something necessary for plants in order to develop and achieve optimality in terms of growth (Esmon et al., 2005). But growth-mediated directional change is not the only way to cope with the contingencies in an ever-changing environment. Plant parts also expand/contract, giving rise to turgor-mediated movements by means of differential changes in volume, instead of differential changes in the rates of growth (Koller, 2000, 2001). In fact, plants exploit a variety of forms of movement, if only typically on a slower timescale than animals. Traditionally, this is certainly one factor that has made it more difficult for plant behavior, let alone cognition, to be taken seriously, although thanks to

speeded up film our appraisal is now changing dramatically. Well-studied phenomena are autonomous movements under an endogenous circadian clock, as well as more direct, environmentally driven movements, such as nastic responses (e.g., nondirectional leaf movement in daytime). Flowers also open regardless of the direction of environmental vectors, and close at night (nyctinastic “sleep”). Or consider the case of the stilt palm. In order to avoid competition for light, the stilt palm (Allen, 1977) “walks” away from shade and into sunlight. The stilt palm grows new roots in the direction of sunlight, allowing older roots to die. Trewavas (2003) even interprets this as an *intentional* form of light-foraging behavior. A more exotic form of movement obtains when a plant moves toward darkness, a routine by the name of skototropism that allows some herbaceous plants to target trees for climbing. Ray (1992) studied the light foraging behavior of five climbing species of *Araceae*; a tropical herbaceous monocotyledon. *Araceae* may shift back and forth between mobile and sessile routines, as meristems disperse from their original seedling location to tree trunks, which they might leave behind for good, should local conditions become disadvantageous. As Trewavas (2003) interestingly observes in relation to such foraging behavior,

the filiform stem explores, locates and recognizes a new trunk and reverses the growth pattern. As it climbs, the internode becomes progressively thicker and leaves progressively redevelop to full size. . . This behaviour is analogous to animals that climb trees to forage, intelligently descend when food is exhausted or competition severe, and then climb the next tree. (p. 15)

Only plastic systems are able to assess the benefits of integrating tropistic responses one way (beneficial) rather than another (detrimental), and exploit the ones that result in an increasing fit to environmental contingencies. This tells plants apart from cartoon versions of hard-wired tropistic, non-adaptive, behavior. Take Philidog, the robot toy whose sad story is amusingly told by Boden (2006). Philidog would track and follow a light source. Unfortunately the robot was so good at it, and so hard-wired(!), that it was run over by a car whose lights could be perceived through the entrance of the hall where Philidog was being exhibited. Of course, this is a cartoon story, and the moral is that, if anything, plants’ soft-wired capacities resemble, not those of Philidog, but rather those of behavior-based AI or biological-based robotics of the sort pioneered by Braitenberg (1984), Beer (1990), and Brooks (1991), among others.

Root Decisions and Self-Acquaintance Plants also exhibit sophisticated forms of decision-making and self-acquaintance courtesy of root growth

(Baluška, Manusco, Volkmann, & Barlow, 2010). Roots have developed computational resources to indirectly sense, for example, the volume of soil potentially available in which plants may display their root network while minimizing the negative effects of self-competition (Trewavas, 2005b). In a series of experiments (McConnaughay & Bazzaz, 1991), belowground space available for rooting was shown to affect the overall performance of plants belonging to the same species. The results were interesting to the extent that the amount of nutrients had been controlled for independently. When the rate of nutrient addition was held constant, those plants with more volume available would score higher in terms of growth and reproductive parameters. Root segregation, the spatial distribution of the root mass, is directly related to pot space availability (in greenhouse controlled conditions), and not to amount of nutrient or water. It seems then that plants compete for physical space itself, regardless of nutrient concentration and the like. Roots actively compete by means of toxic and nontoxic chemical, as well as electric, signaling belowground (Schenk, Callaway, & Mahall, 1999). In fact, competition can be fierce in arid environments, where resources are usually sparse, and adequate decisions as to how to segregate optimally a root network clearly confer an adaptive advantage. In this way, root segregation can be seen further as a genuine form of territoriality akin to what can be observed in the animal kingdom.

Interaction and territoriality indicate that plants must have a way to distinguish own from alien root structures, and those from the same species from root networks belonging to other competing species. In short, some form of self-recognition is needed if roots are to make decisions as to how to segregate. A different set of experiments (Gruntman & Novoplansky, 2004) has lead researchers to defend the view that such a competency is a form of predictive modeling (Trewavas, 2005b). The behavior of twin clones of seedlings set in control experiments to share belowground conditions indicates that they perceive each other as containing alien root structures. The same happens when previously connected ramets, clones with the same genetic constitution, become disconnected and after some time react to one another’s roots as alien.

The ideas of self-recognition and non-self discrimination serve to back up the evidence thus gathered. But what are the mechanisms that underpin the capacity to discriminate self from alien? The aforementioned experiments indicate that the explanation cannot reside in genotype-based discriminations, as seedlings can “tell the difference” between themselves and their clones. Instead, the phenomenon may have to do with the information-processing possibilities of root-brains. Thus, according to the working hypothesis of plant

neurobiology, the identification of self may proceed via different types of “synapses,” courtesy of transport auxin for the purpose of electric communication among cells (neuronal synapses), on the one hand, and mechanisms at the cellular level (immunological synapses), on the other. Either way, what we find once again are mechanisms that resemble those identified in animal communication (Baluška et al., 2005). In fact, plant root decision-making pretty much resembles the sort of processes that underpin decision-making in the bacterium *Escherichia coli* (Adler & Tso, 1974; more below).

