The Smart Plant: A Look into the Controversy Behind Plant Intelligence

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Abstract

Plants have long been excluded from the conversation regarding intelligent functioning in living things. This mindset dates back to ancient times, when plants were assigned a low-functioning and unintelligent rung on the *scala naturae*. In comparison to animals, plants have evolved to respond to their environment with a modular body plan, which lacks a nervous system and 'intelligent' organ, such as a brain. Despite this, research has demonstrated that plants are able to sense their environment, transmit sensory information throughout the entire organism, and respond to this sensory information with appropriate physiological responses. Also, plants have been shown to demonstrate aspects of learning and memory – cognitive functions once thought to be restricted to 'intelligent' beings (i.e. animals). The argument against plant intelligence is largely semantic-based, and stems from the concept that the word 'intelligence' cannot be applied to organisms which lack organs responsible for intelligent functioning. To truly appreciate the intelligent functioning of plants, we must eliminate this semantic barrier through a re-evaluation of our conventional understanding of intelligence. Perhaps this would require us to view intelligence, not as a quality unique to animals, but as a biological property, which in varying degrees is present in all life forms.

There are many definitions of intelligence, and often, the appropriate definition will depend completely on the context in which the word is used. In one definition, intelligence can be defined as the mental ability to learn, reason, and problem solve (Colom et al., 2010). This definition insinuates that to be

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intelligent, an organism must possess a 'mind' (or brain) for the integration of environmental stimuli into intelligent cognitive functions. With this, the brain is argued as the sole organ responsible for intelligent cognition. Under this basic reasoning, it is tempting to believe that indeed all organisms that lack a brain (and the nervous system associated with it) are incapable of intelligent thinking such as learning, reasoning, and problem solving. But is this really the case? Here, I will refute this narrow-minded rhetoric through exploring the many abilities of members of the 'brain-less' plant kingdom.

Historically, plants have been perceived as simple, passive, and immobile masses of vegetative and reproductive tissues (Hall, 2011). This viewpoint dates to the times of the ancient Greeks, when philosophers comprised the hierarchical classification scheme of existence, the *Scala Naturae* (Lovejoy, 1936; Kutschera, 2011). On this scale, plants were assigned a position in between soulless inanimate matter (e.g., soil, minerals, water, etc.), and low-functioning and predominantly sessile animals (e.g., sponges) (Hall, 2011). Although both plants and low-order animals do not have a brain and appear immobile, the low-order animals were believed to be superior because they could perceive tactile and gustatory sensations—mechanisms (incorrectly) thought to be devoid in plants (Lovejoy, 1936). Plants, low-order, and high-order animals (i.e., animals with a brain) were all denied intelligent qualities (e.g., rationality)—qualities which were only bestowed upon humans, angels, and God (Lovejoy, 1936; Hall, 2011). By viewing intelligence as inclusive to only humans and the divine, an impossible barrier was fashioned in recognizing plant intelligence, and thus prompted most to perceive the plant world with disregard and ambivalence (Hall, 2011).

Presently, few people deny intelligence in animals. Plants, however, are so separated from the animal (and human) lineage, that we still tend to perceive them as inferior, or less complex, organisms that generally lack intelligent behavior

(Trewavas, 2014). Plants evolved as sessile organisms and are largely unable to display quick movements in response to environmental stresses, perturbations, or other stimuli. A sessile life habit pressured plants to exhibit modular body plans, with no centralized functional areas (i.e., organs, nervous systems, etc.); this in turn would enable plants to withstand extensive damage or stress (such as mechanical injury or herbivory), and to optimize growth and development in accordance with ambient conditions (Mazzolai et al., 2010). The lack of nervous systems inhibits plants from responding to stress and perturbation with obvious movements. Instead, movements of plants are subtle and often not perceivable on a human timescale (Trewavas, 2014). Animals, however, have evolved as mobile organisms, and unlike plants, are equipped with fight-or-flight responses. These responses require mechanisms for quick integration of environmental stimuli through central and peripheral nervous systems (Jansen et al., 1995). So how is it logical to compare animal and plant intelligence when both Kingdoms were subjected to completely different evolutionary selection pressures? Perhaps to counter the zoocentric view of intelligence, we must provide evidence that intelligent behavior is not solely coupled with a brain or nervous system, at least in the sense that we perceive it.

