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REVIEWS

doings, and habits of animals without turning a blind eye to animal physiology.

Ascribing intelligence and consciousness under a pluralistic approach does provide new directions to study cognitive processes in plants [3]. All we need to do so is to place the discussion outside the framework of old and sterile battles. We lend mainstream plant physiology a friendly helping hand with an eye to enriching discussion with no vetoes over alternative theoretical frameworks. That is the only way forward.

Acknowledgments

This research is supported by the Office of Naval Research Global (Award # N62909-19-1-2015) to P.C.

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https://doi.org/10.1016/j.tplants.2019.12.016

References

1. Sachs, J. (1865) *Handbuch der Experimental-Physiologie der Pflanzen: Untersuchungen über die Allgemeinen Lebensbedingungen der Pflanzen und die Functionen ihrer Organe*, W. Engelmann, Leipzig
2. Hiernaux, Q. (2019) History and epistemology of plant behaviour: a pluralistic view? *Synthese* Published online July 2, 2019. https://doi.org/10.1007/s11229-019-02303-9
3. Allen, C. (2017) On (not) defining cognition. *Synthese* 194, 4233–4249
4. Cleland, C.E. and Chyba, C.F. (2002) Defining life. *Orig. Life Evol. Biosph.* 32, 387–393
5. Taiz, L. *et al.* (2019) Plants neither possess nor require consciousness. *Trends Plant Sci.* 24, 677–687
6. Baluška, F. *et al.* (2006) *Communication in Plants: Neuronal Aspects of Plant Life*, Springer
7. Calvo, P. *et al.* (2017) Are plants sentient? *Plant Cell Environ.* 40, 2858–2869
8. Stolarz, M. (2009) Circumnutation as a visible plant action and reaction: physiological, cellular and molecular basis for circumnutations. *Plant Signal. Behav.* 4, 380–387
9. Calvo, P. *et al.* (2017) Guidance of circumnutation of climbing bean stems: an ecological exploration. *bioRxiv* Published online March 30, 2017. https://doi.org/10.1101/122358
10. Darwin, C. and Darwin, F. (1880) *The Power of Movements in Plants*, D. Appleton and Company
11. Israelsson, D. and Johnsson, A. (1967) A theory for circumnutations in *Helianthus annuus*. *Physiol. Plant.* 20, 957–976
12. Stolarz, M. *et al.* (2014) Circumnutation Tracker: novel software for investigation of circumnutation. *Plant Methods* 10, 24
13. Taiz, L. and Zeiger, E. (2010) *Plant Physiology* (5th edn), Sinauer Associates
14. Bown, A.W. and Shelp, B.J. (2016) Plant GABA: not just a metabolite. *Trends Plant Sci.* 21, 811–813
15. Calvo, P. (2016) The philosophy of plant neurobiology: a manifesto. *Synthese* 193, 1323–1343
16. Gianoli, E. (2015) The behavioural ecology of climbing plants. *AoB Plants* 7, plv013
17. Griffin, D.R. (1981) *The Question of Animal Awareness*, Rockefeller University Press
18. Calvo, P. and Friston, K.J. (2017) Predicting green: really radical (plant) predictive processing. *J. R. Soc. Interface* 14, 20170096

Letter

Consciousness Facilitates Plant Behavior

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The scientific pursuit of nonhuman consciousness and sentience, understood as the capacities to be aware of the environment and to integrate sensory information for purposeful organismal behavior, has been a research priority for decades [1]. Many plant scientists would have no problem in assuming that chimpanzees, dogs, cats, and dolphins are conscious. Marks of ‘the cognitive’ have been identified in such distant animals, taxonomically speaking, as fruit flies [2], archerfish [3], and zebrafish [4]. By contrast, plant consciousness appears to be a different ‘breed’ altogether.

Consciousness appears to bottom-out at some point in evolution and, for Taiz *et al.*, plants mark the borderline in this respect [5]. In their recent opinion article [5] in *Trends in Plant Science*, they claim that ‘plants neither possess nor require consciousness’. However, they base their claim on a cerebrocentric postulate [6] and assume without further ado that a relatively complex nervous system is essential for consciousness. By contrast, on evolutionary continuity grounds, we see biological sentience and consciousness as emerging from certain basic features of living organisms [7]. These features can be partly neural, as in the case of the rise of animal-based forms of sentience, but can also be non-neural, as the very possibility of plant sentience suggests. We are happy to go all the way down. To avoid the ‘emergentist dilemma’ and to stay on an evolutionary track, a basic form of sentience (awareness of environment) is proposed to emerge with the evolution of first cells and is an inherent feature of cellular life [7]. If bacteria evolved biomechanical structures that underlie their own subjective experiences, and facilitate their own goal-directed behavior, communication, and adaptation [7,8], there is no reason to exclude the possibility that plants have also evolved their own subjective sense of environmental awareness.

