Trends in Plant Science

CellPress REVIEWS

Opinion

Plants Neither Possess nor Require Consciousness

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In claiming that plants have consciousness, 'plant neurobiologists' have consistently glossed over the remarkable degree of structural and functional complexity that the brain had to evolve for consciousness to emerge. Here, we outline a new hypothesis proposed by Feinberg and Mallat for the evolution of consciousness in animals. Based on a survey of the brain anatomy, functional complexity, and behaviors of a broad spectrum of animals, criteria were established for the emergence of consciousness. The only animals that satisfied these criteria were the vertebrates (including fish), arthropods (e.g., insects, crabs), and cephalopods (e.g., octopuses, squids). In light of Feinberg and Mallat's analysis, we consider the likelihood that plants, with their relative organizational simplicity and lack of neurons and brains, have consciousness to be effectively nil.

Highlights

Although 'plant neurobiologists' have claimed that plants possess many of the same mental features as animals, such as consciousness, cognition, intentionality, emotions, and the ability to feel pain, the evidence for these abilities in plants is highly problematical.

Proponents of plant consciousness have consistently glossed over the unique and remarkable degree of structural, organizational, and functional complexity that the animal brain had to evolve before consciousness could emerge.

Recent results of neuroscientist Todd E. Feinberg and evolutionary biologist Jon M. Mallatt on the minimum brain structures and functions required for consciousness in animals have implications for plants.

Their findings make it extremely unlikely that plants, lacking any anatomical structures remotely comparable to the complexity of the threshold brain, possess consciousness.

The Vexed History of 'Plant Neurobiology'

Since its debut on the pages of *Trends in Plant Science* in 2006 [1], the subfield of 'plant neurobiology' (PN) has been dogged by controversy [2]. Not surprisingly, the controversy became a publicity bonanza for the new paradigm, transforming some of its more provocative advocates into media darlings [3–5].

As reported by Michael Pollan in his *New Yorker* article, the initial obstacle to PN's acceptance was the group's name. Neurobiology refers to the biology of the nervous system, and plants manifestly lack nervous systems. This particular lexical complaint was soon resolved when the group quietly changed its name a few years later from the Society for Plant Neurobiology to the more acceptable Society for Plant Signaling and Behavior. However, self-identification of the group with neurobiology and its associated terminology has largely persisted, and some proponents continue to use the term plant neurobiology in their internet publications.

The second lexical dispute centered on the PN group's use of the word 'intelligence' in connection with plant behavior. Initial resistance to the term 'plant intelligence' was largely due to the cognitive dissonance occasioned by hearing a term normally reserved for the higher mental faculties of humans and other vertebrates being applied to plants. However, as there are now at least 70 different definitions of intelligence [6], and the terms 'machine intelligence' and 'artificial intelligence' have entered the language, it is appropriate to consider intelligence more generally as the ability to receive and process information from the environment. Living cells are certainly able to do that; so, in this sense, all organisms, with or without a nervous system, are intelligent. In the case of semi-autonomous mitochondria and chloroplasts, one could even speak of 'intelligent organelles'.

The term 'swarm intelligence' has also been applied to plants based on the supposed similarities between individual plant cells and social insects [6–8]. According to this idea, plant behavior emerges from the coordination of individual cells and tissues, analogous to the problem-solving

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that emerges from the communication and cooperation between the members of a bee hive. However, this analogy has several problems [9]. Bees are free to move about inside and outside the hive, while plant cells are permanently attached to each other. Moreover, the interactions between plant cells and tissues occurs with little or no genetic conflict, whereas individual bee behavior in a hive involves a great deal of genetic conflict due to the fact that the queen, in the course of several mating flights, collects semen from multiple males from other hives, giving rise to daughters with diverse genetic backgrounds [10]. According to molecular ecologist Robin Moritz,

> …as with any complex social system, honey bee societies are prone to error, robbery, cheating, and social parasitism. The honey bee colony is thus far from being a harmonious, cooperative whole. It is full of individual mistakes, obvious maladaptations, and evolutionary dead ends. Conflict, cheating, worker inefficiency, and curious reproduction strategies all occur [10].