Plant-Level Communication Communication between plant parts is clearly needed. Think, for example, of plant propagation by grafting and budding. In these cases, asexual reproduction requires that communication channels between roots and shoots are open in such a way that morphology can be controlled for. But, more interestingly, consider inter-plant communication. Beyond already well-researched forms of cell-to-cell transport of proteins, nucleic acids, oligonucleotides, and other macromolecules via plasmodesmata (Ding, 1997), plants communicate aerially not only between conspecifics, but also between members of different species, via a number of volatile organic compounds (VOCs) that plants release into their environment. Plants thus interact and actively search for adaptive defense by means of the VOCs emitted and received. This has been popularized as “talking trees,” although a more precise description of the processes involved would be “eavesdropping” (Baldwin, Halitschke, Paschold, von Dahl, & Preston, 2006). A well-documented case where plants eavesdrop on each other is VOC-based communication between *Nicotiana attenuata* (wild tobacco) and *Artemisia tridentata tridentata* (sagebrush; Karban, Huntzinger, & McCall, 2004). Wild tobacco plants rooting closer to healthy sagebrush do suffer more attacks from herbivores than tobacco plants located in the vicinity of damaged exemplars of sagebrush. Interestingly, VOCs released by the damaged exemplars allow wild tobacco plants to induce defensive mechanisms against herbivory by signaling molecules, achieving thus greater fitness. In some cases, chemical signals such as ethylene are known to trigger defensive genes after traveling aerially (Farmer & Ryan, 1990).

Forms of plant–invertebrate communication abound, with cross-pollination being a paradigmatic case of co-evolutionary success. But other clear expressions of adaptive behavior, such as the manipulation by plants of predatory animal movements for the purpose of defending themselves from herbivorous that can be thus preyed upon (Dicke, 1999; Kessler & Baldwin, 2001), have intrigued plant scientists. Although more research is needed, plant scientists are beginning to

envision even more unexpected forms of communication. Consider plant–invertebrate acoustic interaction. Belowground movement of roots in Maize results in the emission of a cracking noise that some insects may detect and interpret as the presence of a root (Barlow, 2010).

In this section, we have briefly reviewed some aspects of the behavioral repertoire of plants. Plant phenotypic plasticity is the result of signal integration: a process that requires cell-to-cell communication, and that results in adaptive forms of movement not to be interpreted as automatic and programmed or, in other words, as scoring low on an “intelligence test.” We have also seen that plants are territorial. This requires some form of self-recognition, a degree of decision-making, and, of course, communication. Plants need to interact at many levels with other biological systems in their local environment. It is evident that they process information and are anything but hard-wired. Bluntly, what we find, once we look closer, is a highly sophisticated form of adaptive behavior. Insofar as these patterns of performance are clearly adaptive, the cases herewith considered serve to illustrate the notion of plants as acting creatures or, as we shall argue below, as minimally cognitive.

3 Root-Brains and Plant Neurobiology

Integrated behavior often spreads out across large individuals and does require some form of coordinating, signaling structure. While it is obvious that humans and many other animals have brains, the situation is less clear when one moves to the fringes of nervous system carrying animals, or *Neuralia* (Nielsen, 2008). Here the crisp distinction between nervous system tissue and other tissues disappears. In their standard work *Structure and Function in the Nervous Systems of Invertebrates*, Bullock and Horridge (1965) defined a nervous system as follows:

A *nervous system* may be defined as an organized constellation of cells (neurons) specialized for the repeated conduction of an excited state from receptor sites or from other neurons to effectors or to other neurons. (p. 6)

They stressed that this formulation provided anatomical and physiological criteria that can be applied to decide whether a nervous system is present in a specific group or phylum. They acknowledged that the definition itself already excluded coordinating devices in single-celled organisms that do exhibit action potentials and accomplish coordination by subcellular means. For example, the behavior of the single celled *Paramecium*

is regulated by action potentials across its membrane in a way that is basically identical to neural conduction (Greenspan, 2007).

Even though it is now established that—anatomically and physiologically understood—nervous systems are restricted to cnidarians (such as jellyfish and anemones), ctenophores (comb jellies), and bilaterians, together making up the Neuralia, the function of repeated conduction of signals is dispersed much wider. For example, Leys and Meech (2006), working on sponges, stress that all multicellular organisms need a means of communicating between cells and between regions of the body. They subsequently discuss the presence of electrical signaling in sponges by syncytial tissues that are cytoplasmically coupled and so can transmit signals across the body. In an important paper, George Mackie (1970) discussed the notion of *neuroid conduction*, referring to “the propagation of electrical events in the membranes of non-nervous, nonmuscular cells (p. 319),” and providing examples from protists, plants, and animals. In Mackie’s account, neuroid conduction is a basic and widespread form of signaling that is elaborated on in nervous systems. Nervous systems merely provided more specificity in its connections and a dependency on electrical and chemical junctions. However, the presence and possibility for specialized conducting devices is not limited to animal nervous systems but a more general function that can be accomplished in different ways. In the last two decades, this view is further reinforced as it is increasingly clear that all the basic requirements for animal nervous systems—genetic signaling systems, ion channels, and even the components of synapses—are already present in precursor organism (Ryan & Grant, 2009). Nervous systems only organized these components in new ways.

The application of neuroscience terminology and concepts to plants may intuitively seem misplaced. However, from a fundamental organizational and evolutionary perspective, as just sketched, it is actually a logical line of inquiry that follows from general functional considerations. Animal nervous systems arose themselves as a conducting device tailored to specific constraints related to coordinating free-moving behavior. Plants are also highly evolved multicellular creatures that must coordinate their behavior in responses to a wide variety of internal and external signals. One would expect that these creatures have evolved their own conductive devices for this purpose. In particular when the huge size of some plants is taken into account, the presence of long distance signaling seems to be essential and the functional need for a nervous system—or at least a neuroid system as described by Mackie—seems obvious.

The difference between plant neurobiology and other basic disciplines resides in the target of these

interdisciplinary efforts. Plant neurobiology aims to achieve a scientific understanding of the integration of plant sensation and response. The target is the scientific understanding of how metabolism and growth can be regulated by the endogenous integration and processing of information. Plant neurobiology stresses the integrated signaling and electrophysiological properties of plant networks of cells. As Baluška et al. (2006) point out:

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).