Much research has been done in attempts to reveal the complexities and nature of plant intelligence. Perhaps the most recognized pioneers in revealing intelligent behavior in plants were Charles Darwin, and his son Francis Darwin. In the book “The Power of Movement in Plants” (1880), the Darwins provided evidence from hundreds of experiments which supported the idea that plants are not passive, immobile, and unintelligent vegetables, but rather, are actively engaged in sensing, processing, and intentionally responding to numerous environmental cues. Their evidence for intentional plant movements was later confirmed with the invention of timelapse photography; this technology enabled both scientists and the public to see the extensive array of plant movements, which would otherwise be difficult (or impossible) to detect (Trewavas, 2014). This discovery prompted much research into other possible intelligent plant processes such as: sensing, signal transduction and whole-plant communication, information integration and coordination (the root-brain hypothesis), and problem solving and memory.

Contrary to what early philosophers believed to be true, plants are not merely ‘vegetables’ which are deprived of all sensory functions. In fact, plants exhibit all five of the senses which animals possess (sight, smell, taste, touch, and hearing), as well as fifteen others (soil humidity detection, electromagnetic field detection, gravity detection, etc.) (Chamovitz, 2012). Though it is obvious plants do not have the same sensory nerves or organs as animals, analogous structures are present in their modular body form (Chamovitz, 2012; Mancuso and Viola, 2015). Sight is achieved through detection of visual stimuli (i.e., light wavelengths), by specialized proteins called photoreceptors (e.g., phytochrome, cryptochrome, phototropin, etc.) (Briggs and Olny, 2001). Smell is achieved in plants through detection of airborne biogenic volatile organic compounds (BVOCs) via various receptor proteins (Chamovitz, 2012). BVOCs serve as biological signaling molecules, and may be emitted passively as ambient volatiles, or intentionally to communicate with other plants and other organisms (Kessler and Baldwin, 2001; Raguso, 2009; Rodriguez et al., 2013). In terms of taste, receptor proteins on the roots enable plants to perceive soluble nutritional resources (e.g., nitrates, phosphates, etc.) or water gradients in the rhizosphere (Chamovitz, 2012; Mancuso and Viola, 2015). Lastly, both touch and acoustic (i.e. vibrational) stimuli are perceived in the plant through activation of mechanosensory channels, predominantly located on the epidermal cells (Braam, 2004; Appel and Cocroft, 2014). Thus, plants can sense the environment surrounding them, but how are they able to transmit these sensory messages and coordinate whole-body responses in the absence of peripheral and central nervous systems?

Analogous to animals, plants transmit sensory information through both electrical and hormonal signaling pathways to initiate physiological responses (Trewavas, 2014). Electrical signaling in plants was first revealed in a book titled “The Nervous Mechanism in Plants” (1926) by Jagadesh Chandra Bose. Bose outlines his discovery of electrical signals, or action potentials (APs), in *Mimosa pudica* (Mimosa), a sensitive plant which defensively drops its branches through a quick, turgor-based physiological response to touch. Electrical signals are also involved in whole-organism transmission of information regarding temperature changes, pollination, and wounding (Davies, Ramaiah, and Abe, 1986; Fromm and Bauer, 1994; Fromm et al., 1995).

Animals transmit electrical signals through complex nerve networks, whereas plants transmit electrical signals locally, via the plasmodesmata (microscopic channels connecting the cell walls of plant cells) (Van Bel and Ehlers, 2004), or throughout the whole plant *via* the vascular system (e.g., sieve tubes in the phloem) (Fromm and Lautner, 2007).