Although competition for resources occurs within individual plants, for example, between leaves and tree branches competing for sunlight, between roots competing for water and minerals, and between various carbon sinks within the plant [6], these are 'physiological' conflicts within a single organism, not genetic conflicts between individuals in a colony.

A third lexical dispute centers on the use of the term 'cognition' in relation to plant intelligence and 'learning' [11,12]. Once again, cognitive dissonance comes into play. Plant neurobiology proponents (PNPs) have appropriated a term that is normally applied to conscious learning and comprehension in animals. The philosopher Emanuele Coccia has argued that in plants, 'knowing' is both 'innate' and 'unconscious'. Plant seeds are innately 'cerebral' because

> …the operations of which the seed is capable cannot be explained except by presupposing that it is equipped with a knowing, a program for action, a pattern that does not exist in the manner of consciousness, but that permits it to accomplish everything it does without error [13].

Here, Coccia conflates cognition with 'a program for action that does not exist in the manner of consciousness,' which seems like a contradiction. Plant neurobiology opponents (PNOs), and biologists in general, prefer to think of such innate programming simply as genetic information that has been acquired through natural selection and which is fundamentally different from cognition or knowing, at least as these terms are widely understood.

Despite the above-mentioned lexical contretemps, excellent papers have been published by both PNPs and PNOs on plant signaling and behavior that have not been the least contentious. Many are noncontroversial studies on the role of signaling in ecological responses. Others have focused on plant processes that show some analogy (but not homology) to animal nervous systems. For example, the involvement of electrical signaling in rapid leaf movements and defense responses [14–16], the role of glutamate receptor-like genes in regulating electrical signaling [17], and 'counting', a type of short-term memory, in Venus flytrap trigger hairs [18].

More controversial has been the claim by some, but not all, PNPs that plants possess the equivalents of animal **neurons** (see Glossary) and synaptic junctions, where **auxin** is purportedly released to abutting cells via the fusion of '**presynaptic vesicles**' similar to the process of **neurotransmitter** release at synaptic junctions in animals [19–22]. According to this hypothesis, auxin functions as a plant neurotransmitter that initiates **action potentials** during plant signaling in response to various stimuli. However, the data supporting this hypothesis have been heavily criticized on technical grounds [23], and the hypothesis itself has been rejected on theoretical grounds [24].

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Electrophysiological experiments by Masi *et al.* led to the proposal that the electrical signals in the cells of the elongation zone of root tips exhibit brain-like 'synchronized oscillation'. The authors went on to suggest

> …that this region of the growing root apex is some kind of sensory zone, specialized for integration of diverse sensory input formation that enable the growing apex to continuously monitor diverse environmental parameters and to mount appropriate adaptive output responses [25].

Accordingly, Baluska *et al.* have dubbed this region of the root tip a 'brain-like command center' that integrates signals from all over the plant [26]. However, in an emphatic rebuttal, Rehm and Gradmann have provided compelling arguments that the data purportedly demonstrating brain-like synchronized oscillations in the root tip are actually electrode artifacts [27].

PNPs frequently cite no less an authority than Charles Darwin as the source of the plant brain hypothesis. In the final paragraph of *The Power of Movement in Plants*, Darwin wrote the following:

> It is hardly an exaggeration to say that the tip of the radicle thus endowed [with sensitivity] and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements.

Although Darwin got a lot of things right, his brain analogy simply does not stand up to scrutiny. Darwin, it will be recalled, is also famous for his demonstration that the tips of grass coleoptiles and tomato hypocotyls control the light-induced bending of the more distal regions of their respective organs. Shoot tips also regulate the growth of axillary buds and the vascular cambium. If root tips and shoot tips both exert influences on the growth of their 'adjoining parts', why did Darwin not compare shoot tips with brains? There are other instances of one plant structure affecting the growth or development of another: the leaves of photoperiodic plants respond to a photoperiodic stimulus by causing the shoot apical meristem to form flowers, fruit development can trigger whole plant senescence in monocarpic plants; the starch sheath regulates gravitropic bending in eudicot stems. The list goes on. No single plant organ or tissue functions as 'the plant brain', integrating all of the signals affecting plant growth and development. If the root tip is a brain-like command center, then so, too, is the shoot tip, the coleoptile tip, the leaf, the stem, and the fruit. Because regulatory interactions are occurring throughout the plant, we could regard the entire plant as a brain-like command center, but then the brain metaphor would lose whatever heuristic value it was originally supposed to have.