The working hypothesis of plant neurobiology is that the integration and transmission of information at the plant level involves neuron-like processes such as action potentials, long-distance electrical signaling, and vesicle-mediated transport of (neurotransmitter-like) auxin (Brenner et al., 2006).

Brenner et al. (2006) discuss three issues that link plant signaling to signaling in animal nervous systems: (1) long-distance electrical signaling, (2) the role of homologous molecules from plants that are similar to neuroreceptors and neurotransmitters in animal nervous systems, and (3) the neurotransmitter-like characteristics of the phytohormone auxin (p. 414). We will consider these in turn.

1. The presence of action potentials in plants was already established by around 1880 (Stahlberg, 2006). However, for a long time it was thought that these were limited to a small number of specialized, fast-moving plants like *Mimosa* (sensitive plant) and *Dionaea* (Venus flytrap). Even after the discovery of action potentials in “normal” plants around 1963 this fact did not disseminate readily into mainstream plant science (Brenner et al., 2006). These action potentials can travel large distances via vascular bundles along the plant axis. While it remains open to further investigation how this long-distance signaling is more generally connected to systematic responses in plants (Brenner et al., 2006), Barlow (2008), after Fromm and Fei (1998), mentions the example of the response of droughted maize plants to the rewetting of their soil: “An action potential was then induced in the roots which, in a matter of minutes, passed via the phloem to the leaves where the rate of CO₂ assimilation was affected. (p. 134).”

2. Another similarity between plants and Neuralia consists in the mutual presence of substances like acetylcholine, serotonin, dopamine, GABA, glutamate, and other substances that are well-known neurotransmitters in animals. At present it remains uncertain to what extent these substances have a similar signaling function in plants; however, there is strong evidence that glutamate acts as a signaling molecule in plants, playing the role of a neurotransmitter for the purpose of intracellular communication (Brenner et al., 2006). In fact, glutamate receptors resemble neuronal receptors, with glutamate serving to induce action potentials in plants (Baluška, 2010).
3. Finally, there is a (brain-like) plant equivalent of synapses, defined as “acting-based asymmetric adhesion domains specialized for rapid cell-to-cell communication which is accomplished by vesicle trafficking” (p. 9) (Baluška et al., 2004). The transported substance here is auxin, a hormone that is known to induce fast electrical responses when applied extracellularly.

However, physiological similarities between plants and Neuralia are only to be expected as many of the molecular and macromolecular ingredients of nervous systems were already present in single-celled ancestors (Ryan & Grant, 2009). Nevertheless, the significance of these physiological similarities is reinforced by the recent resurfacing of an idea that goes back to the work of Charles Darwin (1880). This is the last sentence of *The Power of Movement in Plants*:

It is hardly an exaggeration to say that the tip of the radicle [root] thus endowed, 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. (Darwin, 1880; see also Baluška et al., 2009)

This early proposal drew attention to the finding that a large part of plant activity takes place underground. Here many of the most difficult decisions must be made concerning the direction of growth, the amount of investment in new growth and so on. From this perspective it makes sense to think of the roots of a plant as its anterior pole and the root apices as the plant's forward command centers (Baluška et al., 2004). It is the distinctive decision-making capacities of the *transition zone* within the root-apex that led to the formulation of the root-brain concept.

The transition zone is a distinctive area of the root-apex that plays a critical role in the circuitry of auxin transport, and the integration of different types of

signals. Cells in the transition zone area depolarize in response to glutamate activity (Baluška, 2010). Vesicle recycling and transport of auxin throughout the whole plant body permits the integration of sensory-motoric signaling circuits (Baluška et al., 2009). This results in forms of cell elongation that underlie root-apex tropisms with an adaptive value under the face of biotic and abiotic perturbations, both endogenous as well as exogenous. The transition zone is special. It is the one and only plant area where electrical activity is known to synchronize (Masi et al., 2009) and where—brain-like—decision-making takes place that controls phenotypic changes by exchanging information vascularly all the way up from the roots themselves to the shoots and organs at the opposite end of the plant.

However, even though there are many similarities, rather than stressing the similarities or dissimilarities with animal nervous systems, the current discussion on plant neurobiology is important as a way to develop a deeper understanding of how signaling and adaptive behavior in plants is organized. Mackie's notion of a neuroid system can be applied to plants as a way to signal the presence of similarities to, as well as differences from, animal nervous systems. In addition to being an important field of research in its own right, the development of plant neurobiology—whether under this name or another—will also be beneficial for research on animal behavior and neuroscience as it allows a comparative approach to understanding what is specific rather than general to animal intelligence.

4 Requirements for Minimal Cognition

The notion of cognition is notoriously hard to define. For example, Ulrich Neisser (1967) defined cognition as: “all processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used.” (p. 4) However, his definition does include many artifacts, such as tape recorders, as well as organisms, such as plants, that can hardly be intended by him as being cognitive. The implicit assumption at the time was that cognition applies to human forms of information processing and to artificial systems that mimic human performance. Because embodied cognition breaks the intrinsic connection between humans as prime examples from cognition in a more general sense, work has begun to provide a systematic account of cognition that is not based on human examples alone (e.g., Barandiaran, 2008; Keijzer, 2001, 2003, 2006; Lyon, 2006a, 2006b; Moreno & Etxeberria, 2005; Moreno, Umerez, & Ibañez, 1997; van Duijn et al., 2006). The main idea that is developed here is that cognition is (or that it originated as) a biological

phenomenon, and that it exhibits itself as a capability to manipulate the environment in ways that systematically benefit a living organism. This metabolic organization provides a basic form of normativity (Bickhard, 2008), differentiating “bad for me from good for me,” while cognition itself is cast in sensorimotor terms. In this context, the question concerning minimal cognition is important (Beer, 2003): what is the minimal biological system to which the notion of cognition applies?