Like electrical signals, hormonal signals are also generated in response to sensory stimulation in plants. This, not surprisingly, is possible despite the absence of an endocrine or circulatory system (Davies, 1995). Plant hormones are produced in unspecialized cells and transported to target cells and tissues locally through cellular streaming, or over long distances through the vascular tissues (both xylem and phloem). The specific physiological response that is induced will depend completely on the phytohormones that are at work. So, the mechanism behind transmission of information has been identified, but how is a plant able to integrate and coordinate this information to generate the most appropriate physiological or behavioral responses?

At any given moment, plants are responding to numerous environmental cues, and are in turn responding to these cues through various behavioral mechanisms. When stimulated by light (or lack of light), mechanical stress, water or nutrient concentrations, or potential herbivores, plants must 'choose' which stimuli to respond to (Mancuso and Viola, 2015). For example, will it avoid shading and grow towards the light (phototropism), or will it grow away from a touched surface (negative thigmotropism)? Will roots grow in the direction of water (hydrotropism), or will they grow in the direction of nutrient pools (chemotropism)? Will it invest energy in vegetative growth, or will it invest energy in reproduction?

The coordination of these responses has been predicted to occur in the roots, specifically the region of the root-tip, termed the transition zone (Baluška et al., 1996; Baluška et al., 2004). Darwin (1880) was the first to propose this idea, which would later be termed the "root-brain hypothesis". In this hypothesis, it is suggested that the roots act as data-processing centers that continuously integrate information from the rhizosphere (parameters such as gravity, nutrient and water content, temperature, electrical fields, and defense compounds), and signals generated from above-ground stimuli (Baluška et al., 2004). The integration of this information permits a sort of cost-benefit calculation, which dictates how the plant will respond (Mancuso and Viola, 2015). For example, Cahill et al. (2010) demonstrated that *Abutilon theophrasti* expressed differential root placement when grown under competitive and non-competitive environmental conditions. Specifically, results revealed that *A. theophrasti* roots exhibited a broad foraging strategy when growing alone and roots remained indifferent to any nutrient gradients. Alternatively, when planted alongside a neighbor, *A. theophrasti* adopted a restricted foraging strategy where root placement would depend on the direction of highest nutrient concentration. Remarkably, this effect was strongest when nutrient concentrations were in the same direction as the neighbor.

Thus, *A. theophrasti* demonstrated its ability to detect the presence or absence of a competitor and respond to this stimulus via allocating or not-allocating energy toward competitive foraging strategies. But what about learning and memory, are plants capable of these higher intelligent functions as well?

Learning, error correction, and memory in plants is associated with the acquisition of information, information storage, and adaptive behavioral changes resulting from experience (Gagliano et al., 2014). Perhaps the most basic example of memory in plants is displayed by the carnivorous Venus flytrap (*Dioneae muscipula*). This learning response is based on generation of action potentials through prey stimulation of trigger hairs on the inside surface of the trap; however, the trap will not close if only a single action potential is generated (Guo et al., 2015). Instead, trap closure requires a second action potential generated by a different trigger hair within a period of twenty to forty seconds. This suggests that *D. muscipula* must remember the first action potential generated, in order to successfully close its trap (Shepherd, 2005). The second action potential is suggested to act as a safeguard against unnecessary trap closure (which is energy costly), such as trigger hair stimulation from debris or water (Guo et al., 2015).