Even more controversial have been Monica Gagliano's intriguing behavioral studies on **habituation** and associative learning, which have captured the public's imagination in a way not seen since the 1973 publication of *The Secret Life of Plants* [28,29]. Habituation, considered the most basic form of learning in animals, is a decrease in a behavioral response with repeated stimulation that does not involve either sensory adaptation or motor fatigue [30]. Putative habituation was reported by Gagliano *et al.* for the rapid leaf folding of the sensitive plant *Mimosa pudica* in response to a mechanical stimulus [28]. Gently dropping potted mimosa plants from a short height caused rapid leaf folding, and the response declined to zero with repeated dropping. Nevertheless, they were still able to fold their leaves in response to lateral shaking, indicating that the decrease in the response was specific for dropping and was not due to motor fatigue. The authors concluded that the mimosa plants exhibited genuine habituation, consistent with an ability to learn. However, Biegler has cautioned that such a conclusion is premature and that

Glossary

Action potential: an electrical impulse indicating that a cell (nerve cell, sensory cell, or muscle cell) has been activated. Action potentials of a given cell type have a stereotypic waveform and can propagate to other cells or organs at velocities between 0.5 and 100 m/s.

Affective: relating to, arising from, or influencing feelings or emotions.

Amygdala: the 'corpus amygdaloideum' or almond-shaped nucleus is a part of the mammalian brain located deep within both temporal lobes (the lateral to bottom portion of the brain). The amygdala is strongly involved in processing adverse stimuli and emotions such as fear.

Anesthetic: a common name for drugs reducing awareness or sensation. Anesthetics cover a broad range of substances. Local anesthetics prevent signal transduction from a specific area (e.g., a finger) to the spinal cord and allow operating on a fully conscious patient. General anesthetics leave the patient unconscious and are used for more invasive procedures.

Auxin: a class of plant hormones, produced mainly in the shoot tip, that promote cell division, cell elongation, and play an important role in coordinating plant development and behavioral responses; can be polarly transported cell to cell throughout the plant via specialized membrane proteins.

Brain stem: a section of the vertebrate's nervous system at the interface between the brain and the spinal cord. The brainstem contains critical areas such as the centers for breathing or for regulation of heartbeat and blood pressure, as well as networks mediating arousal reactions (called the 'reticular formation').

Cephalization: an evolutionary trend in which the mouth, sense organs, and nerve ganglia become concentrated at the anterior end of the organism to produce the head.

Classical conditioning: a type of learning in which a stimulus that evokes a response is associated with a second stimulus that normally does not evoke the response, such that the second stimulus acquires the ability to evoke the response.

Frontal neocortex: the frontal part of the neocortex contains several areas with different functional specializations. Major parts are involved in the preparation and execution of additional controls are required to establish the specificity of the response as well as to definitively rule out the effects of sensory adaptation and motor fatigue [31].

Gagliano *et al.* also carried out Pavlovian-type experiments that seem to demonstrate **classical conditioning** during phototropism [29]. This is an astonishing result, so it is worth examining it in some detail. During classical conditioning, associative learning occurs when a physiologically neutral environmental cue, the conditioned stimulus (CS), is paired with the physiologically active signal, the unconditioned stimulus (US). Pavlov famously trained dogs to salivate in response to various stimuli, such as the sound of a metronome, by associating the sound stimulus (CS) with feeding (US). Pea plants were allowed to grow into one or the other arm of a Y-maze, with blue light-emitting diode lights serving as the US and airflow produced by a small fan serving as the CS. Before testing, the plants were trained in the maze for an hour on three consecutive days. In one group of plants, the fan and blue light were placed on the same arm of the maze, while in another group the fan and blue light were placed on opposite arms of the maze. To avoid predictability, the position of the light with respect to the arm of the maze was changed (or not changed) according to a fixed pattern.