It can be argued that bacteria already provide examples of minimal cognition (e.g., di Primio, Müller, & Lengeler, 2000; Lengeler, Müller, & di Primio, 2000; Lyon, 2006a; van Duijn et al., 2006). Consider chemotaxis in *E. coli*. These free-moving bacteria use flagella to move around and can travel up or down gradients of several substances that they can ingest or that they need to avoid. All of the basic ingredients for a minimal form of cognition are already present here: manipulating the external environment at larger scales to enable or enhance metabolic functioning.

Manipulating the extra-organismal environment is a very general biological strategy. Sponges pumping water through their bodies, plants growing leaves oriented toward the light, lions stalking their prey, and even humans discussing which restaurant to go to, can be considered as examples. Why would all of these activities be cognitive? So far, embodied cognition used a clear, intuitive cut-off point which limits cognition to systems that show a form of sensorimotor coordination. Cognition is thought to apply to free-moving agents, capable of reversible movements and perception. In this view, bacterial chemotaxis is a plausible example of minimal cognition, as it uses sensorimotor coordination to expand metabolic forms of adaptation and, in this way, provides a basic example of an organization that is also present in human cognition. Plants, fungi, and sessile animals, however, would be left out of the cognitive domain insofar as they (seem to) lack this additional requirement.

Setting up an adequate sensorimotor organization requires a particular physical embodiment of an organism, be it bacterium or monkey. For bacteria, this comes in the form of specific chemical receptors such as methyl-accepting proteins, and actuators such as flagella or pili that enable the bacterium to move about (Berg, 2000). It also involves a control system that enables the organism to initiate motion and use the perceptual feedback it generates to guide this motion. It is customary here to differentiate between online processing that is under direct perceptual control, and offline processing which is to some extent decoupled from immediate perception–action coupling. Online processing is cast as being more basic, while offline processing is thought to be involved in more complex cognitive tasks, like those relating to memory or planning. In

this way, one can see the general outlines of a progressive change from minimal cognition to more elaborate forms.

Thus, within embodied cognition one often encounters a fairly open-ended interpretation of cognition and intelligence. The upshot of this enterprise can be summarized in five different constraints on cognition:

1. Metabolism provides a basic form of biochemical normativity for cognition.
2. Cognition proper (initially) consists of exploiting the spatiotemporal dispersal characteristics of metabolically relevant environmental features.
3. The spatiotemporal structure of the environment is accessed by free and reversible bodily movement enabled by various sensorimotor organizations.
4. A basic sensorimotor organization operates online—being under direct stimulus control—but can be expanded to include offline control structures.
5. Such a sensorimotor-based cognitive organization is a globally organized cohering unit, not a collection of individual stimulus–response relations.

The question to ask now is whether and (if so) how does this set of constraints apply to plants. To begin with, we must stress that the application of the first two constraints is not disputed. Plants metabolize, of course, giving them a basic motivation for doing things. There is no doubt either that plants manipulate their environment in a second-order way such that their metabolic functions profit from this manipulation. Growing roots downward and light-catching parts upward suffice in this respect (Keijzer, 2001).

The real rub for minimal cognition in plants comes from constraints 3 to 5. Constraint 3 imposes being *free-moving*, having a sensorimotor organization, as a requirement for cognition. It is here that the option of plant cognition seems highly problematic within an embodied perspective. However, adhering to being free-moving as an *intuitive* criterion is unsatisfactory. Within the biological domain, free-moving organisms may stand out as potentially intelligent beings, but why should we trust these intuitions? The question should instead be: why should we consider free-movement to be so important?

Up to now, plants have not received much attention within embodied cognition. Most of those working in the field have employed a default assumption that intelligence is at a minimum an animal thing that was best caught in studies with free-moving agents such as robots, while excluding sessile plants. However, Hans Jonas (1966, 1968), who is now receiving renewed attention as an important thinker on the connections between biology and mind (Barandiaran, 2008; di Paolo, 2005; Keijzer, 2006), did take plants into

consideration. Jonas tried to articulate the differences between plants, animals, and humans in a way that highlights the relevance of being free-moving. In his view, the capacity for free movement is a key feature that is required for the development of intelligence as exhibited by animals, and a precondition for the evolution of human thought. Jonas' work can be used to argue that there are fundamental differences between intelligence in plants and animals (e.g., Barandiaran, 2008). At the same time, by clarifying why being free-moving is so important, he provides a clearer target for challenges on empirical and theoretical grounds. Despite being unable to move about in the way animals do, plants may well fulfill these constraints instead by means of signal integration into phenotypic change.

Jonas provides an analysis of why motility, and in its wake sensing and emotion, are key features when it comes to cognition. For Jonas (1966), motility and perception are also intrinsically linked to emotion and the presence of an inner, phenomenal dimension. We will not discuss these further complexities here. He argues that animal motion is more than an intensified case of vegetative motion, from which it differs in a number of physical respects: "in speed and spatial scale; in being occasional instead of continual; variable instead of pre-defined; reversible instead of irreversible." (Jonas, 1968, p. 248). These criteria are important for differentiating between being free-moving—which plants are not, generally speaking—and having self-induced motility, which is present in plants. Jonas uses these physical differences as the foundation for a further argument that animal motion leads to a principled new method of coordinating with the geometry of environmental space (1966; see also Barandiaran, 2008). Jonas (1966) makes the point as follows:

Now it is the main characteristic of *animal* evolution as distinct from plant life that *space*, as the dimension of dependence, is progressively transformed into a dimension of freedom by the parallel evolution of these two powers: to move about, and to perceive at a distance. (p. 100).

In his view, only by free-moving and perceiving at a distance, most notably by vision, is "space really disclosed to life." The key issue is that (aspects of) the global spatial structure of the environment must become a feature that is present and accessible for an organism. A fly, for example, is able to orient itself within its environment and home-in on places with sweet stuff, while avoiding swatting hands. Animals are sensitive to the spatial layout of the environment, for example in the form of patterns on a sensory surface like the retina or the skin, and their behavior is globally organized as a unit in relation to this layout.