In Gagliano et al., (2014), both learning and memory were demonstrated in the sensitive Mimosa (*M. pudica)*. Individuals were subject to repeated mechanical stimulation of the leaves through water-drop stimuli. This stimulus triggered the classic folding response of the leaves but was otherwise considered no real cause for stress. Because the water-drops were not a source of true stress for *M. pudica*, the authors hypothesized that each plant could learn the harmlessness of the stimulus and cease to drop its leaves (which is an energetic cost) in response. Results revealed that *M. pudica* eventually habituated to the water-drop stimuli. To associate this response with learning (rather than fatigue or sensory adaptation), the authors applied a novel stimulus (shaking) to habituated plants and followed this with the original water-drop stimulus. The novel stimuli induced defensive folding, whereas the subsequent water-drop stimuli continued to induce a habituated response, thus showing that fatigue was not a factor. Most remarkably, this habituation was shown to continue for 28 days—suggesting long-term memory of the water-drop stimuli. Though the precise biological mechanisms behind learning and memory in plants is unclear, researchers have suggested the involvement of the calcium and calmodulin signaling system—which also has been shown to be involved in learning and memory in animals (Bose and Karmakar, 2003; Kim et al., 2009; Esdin et al., 2010). Despite these remarkable discoveries of higher cognitive functions in plants, critics are still attempting to discredit and dismantle the argument behind plant intelligence.

A large portion of criticism on plant intelligence does not directly stem from denying plants intelligent qualities per se, but rather, is based on semantics. Firn (2004) provides thought-provoking, but nonetheless, semantic-based arguments against the concept of plant intelligence. First, he argues that intelligence is a property of the 'the individual', and individuality is a much vaguer concept with respect to plants vs. animals (e.g., clonal patches of *Rosa spp*.). Because the concept of individuality is ambiguous in plants, he argues intelligence cannot be applied to whole organisms, but only to cells or tissues. He then goes on to argue, based on dictionary definitions, that the key characteristics of intelligence are choice, comprehension, and discernment—characteristics predominantly present in higher mammals. Trewavas (2004) rebuts with the argument that biologists need not follow general dictionary definitions, but instead should explore concepts with new and imaginative approaches.

Another prominent criticism is the use of the term 'plant neurobiology' by researchers who see similarities between plant and animal methods of signaling and information integration (Alpi et al., 2007). Alpi et al. (2007) argue that the words ‘neuron’, ‘brain’, and ‘neurobiology’ are misleading to use in a plant context, for there is no evidence of these structures (as we know them in animals) within the modular plant body. They believe the use of these words does not promote new research and is encroaching on the realms of pseudoscience. Again, Trewavas (2007) rebuts by stating that the use of metaphors such as these, in describing signal transduction and information integration, is an “essential adjunct to the imaginative scientific mind in confronting some of the most recalcitrant problems in plant biology” (p. 232).

Conclusion

Science has come a long way since the time of the Ancient Greeks. Through decades of research, it is now obvious that plants can evaluate their environmental surroundings and respond to environmental cues by coordinating appropriate physiological responses. Plants exhibit signs of memory, error-detection, and error-correction—cognitive functions which were once thought only to occur in animals. All of these processes are achieved in plants without the presence of a true nervous system or ‘intelligent’ organ.

The word “intelligence” in itself is a loaded term, and frankly, posits heavy ties to the animal kingdom (Chamovitz, 2012). This, perhaps, is a result of our ignorance in acknowledging intelligent qualities in life-forms which are so very different from our own. It is of no doubt that humans display the highest intelligence of all life, but that does not mean we have the authority to compare our intelligence to plants, and deny them their extraordinary abilities in dealing with the natural world—even if these abilities do not comfortably fit within our framework of understanding intelligence.

To eliminate this semantic-based argument against plant intelligence, I suggest we re-evaluate our conventional understanding of the word ‘intelligent’. We must approach the concept of intelligence as not something mutually exclusive to humans (or the animal kingdom in general), but, as Darwin (1871) states: “[something that] is based on how efficient a species becomes at doing the things they need to survive”. I agree with Trewavas (2014) in saying that this vantage point would allow us to view intelligence as more of a biological property which is universal to all organisms, rather than an emergent quality exclusive to the animal kingdom. Perceiving plants in this light would result in a deeper understanding and appreciation of the green world which so abundantly surrounds us.

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