In the control experiments, when plants trained with the light and fan on opposite arms of the maze were tested in the absence of the two stimuli, 100% of the plants grew into the arm of the maze where blue light had been presented during the last training session. This is very surprising in and of itself, because it suggests that the plants ‘remembered’ the direction of light given on the previous day and grew into the correct arm, despite the absence of a light cue. To our knowledge, this phenomenon has not been reported before in the long and storied literature of phototropism. The only similar case of ‘resetting’ following the completion of a phototropic response occurs during heliotropism in sunflowers that track the sun from east to west during the day and then return to face the east during the night [32]. Curiously, the authors described this result as ‘expected’, citing a review article on phototropin receptors that makes no reference to the putative memory phenomenon.

In our view, the 100% response to the previous day’s US is not expected. During phototropic bending, the shaded side of the stem elongates at a faster rate than the illuminated side, thereby causing bending toward the light source. There is a complex relationship between the growth rate during phototropism and the rate and amplitude of circumnutation in response to light and dark [33]. The growing tip typically undergoes strong circumnutation in the dark, which weakens in the light or during phototropic bending. In the dark, circumnutation increases and the tip gradually reverts to vertical growth due to the effects of gravitropism. The presence of the Y-maze adds another layer of complexity to the experiment. If the shoot tip happens to enter the arm of the Y-maze where light was last presented during the previous day’s training session, it would be mechanically prevented from reverting to vertical growth and would therefore resume growth the next day in the same arm. In this case, the control plants would appear to grow toward the arm where light had previously been presented, whereas in the absence of the Y-maze the control plants would grow randomly.

Gagliano *et al.* reported that when the plants were tested on the fourth day, ~65% of the plants grew into the arm of the maze where the fan was positioned in the absence of light [29]. Compared to the apparent 100% response of the controls, the finding that 65% of the plants grew toward the CS represents a significant classical conditioning response (P values <0.005). However, if the control response is actually an artifact caused by the Y-maze, and the plants would have grown randomly in its absence, the significance of the 65% response to the CS would have been greatly diminished, although not necessarily abolished.

movements while other, even more frontal parts are required for decision making and cognitive control of spontaneous impulses.

Ganglion: a cluster of neurons that provides relay points and connections between different neurological structures in the body.

Habituation: the most basic type of learning in which a behavioral response declines with repeated stimulation, and the decline is not caused by sensory or motor fatigue.

Hypothalamus: a group of neuronal networks or nuclei located below the thalamus, close to the base of the middle portion of the vertebrate’s brain. It is involved in homeostatic reactions such as release of hormones, sleep-wake-cycle, stress reactions, and food intake.

Insular cortex: a section of the lateral mammalian brain hemispheres located in a deep indentation or furrow. The insula is involved in multiple sensory and emotional functions which are not yet fully understood.

Neuron: the information processing cell of the nervous system that uses action potentials to send signals along the length of the cell toward the synapse, which communicates the signal to a neighboring neuron via synaptic vesicles.

Neurotransmitter: a chemical that is released by presynaptic vesicles upon stimulation and then activates postsynaptic receptors.

Nucleus (neuro-anatomy): a compact cluster of neurons deep in the brain.

Pain: an unpleasant sensation that can range from mild, localized discomfort to agony. Pain has both physical and emotional components. The physical part of pain results from the stimulation of pain receptors (nociceptors), which transmit electrical signals to the spinal cord and the brain.

Presynaptic vesicle: a membranous vesicle containing neurotransmitters, located in the presynaptic component of a synapse, that is, in the neuronal compartment that releases the neurotransmitters in response to an action potential.

Primary consciousness: sensory consciousness, the basic ability to have subjective experiences, ‘something it is like to be’.

Somatosensory cortex: the part of the mammalian brain hemispheres receiving sensory signals from the body surface such as pressure, temperature, or damaging, painful stimuli.

A recent attempt to duplicate Gagliano *et al.*'s results under more stringent conditions indicates that the control plants do, in fact, grow randomly toward both arms of the maze, rather than bending uniformly toward the arm where the light had last been presented (K. Markel, personal communication, 2019). In these experiments, care was taken to ensure that the growing tips of the plants did not enter a maze arm during the training sessions. Interestingly, there did seem to be a slight tendency of the plants to 'remember' the light direction from the last training session. In view of these preliminary results, further studies are called for to clarify the control response. Importantly, the interactions of phototropism, gravitropism, and circumnutation in the Y-maze experiments need to be elucidated. In the words of Carl Sagan, 'Extraordinary claims require extraordinary evidence'.