Barandiaran (2008) uses the nice phrase of being sensitive to the "geometric space where objects can be freely explored" (p. 198). Such sensitivity comes in different grades, as the fly will not be sensitive to the highly relevant fact for me that it is trying to land on my child's birthday cake. However, we are both sensitive to, or "aware" of, the environment as a spatially and temporally extended structure in which we can act.

In contrast, plants are presumed to act on local stimuli, which may guide their behavior in globally appropriate ways, but without being directly sensitive to the spatial patterning of the environment. Thus, plants may grow their roots systematically downward strictly based on the locally available perception of gravity in every root. In this way, they can exploit this geometric structure without being sensitive as a single unit to geometric space as induced by free motility. The issue is the extent to which plants are sensitive to and act upon this global spatial structure of the environment. Or do they get by on the basis of a multitude of local interactions or decision-making processes? Thus, the important challenge that Jonas highlights for plant cognition is that only free motility seems to lead to an independent world—a geometric space—in which an agent can act.

Importantly, Jonas shifts the issue from a general unspecific commitment to a sensorimotor organization that plants just do not have, to different, more specific demands that require empirical data to settle. In line with constraint 3, Jonas changes the issue from having an animal-like sensorimotor organization to motility and possible differences in the speed, variability, and reversibility of motility. As we will see, recent developments in plant science provide good empirical reasons to downplay the differences between being free-moving and self-induced motility, as imposed by constraint 3. Similarly, sensitivity to the geometric layout of the environment, as stressed by Jonas, may be something that plants are quite capable of without us knowing it. Thus, plants could also very well fulfill constraint 5, also making this an empirical issue rather than a theoretical one.

Constraint 4 stresses the importance of offline control as a way to expand the options of an online operating control structure. Offline control is often considered a very important sign of cognition. Offline control allows an organism to dissociate its behavior from the immediately impinging stimuli and to act in ways that are guided by forms of knowledge. It is ironic then that these more cognitive offline aspects can be comparatively easily established in plants compared with the motility issue.

In what follows we will discuss examples from plant science and discuss to what extent it is plausible that plants can fulfill constraints 1–5 to some degree, and

thus exhibit forms of minimal cognition as described above.

5 Intelligent Behavior Can Take Different Forms and Speeds: Learning, Memory, and Offline Cognition

Most of the examples reviewed in Section 2 are, contrary to conventional wisdom, congenial with the idea that plants are directly sensitive to the spatial patterning of the environment. Root territoriality, for instance, clearly illustrates the exploitation of the geometric structure itself, which in turn backs up the idea that the behavior of plants is guided globally rather than locally. We may thus consider plants to be sensitive, as a single unit, to geometric space.

It is of course difficult to grasp such tuning in the absence of plant forms of learning and memory. Trewavas (2003) considers learning by seedlings, and draws a useful analogy between learning being reinforced in neural networks, as happens in the case of dendrite ramification and modification for the purposes of optimal signaling flow, and the transduction network of plants. Plant reinforcement takes place once we understand signal transduction networks similarly. As further signaling is transduced along the same incoming channel (e.g., specific root surface areas or root cap), an initial signal flow through gets reinforced (Trewavas, 1999). In fact, at the molecular level, learning by animals and plants shows remarkable similarities in terms of signal transduction (Trewavas, 2003). Furthermore, learning takes place thanks to feedback mechanisms that permit the system, plant or animal, to compute an error measure, and assess which changes would get the system closer to the goal. Of course, “computing” an error signal may sound artificial, but in an ecological setting it is no more, and no less, than the active maintenance of reciprocal channels of communication among different parts of the plant (meristems at the local area, but also parts further away), and the local environment. Such a constant exchange does furnish plants with full-fledged trial-and-error learning mechanisms.

This trial-and-error strategy is consistent with the soft-wired, global view of plastic tropic responses. Plants would not have survived in evolutionary time by being pre-programmed; quite the contrary, they have succeeded thanks to their ability to change the course of growth and development in the face of local disturbances of all sorts. Examples of plant learning abound; acclimatization under different forms of short and long-term stress, such as heat, cold, floods, or droughts easily come to mind. Optimization of stomatal aperture in situations of water stress, goal-oriented over-compensatory growth (Clifford,

Fensom, Munt, & McDowell, 1982), and oscillations in gravitropic behavior due to variations in the vector of orientation are well-researched illustrations. In all these cases, phenotypic plasticity delivers the goods. An extensive literature now shows that they all have to do with error-correcting mechanisms that are explained by complex networks of interconnected feed-forward and feedbackward connections, where particular flows of information are selectively enhanced (Trewavas, 2005b).

Likewise, phenotypic change underlies the ability to memorize. The genesis of dendrites delivers the goods in animal brains by effectively altering the architectural features of the network. Different patterns of connectivity permit the network to acquire new functions, with plant cell divisions continuing at any stage of development. This means that the method of acquiring different functionalities throughout the life of the plant will involve architectural changes somehow. Trewavas (2003) points out where the architectural divergence between plants and animals may lie:

Just as the process of learning in a brain could be represented as a time series, a set of snapshots of developing brain connections, in plants, each snapshot may possibly be represented by developing plasmodesmatal connections or equally, successive new tissues. So, instead of changing dendrite connections, plants form new networks by creating new tissues, a series of developing brains as it were (p. 14).

In this view, it is not the modification of patterns of connectivity that allows the plant network to remain competent. Rather, as new tissue accumulates, new networks with different computational resources are stored on top of each other. Note that newer tissue networks do not replace former ones; instead, we have a succession of operative serial networks that are obtained as cells continue to divide throughout the life of the plant.

Basic forms of short-term memory have been known for some time now. Consider for the sake of illustration the carnivorous plants *Dionaea muscipula* and *Aldrovanda vesiculosa*. In the case of *D. muscipula*, an action potential (AP) is generated whenever an upper trap hair is bent. Crucially, a single stimulation of the hair does not trigger the closure of the trap. For the trap to close, a second AP that takes place only when another hair is bent within 40 s after the first AP has been generated is necessary (Baluška et al., 2006). This setup comprises a basic form of memory, similar to the TCST system in bacteria (di Primio et al., 2000), as well as basic forms of animal memory. Or take the avoidance responses of plants in relation to drought (Trewavas, 2003). Drought avoidance behavior results in a reduction in the rate of cell growth that involves, on the one hand,

changes in cytosolic Ca^{2+} , $[\text{Ca}^{2+}]_i$, and in other secondary messengers, and, on the other hand, phosphorylation changes in ATPases and associated ion channels related to turgor (Palmgren, 2001). Trewavas (2003) compares drought avoidance responses in plants with the avoidance behavior of *Aplysia*. The pattern of avoidance of this marine slug involves a form of short-term memory whose mechanism includes Ca^{2+} and, in addition to the second messengers, cyclic nucleotides and several protein kinases that operate as a temporary memory (Greengard, 2001) by phosphorylating ion channels.

The key issue nevertheless resides in the possibility of converging on a nonbiased approach to intelligence. As Trewavas (2003) notes, elaborating on the work of Stenhouse (1974), Stenhouse had

regarded the early expressions of intelligence in animals as resulting from delays “delays in the transfer of information between the sensory system and the motor tissues acting upon the signals. The delay enabled assessment of the information and modification of information in the light of prior experience, and it was that assessment that formed the basis of intelligence.” (p. 1).

Ultimately, those willing to stick to a dividing line that sets plants and animals apart, must exploit the idea that whereas plant behavior is to be equated with the lack of delays in the transfer of information, animal behavior is to be equated with the (intentional) inference-based transfer of information, courtesy of those delays that mediate in between sensory input and motor output, and that plants apparently lack.

However, the organization of both animals and plants can be understood by appealing to the same constraint Stenhouse calls for. Both neural synaptic modification and successive plasmodesmatal connections rely upon delays in the transfer of information for the purposes of signal-integration. We may put this in artificial neural network (Rumelhart, McClelland, & the PDP Research Group, 1986) terms, and read delays in transfer, and lack of, with nonlinearly separable functions being approximated by an intermediate neural layer in between the sensory and the motor layers, and linearly separable functions being approximated directly by a sensory-to-motor synaptic matrix. But as Bose and Karmakar (2003) point out, animal neuronal networks and plant calcium signaling systems are not that different in terms of nonlinearities. In the case of plants, nonlinearities are obtained by means of the succession of signaling networks. Chakrabarti and Dutta (2003) have put forward an electrical network that models plant calcium signaling systems. Open/closed ion channels play the role of neurons in

networks of plants. As calcium ions are released, diffusion across nearby channels gives rise to further calcium release, ultimately giving rise to a calcium wave that flows throughout the whole network. This modeling of calcium signaling networks illustrates how memory mechanisms can be implemented in plants (Bose & Karmakar, 2003). In this way, transfer of information delays cancel out a rendering of plant forms of memory with some class of developmental progression, where previous cellular states determine future outcomes *linearly* (Firn, 2004). Thus, despite taking different forms and speeds, learning and memory functionally resemble animal-based competencies. The dynamics of the calcium wave are governed by nonlinear equations, opening up the possibility of integrating and computing all incoming data (Trewavas, 2002); a strategy pretty much deployed by animals and plants alike, and architectural constraints and processing speeds apart.

It is noteworthy, nonetheless, that plant scientists stress internal organization of intelligence (like learning or memory), while recent developments in embodied cognition tend to stress the way in which the ongoing interaction between the agent (or plant) and its environment result in intelligent solutions. Cvrčková, Lipavská and Žárský (2009), for example, propose a restricted use of the term *plant intelligence* which requires in their opinion at least some form memory, which they interpret as some form of offline control. In this way they would regard many of the basic forms of animal intelligence as not being “intelligent” because they result from online control. It is usually assumed that decoupled, offline modeling tasks are what distinguish sophisticated forms of behavior from merely tropistic online routines of the sort reviewed in Section 2. That being said, nocturnal reorientation of the sort performed by some plant leaves represents a qualitative change with respect to online sun-tracking. Consider the following illustration from a behavioral perspective of plant offline competencies.

Offline nocturnal reorientation by plant leaves of *Lavatera cretica* represents a qualitative change with regard to stimulus-controlled online behavior. Leaf heliotropism involves a correlated response to changes in sunlight orientation as the day changes from sunrise to sunset. Leaf laminae reorient during the night toward sunrise, and are able to retain such anticipatory behavior for a number of days in the absence of solar tracking (Schwartz & Koller, 1986; see also Calvo & Keijzer, 2009). Nocturnal reorientation is clearly an adaptation insofar as it allows plants to optimize their light intake (Kreps & Kay, 1997) while avoiding the overlap of incompatible metabolic processes in between nighttime and dawn. It is cellular circadian oscillations that permit nocturnal reorientation. The genes and proteins implicated in plant circadian time-keeping are

now being unearthed (see García Rodríguez & Calvo Garzón, 2010, and references therein), and although the proteins involved in time-keeping in plants differ from those found in animals, the oscillatory-involving roles are similar across eukaryotes (Cashmore, 2003).

As we saw earlier, the types of restrictions imposed by constraints 3 and 4 serve to stress the importance of having a sensorimotor organization on the one hand, and improving the offline and information processing capacities of the system on the other. Offline plant behavior may thus be considered to be minimally cognitive insofar as information is processed flexibly and adaptively in accordance with the aforementioned restraints. Constraint 5, nonetheless, remains an open empirical question, although there are reasons to be optimistic, as we point out in the closing section.