The most provocative, controversial, and least testable of all the PN hypotheses is the contention that plants possess consciousness, feelings, and intentionality [6,34–36]. Extrapolating from her results on associative learning in pea plants, Gagliano augmented her hypothesis to include consciousness, which she claims is integral to 'the ability to learn':

> The ability to learn through the formation of associations involves the ability to detect, discriminate and categorize cues according to a dynamic *internal value system*. This is a subjective system of *feelings* and *experiences…* [Since] feelings account for the integration of behavior and have long been recognized as critical agents of selection, plants too must evaluate their world *subjectively* and use their own experiences and feelings as functional states that motivate their choices [35].

Even if Gagliano's proposal that plants exhibit associative learning turns out to be correct, it by no means follows that plants possess consciousness, feelings, and intentionality, for which there is no real evidence.

Despite the claims that the root tip represents a brain-like command center, PNPs generally do not regard the lack of a bona fide brain as an impediment to consciousness in plants. In a Forbes magazine interview about her work, Gagliano provided the following infelicitous description of the human brain:

> …a blobby mass of electrochemical impulses and there are all of these other cells which are very specialized at their job. They transfer chemicals and, in particular, electrical signals and that's how the information goes through the body. So in that sense, we shouldn't focus so much on saying 'it's the brain doing things, it's the nervous system doing things,' but actually look at the functional aspect of the story… plants do it with electricity, animals do it with electricity, bacteria do it with electricity [5].

From this risibly oversimplified picture of the brain, the naïve reader could be forgiven for inferring that the brain, the seat of consciousness in animals, is no more complex than a sponge, the only multicellular animal lacking neurons. But it serves the author's rhetorical purpose, for by neglecting the brain's amazing complexity, which is the very essence of brain function, she makes the existence of consciousness in plants seem much more plausible than it really is.

While it is true that some plant cells are electrically excitable and that electrical signaling is involved in some plant stress responses, not all electrical excitability represents communication with other cells. Most plant action potentials generate a net export of KCl salt, while animal action potentials are osmotically neutral. Some unicellular algae are electrically excitable but, being unicellular, do not communicate with neighboring cells. They use action potentials to regulate their osmotic balance [37–39], a function that is still maintained in guard cells of higher plants [40]. There are many arguments, which are rarely mentioned, that excitability for osmotic regulation is evolutionarily much older than excitability for information transmission.

Oversimplification in the service of plausibility also has been deployed to infer the ability of plants to feel **pain** from the inhibitory effects of **anesthetics** on autonomous and touch-sensitive plant movements and action potentials. In addition, anaesthetics inhibit a broad spectrum of cellular and biochemical processes, including germination, chlorophyll accumulation, and endocytic vesicle recycling [41]. The International Association for the Study of Pain defines pain as 'an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage' (IASP terminology. https://www.iasp-pain.org/terminology?navItemNumber=576#Pain). This definition emphasizes the subjective character of pain as a complex experience, far beyond a stereotypic reaction to the stimulation of peripheral nociceptive (pain) receptors. Pain can have different qualities and temporal features depending on the stimulus, such as piercing, stabbing, burning, throbbing, cramping, and aching. Indeed, ascending nociceptive signals activate a large network of different **nuclei** in the brain that, in mammals, includes **somatosensory**, **insular**, and **frontal neocortex**, the **amygdala**, **hypothalamus**, and **brain stem** [42,43]. These regions correspond to different sensory, **affective**, cognitive, motor, and vegetative components that together form the complex psychophysiological experience of pain [44].

It is therefore incorrect and misleading to use the word 'pain' for adaptive responses to damaging conditions. Adaptive responses are basic properties of living organisms that have nothing in common with the complex psychophysiological experience of pain. It is equally fallacious to cite experiments performed on plants with anesthetics as indirect evidence for subjective experience in plants. While it is true that substances such as diethyl ether interfere with touch-sensitive action potentials and rapid leaf movements, this inhibition represents a general effect of anesthetics on membrane properties. As is discussed next, consciousness emerges only at higher levels of biological organization and complexity. To infer that plants have consciousness and feel pain on the basis of responses to anesthetics is a bridge too far.

A New Paradigm for Consciousness in Animals

But to rule out consciousness in plants we first need to have some idea of how much organizational and functional complexity is required for consciousness in animals. Until recently, consciousness has been viewed as a nearly impenetrable black box, which philosopher David Chalmers called the 'hard problem of consciousness' [45]. In his influential paper 'What Is It Like to Be a Bat?', the philosopher Thomas Nagel defined the subjective experience of consciousness as 'something it is like to be' [46]. Yet, there exists, in the words of philosopher Joseph Levine, an 'explanatory gap' between the physical brain and the experience of subjectivity [47].

According to the philosopher John Searle, the problem of consciousness is so challenging because any direct observation of the brain itself inevitably leaves out the subjective experience we are trying to explain: 'You can neither reduce the neuron firings to the feelings nor the feelings to the neuron firings, because in each case you would leave out the objectivity or subjectivity that is in question' [48]. Nevertheless, neurobiologists are virtually unanimous in believing that the link between the brain and consciousness is neither magical nor mystical and does not involve any new physical laws, although the mechanism of consciousness is probably unique to the brain.

Recently, Todd E. Feinberg and Jon M. Mallatt conducted a broad survey of the anatomical, neurophysiological, behavioral, and evolutionary literature from which they were able to derive a consensus set of principles that allowed them to hypothesize how and when **primary consciousness**, the most basic type of sensory experience, evolved [49–51]. First, consciousness and the creation of feelings are fundamentally grounded in living processes. Second, only multicellular animals with a nervous system and a basic core brain can be said to exhibit primary consciousness with any certainty. Third, to create consciousness, the animal nervous system must also possess 'the numerous and neurobiologically unique special neurobiological features of complex nervous systems, especially of complex brains, that all together create consciousness.' In addition to these three requirements, the evolution of consciousness involved 'an explosion of senses (eyes, good hearing, keen smell), a multitude of new neural processing subsystems, more combining of information from the different senses, more levels of information processing at the top of the brain, more back-and-forth communications between brain levels, and more memory'.

How might all of these unique brain features work together to create consciousness?
Consider that a brain with a threshold level of complexity can represent some mapping of sensory experience, that is, sight, smell, hearing, taste, and touch. Each sensory pathway consists of several hierarchically arranged neurons that carry signals up to the brain, while keeping a point-by-point mapping of a body surface, a body structure, or the outside world. In most cases the maps correspond to spatial features in the sensory world. For example, in the visual system there are maps of visual space, in the auditory system there are maps of sound frequency, and in the touch/pain system there are maps of the body surface. The maps of the chemical senses (taste and smell) differ from those of sight, sound, and touch in that they have no meaningful spatial properties. Instead of spatial maps, gustatory and olfactory systems use population coding to identify specific tastes and smells [52]. That is, the brain sorts out information from large numbers of receptors that differ in their sensitivities to different types of molecules and organizes them into a functional map, like the periodic table.

When such a brain senses a large number of spatially mapped sensory stimuli, it will generate a flood of inputs (millions in complex mammalian brains) that are closely associated in time and that can lead to mental images. We can think of these mapped mental images as the sensory dimension.

Next, consider that this 'threshold brain' possesses a genetically programmed panel of emotional reactions: appetite/consume food, fear/avoidance of threat, love/sexuality, anger/confrontation-attack, pain/anxiety. These can be thought of as the emotional dimension, the palette of feelings.

Finally, consider that such a brain can associatively learn – that is, link – cues, even context, to the feelings and related sensory experience. These associations can be thought of as a learning dimension, in which patterns from the sensory and emotional dimensions are remembered so that they can be reinforced and/or avoided.

It follows, therefore, that with millions of neurons and billions of synapses that interconnect the neurons to form networks, the totality of these dimensions could emerge, that is, be integrated as an extraordinarily complex series of images over time (even fractions of a second) that could contribute to consciousness.