We have highlighted the similarities between plant growth and animal memory, and try to show why the behavior of plants, as they are coupled to their environment, allows for a cognitive interpretation of their adaptive responses. Although perception, memory, and action are capacities that can be present in both animals and plants, they take different forms. Animals, insofar as they are heterotrophic organisms that require organic foodstuff to survive, exploit a number of mobility-related competencies in order to navigate in complex and contingent environments (Neumann, 2006). Animals also appear to be better fitted to escape from predators or harmful environments. Plants, by contrast, do not require contractile muscles for fast responses to environmental contingencies. Insofar as plants are autotrophic organisms, they operate on slower time-scales, since inorganic substrates can be synthesized into organic compounds while remaining stationary. This also means that the computational solutions found by both plants and animals can diverge even when they exhibit similar complex functions.

Differences in speed and architecture have fostered the idea that plant behavior, compared with animal behavior, is strictly determinate and invariant under a variety of conditions. However, animal and plant avoidance responses are both graded as a function of the stimulus strength and both involve modifications in cellular morphology. Current evidence easily shows that plant behavior is not predefined at all, as Jonas claimed, but highly variable. If anything, learning and memory, when coupled to perception and action, are common currencies across phylogeny. We have seen that differences in speed and form do not serve to exclude a cognitive interpretation of plant behavior. In our view, the issue is not whether plants can move about, acting intelligently in this way, but rather whether plants, being autotrophic organisms, integrate information, have memory, can make decisions, in such a way that their adaptive coupling to their environment

can be called “cognitive.” Light, gravity, moisture, and touch are signals that plants integrate and respond to in complex, nonlinear ways. Roots make decisions in particular contexts as to which type of signal(s) to honor (Li & Zhang, 2008). Furthermore, phenotypic plasticity in ever-changing environments requires the exploitation of memory resources. Plants integrate exogenous and endogenous information channels in an attempt to phenotypically adapt to environmental contingencies; a sophisticated form of competency that, we believe, is comparable with animals’ predictive behavior.

Concluding, we hope that we have shown here that, in a number of specific issues relating to cognition, animals and plants do not differ fundamentally, and that plants are cognitive in a minimal, embodied sense that also applies to many animals and even bacteria. The scientific target in both cases is to understand the continuous interplay of animals and plants in relation to the environmental contingencies that impinge upon them. Plant cognition is, from this viewpoint, not a contradiction at all, but an empirical issue that requires much more attention, not only from plant scientists but also more generally from cognitive scientists.

6 Prospects and Challenges

The last few years have seen a lot of work on intelligent behavior, neurobiological phenomena, and basic forms of cognitive processes in plants. Above, we discussed how plants exhibit adaptive behavior, stimulus integration, learning, and decision-making. We discussed how plants incorporate specific signaling structures to transfer information across their sometimes huge bodies and how they even incorporate a more centralized decision-making structure—a root-brain—in their forward looking root-tips. We also discussed the possibility that plants exhibit a form of minimal cognition, interpreted in a wide sense as used in embodied cognition. Much of this work remains controversial as far as the use of concepts that stem from an animal and even human context is concerned. At the same time, the empirical findings on which the use of such concepts is based are well established.

We think that not only the common sense but also the scientific use of concepts such as intelligence, memory, behavior, nervous system, brain, and cognition remains to a significant extent based on intuition. We often cannot tell *why* we apply these concepts in specific cases, even when it remains intuitively self-evident and without much discussion when and where we apply them. Of course, we also develop definitions for these notions, like Ulrich Neisser did for cognition, but it is intuitive usage that drives the definitions rather than the other way round.

The study of behavioral, neural, and cognitive phenomena in plants that to a large extent goes counter such intuitions is not only important in its own right, but also because it holds up a mirror for similar research on animals and humans as it enforces a more explicit treatment of notions that are often taken for granted here. As a result, one can expect that ongoing work on plant intelligence will have a major and general impact on the fundamental issues related to research on the behavioral, cognitive and neurosciences. To close, we will very briefly introduce and discuss some possible—and sometimes speculative—prospects and challenges that may arise from this research for the study of behavior and cognition more generally.

Swarm Intelligence and Dispersed Underground Sensing While the occurrence of swarm intelligence is well-known in embodied cognitive science, plants allow a new application of this phenomenon (Baluška, Lev-Yadun, & Mancuso, 2010). As individual roots behave in their forward growth as active animals, the root tips act like different individuals. At the same time, rather than wholly separate individuals, they also remain connected to one another. This allows for different and additional forms of communication between the “individuals.” Baluška, Lev-Yadun et al. (2010) describe three possible communication channels between root tips. Secreted chemicals and released volatiles allow rapid communication between roots, which amounts to ordinary chemical signaling between individuals. There is also the possibility that electric fields generated by each growing root might allow electrical communication among roots, which would add to these “horizontal” signaling possibilities of individual roots. However, the sensitive root tips can also signal internally—vertically—through their connecting tissues, which combines ordinary swarm phenomena with more direct and specific signaling between individuals.

An interesting possibility here is that the dispersed root-tips are combined to act as a single but widely spread sensor array, like the eye’s retina. Acting like huge “underground eyes” such arrays could be used to sense the physical and chemical lay out of the underground environment at a more global level. On the one hand, this could be a way of further developing the notion of a plant root-brain as discussed above. On the other hand, it offers a handle for developing artifacts capable of negotiating the world underground. Mazzolai, Laschi, Dario, Mugnai, and Mancuso (2010) describe the notion of a *plantoid*, a plant-inspired robot with branching sensory roots that could explore the soil in a more efficient way for purposes such as in situ monitoring analysis and chemical detections, water searching, anchoring capabilities, and many others. Even without any recognizable animal movements

involved, this is an important and interesting domain of intelligent phenomena.

Genomics and Plant Behavior Ongoing genomics research on plant mutants promises a better understanding of the potential role of model organisms in our understanding of phenotypic plasticity (Esmon et al., 2005), and adaptive behavior more generally. Similarities between animal and plant mechanisms (e.g., neuronal axons and particular plant cells) can even help us better understand specific disorders. The SPG3A gene, which encodes the protein atlastin and whose mutations are related to hereditary spastic paraplegia (HSP; Baluška, 2010) in humans, and the RHD3 (Root Hair Defective 3) gene, which encodes a protein required for cell enlargement in *Arabidopsis* (Wang, Lee, & Schiefelbein, 2002), are homologous. In other words, we may venture to say that *Arabidopsis* shares with *Aplysia*, *Drosophila*, and the like, more than is at first sight expected; namely, their scientific status as model organisms for the understanding of adaptive behavior and minimal cognition, writ large.

Animal Nervous Systems The claims concerning the neural signaling properties present in plants, and even in single-celled organisms (Greenspan, 2007; Mackie, 1970), sets the whole topic of animal nervous systems in a new light. While the many similarities with other signaling structures seem now beyond dispute, it is also clear that there are important differences too. Previously, basic nervous systems were not generally considered to be a key topic for understanding the human brain. However, if the brain is not essential for intelligent information-processing it becomes a more important issue to investigate what the specific contribution of nervous systems was (and is) to animal intelligence.

In this new situation, it becomes much more urgent to articulate and investigate the specific characteristics of nervous systems compared with the more general forms of neuroid conduction (de Wiljes, Van Elburg, Biehl, & Keijzer, 2010; Keijzer, Franken, van Duijn, & Lyon, 2011).

Fungi As Sessile Heterotrophs Once one starts thinking about behavior and intelligence in organisms that are not like animals, then it becomes self-evident that the present attention for plants should be extended to include fungi. In contrast to most plants, most fungi are sessile heterotrophs and presumably have an even more active life-style than plants. Considering how long it took to become aware of plant intelligence, it seems appropriate to develop a more active attitude here in studying the behavior and intelligence of fungi, which has to our knowledge not yet been pursued in a systematic way. To mention one intriguing example, some fungi trap nematodes by growing constricting rings that operate like a lasso (Hauser, 1985). While this can be seen as merely automatic behavior, it seems

appropriate to investigate further before coming to a more definite verdict. If plants are so rewarding as a domain for studying intelligent phenomena, fungi should not be neglected either.

Information-Processing and Minimal Cognition in the Wild As presented in the opening stages, the objective of plant neurobiology is, in the words of Brenner et al. (2006), “to illuminate the structure of the *information network* [italics added] that exists *within* [italics added] plants.” (p. 413). Now, given the concept of information-processing, as it has percolated throughout the article in relation to learning, memory, decision-making, and the like, the following two final caveats are in order.

First, a word of caution regarding the employment of the very phrase “information networks” seems appropriate, especially considering the emphasis on the sensorimotor-based (minimally) cognitive organization put forward in the foregoing. A narrow reading of “information networks... within plants” would match the integrated signaling and electrophysiological properties of networks of cells to the idea of a “sensorimotor sandwich” (Boden, 2006). This is compatible with Stenhouse’s (1974) own approach to intelligence, insofar as it consisted of “delays in the transfer of information between the sensory system and the motor tissues acting upon the signals.” But note that this narrow reading will not take us far enough since the “sensorimotor sandwich” metaphor entails an implicit endorsement of the view that cognition, minimal or not, has to do with whatever information-processing takes place, inferentially, in between a sensory and a motor layer. By contrast, we have emphasized precisely the sensorimotor-based (minimally) cognitive organization itself. Thus, we call for a wide reading of expressions such as “information-processing” with an eye to making compatible the existence of plasmodesmatal connections that rely upon delays in the transfer of information with an ecological understanding of the very process of signal-integration.

By an “ecological” understanding we mean an embodied, situated or distributed approach, broadly construed (Gomila & Calvo, 2008), that stresses the ongoing, dynamic interactions between the plant and its surrounding environment by means of perception and action, such that perception–action processes become the starting point for intelligence (Calvo & Keijzer, 2009). We may say that the adaptive behavior of plants must be studied “in the wild,” to borrow Hutchins’ (1995) catchphrase. Bluntly, the adaptive/cognitive ecosystem is the proper unit of analysis. In fact, we have only been able to grasp that the narrow information-processing reading was a dead end thanks, for instance, to research in genomics, or courtesy of time-lapse photography. Plant scientists have been able to identify competencies literally unknown by

making phenomena more pronounced; phenomena that from the standpoint of the observer’s timescale were too subtle to be noticed, as systematic, time-lapse, gathered observations are now evidencing.

Nonetheless, the target is not the identification of new forms of behavior per se, but rather of new forms of behavior that are *adaptive*, and here we enter our second and final caveat. In many cases, even the time-lapse study of plants in laboratory conditions is a non-starter. Minimal forms of cognition, be it plant, bacteria or animal, cannot be studied detached from the natural habitat in which they take place. If adaptive behavior is to be studied “in the wild,” controlled laboratory conditions of model organisms only foster the illusion that minimal cognition is easy to grasp. *Arabidopsis* grown in the laboratory is neither forced to compete ecologically with other individuals of the same or different species, nor exposed to chaotic changes in environmental conditions. In this way, we seriously run the risk of studying controlled but, otherwise, toy phenomena.

This is a problem that afflicts the cognitive sciences overall. For the sake of illustration, consider Chomsky’s (1965) seminal competence/performance divide; a distinction exploited to identify grammaticality itself, and not the actual parsing and production performed by cognitive agents, as the phenomenon in need of explanation. But, as research in (embodied) cognitive linguistics shows, the behavior of a cognitive system unfolds in time, matching thus with performance itself and not with an idealized grammatical competence that is only in the eye of the theorist. In fact, by shifting to performance in ecological settings, we may find that plants are sensitive to the geometric layout of the environment, as hinted in previous sections. Likewise, once we target performance in ecological settings, plant communication, learning, memory, and the like, may be assessed in a context of distributed minimal cognition, and may well fulfill constraint 5: understanding sensorimotor-based cognitive organization as a globally organized cohering unit in an ecological context.

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