As subjectively experienced, consciousness is multidimensional, that is, it includes sensory mapping, emotional reactions, and memory filing and recall. Importantly, at successive instants in time, consciousness is a fusion of all these dimensional representations into multidimensional 'snapshots' over time. 'Working memory', for which there are observed electrophysiologic and, more recently, early brain imaging correlates, allows humans to preserve conscious fusion-images for prolonged temporal intervals. This working memory of fusion images in the brain makes it possible to construct and compare elaborate hypothetical scenarios and their likely outcomes before deciding on a particular behavior and acting on it.

Based on their evolutionary analysis of the structure, organization, and functional specialization of the brain required for the emergence of consciousness, Feinberg and Mallatt concluded that the only animals that satisfied their criteria for consciousness were the vertebrates (including fish), arthropods (e.g., insects, crabs), and cephalopods (e.g., octopuses, squids).

Many questions remain, but Feinberg and Mallatt's detailed anatomical studies on the level of complexity that the brain had to acquire before consciousness could evolve should give PNPs pause before speculating about consciousness, feelings, and intentionality in plants. Time-lapse videos of growing roots or twining stems, which have been speeded up to make them look more animal-like, do not constitute evidence for consciousness or intentionality. Animals can move about quickly because they possess motor systems composed of muscles and the neurons that control them. The slow growth movements of plants are caused by entirely different mechanisms involving cell wall expansion and water uptake, while rapid leaf movements, as in the case of *M. pudica*, are mediated by rapid changes in cell turgor pressure.

Neurons are thought to have evolved in animals ~500 million years ago, concomitant with the initiation of predator–prey interactions for the purpose of obtaining food [53,54]. During **cephalization** and brain development, the mouth, sense organs, and nerve **ganglia** concentrated at one end of the organism to form the head region, a process associated with bilateral symmetry. The evolution of bilateral symmetry, in turn, enhanced the mobility required for foraging, predator–prey relationships, and reproduction. The evolution of a brain capable of consciousness, feelings, and intentionality clearly enhanced the evolutionary fitness of animals.

Plants, being sessile, photo-autotrophic organisms, are adapted to be paragons of energy efficiency, relying on water uptake into vacuoles for cell expansion and growth instead of energy-costly protein synthesis. As biological solar collectors, plants evolved to compete for sunlight and to cover space, which they accomplish through indeterminate growth. They did not evolve to chase prey or evade predators. In angiosperms, coevolution with insects and other animals harnessed the motility and intentionality needed for cross-pollination, obviating the need for the evolution of these traits. There is no evidence that plants require, and thus have evolved, energy-expensive mental faculties, such as consciousness, feelings, and intentionality, to survive or to reproduce. Plant development and behavior can be regarded as a series of nonintended consequences emerging from internal and external signaling networks that have evolved through natural selection.

Although plants lack the higher order neuronal complexity required for consciousness in animals, they are nonetheless remarkable organisms, worthy of our admiration, respect, study, and efforts to conserve. It is quite enough that they are capable of converting sunlight, carbon dioxide, and water into the complex carbon compounds that support all of multicellular terrestrial life on earth. We should not demand that they also be conscious of doing so.

Concluding Remarks

Plant neurobiologists are hardly the first biologists to ascribe consciousness, feelings, and intentionality to plants. Parallel claims were made by the Romantic biologists of the 18th and 19th centuries. Romantic biology began as a rebellion against the Cartesian/Newtonian vision of a deterministic, mechanical universe operating entirely by physical laws and was codified in the writings of German philosopher Friedrich Wilhelm Joseph Schelling as *Naturphilosophie*. The ultimate goal of German *Naturphilosophie* was to demonstrate that nature, mind, and spirit are one.

The earliest examples of Romanticism in plant biology occurred in the wake of the discovery of sex in plants [55]. Following Nehemiah Grew's proposal that pollen grains were the

Outstanding Questions

Can plant behavioral responses be habituated? Thus far, there is only one positive report, in *Mimosa pudica*, but additional controls are needed. These experiments with mimosa need to be repeated by other labs, and the findings extended to other plant responses and other organisms to establish their generality.

Do plant behavioral responses show classical conditioning? Thus far, there is only one affirmative report based on phototropic bending, but this study did not control for the contributions of circumnutation and gravitropism. These studies need to be repeated with additional controls by other laboratories.

Is attributing consciousness to plants necessary as a psychological tactic to convince the general public of the urgent need to preserve the biosphere, whether or not it is true? If the answer is yes, we are put in the intolerable position of having to choose between asserting a falsehood to promote ecological awareness, and maintaining objectivity as an uninformed populace pursues ecological catastrophe.

equivalent of animal sperm, and Camerarius's demonstration that pollination is required for seed production, some botanists leaped to the conclusion that if plants had sex like animals they must also experience animal-like passions and lust. Thus, in 1717 Sébastien Vaillant gave a lecture on pollination at the Jardin des Plantes that could have been written by D.H. Lawrence:

> …the tension or swelling of the male organs occurs so rapidly that the lips of the bud, giving way to such impetuous energy, open with astonishing speed. At that moment, these excited organs, which seem to think only of satisfying their own violent desires, abruptly discharge in all directions, creating a tornado of dust which expands, carrying fecundity everywhere; and by a strange catastrophe they now find themselves so exhausted that at the very moment of giving life they bring upon themselves a sudden death (see [55]).

Linnaeus, a great admirer of Valliant, was inspired by him to base his taxonomic scheme on the new sexual theory, but as the son of a Lutheran minister he couched his student dissertation on pollination in terms of lawful marriage:

> The actual petals of the flower contribute nothing to generation, serving only as Bridal Beds, which the great Creator has so gloriously arranged, adorned with such noble Bed Curtains and perfumed with so many sweet scents, that the Bridegroom there may celebrate his *Nuptias* with his bride with all the greater solemnity. When the bed is thus prepared, it is time for the Bridegroom to embrace his beloved Bride and surrender his gifts to her.

Later in life, Linnaeus seems to have enjoyed coining terms for the more scandalous aspects of plant sex, including 'promiscuous intercourse', 'barren concubines', and 'one wife, two husbands', which shocked pious botanists and made the job of textbook authors more difficult, inasmuch as botany was then the only scientific discipline deemed appropriate for young women [55].

Erasmus Darwin, Darwin's grandfather and a believer in free love, was so taken with the Linnaean sexual system of classification that he wrote an epic poem, *The Loves of Plants*, in which he personified stamens and pistils as 'swains' and 'virgins' cavorting on their flower beds in various polygamous and polyandrous relationships. Although he stated that his personification of stamens and pistils was a heuristic device, he also believed that 'the anthers and stigma are real animals', capable of feelings and emotions. His contemporary, René-Louis Desfontaines, Professor of Botany at the Jardins des Plantes, described the quivering of sexually aroused stamens in response to 'the action of the pistil itself, which incites each stamen to orgasm, similar in a sense to the familiar orgasm that occurs in the sexual parts of animals'.

Of course, contemporary plant neurobiologists have not gone so far as to attribute passion and lust to stamens and pistils. However, they repeatedly scold mainstream biologists for treating plants as 'passive automata' with neither agency nor feelings of their own. They urge PNOs to think more like poets and embrace metaphors.

Why is anthropomorphism resurgent in biology today? In the most extreme case, all forms of life, even prokaryotes, are said to possess consciousness. This new wave of Romantic biology appears to have been inspired by a justifiable concern about humanity's continuing ecological degradation of the biosphere: the loss of habitats and biodiversity, the over-exploitation of natural resources, and the crisis of climate change (see Outstanding Question). PN has its roots in plant ecology and its philosophical offshoot, the Gaia hypothesis, rather than plant physiology, and an ethical perspective permeates its intellectual foundation. Monica Gagliano makes this clear in the concluding paragraph of one of her articles:

> And lastly, questions about the cognitive capacities of animals and specifically, animal consciousness often play a role in discussions about animal welfare and moral status. This debate has been recently extended to include plants and as experimental evidence for the cognitive capacities of plants accrues, the controversial (or even taboo) topic regarding their welfare and moral standing and our ethical responsibility toward them can no longer be ignored [35].

While we agree entirely that biodiversity needs to be protected, we strongly object to the implication that plant consciousness, intentionality, and cognition are moral or ethical questions. A scientific understanding of nature requires only that we seek the truth.

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