Can we rely upon scientifically grounded indicators for the ascription of sentience to plants? We find justification for the ascription of consciousness to plants on the grounds that doing so furnishes the best explanation of the mounting available data. Which data? Indicators for the ascription of plant consciousness are the same ones we use for the study of animal-based interactions. To wit, anatomical and morphological traits, (electro)physiological responses, and behavioral/ethological data, among other evidence pools. Plant bodily actions, together with electrochemical activity, and phytohormone secretion and transport, serve among other roles to achieve purposeful movements [9], and sophisticated forms of plant behavior [9] have been comprehensively linked to plant electrophysiology [10].

How widespread is consciousness across the Tree of Life? Current trends are orthogonal to Taiz *et al.* [5]. Their ‘ladder approach’ privileges some phyla over others and, in doing so, swims against the stream of research in evolutionary and comparative biology. The investigation of consciousness in plants is fully justified to better understand how these processes contribute to the life cycle in real-world circumstances, which is the real target of selection [11]. Plant consciousness could have emerged from the phytoneural features of the vascular system of higher plants as well as from synaptic-like cell–cell communication in root apices.

Can we effectively determine whether plants are conscious? The capacity of a plant for sentience and sophisticated behavior could be told from the degree of complexity of vascular interactions. Our working hypothesis is that changes in levels of plant sentience will be consistently linked to changes in long-distance electric signaling and vascular complexities. We may measure the integration of information in plants by probing their vasculature directly via causal interaction and assessing to what extent different vascular areas interact and deliver differentiated responses.

The case of plants under anesthesia [12–14] constitutes a specially promising avenue of research in this respect. As in human and nonhuman animals, behavior and sensory responsiveness of plants are also sensitive to anesthetics. Following in the footsteps of Claude Bernard's pioneering work [15] (in his view, sensitivity to anesthesia marked the borderline between sentience and reductive chemical phenomena across phyla), we now know that plants not only biosynthesize anesthetic chemical compounds if stressed or wounded [16,17], but are also subject to reversible anesthetic treatments.

Venus flytrap anesthesia induced with diethyl-ether blocks long-distance electric signaling via plant action potentials and also inhibits jasmonate accumulation and impairs jasmonate signaling, leading to the expression of jasmonate-responsive genes [13]. External application of jasmonic acid restored jasmonate signaling even under anesthesia, implicating that jasmonate signaling is linked to plant anesthesia [13]. Given that jasmonate signaling is also relevant for long-distance electric communication in noncarnivorous plants, we can expect that unraveling of mechanisms behind the interactions between plant action potentials and jasmonate signaling will illuminate how plant sentience and consciousness impact plant defenses and adaptations to stress situations. It is relevant in this respect that plants produce their endogenous anesthetics [17] typically under stress situations and wounding [16].

Given that glutamate and GABA signaling are shared by animals and plants [18,19], the loss and recovery of overt plant behavioral patterns might be due to the inhibition of action potentials. Insofar as anesthesia effectively blocks plant action potentials [12,13], we can expect similar effects on long-distance signaling in the plant body as we find in the animal literature. Extensive breakdowns in vascular connectivity in plant subjects under anesthesia will enable us to observe a lack of correlation between plant arousal and awareness. As plants come out of pharmacological coma (anesthesia) and their physiology reverts to normal, the two components, arousal or wakefulness, on the one side, and awareness, on the other, will stop being dissociated, reaching a higher level of sentience. Future studies can clarify the nature of roles of consciousness in behavior, adaptation, and evolution of living organisms.

If speaking about animal consciousness remains a taboo in some quarters, plant consciousness represents the ultimate frontier. We are aware that the very idea of plant consciousness can prove elusive, and that it is easy to fall prey to conceptual, zoocentric traps. However, theories of consciousness must make evolutionary sense. It is precisely paying due respect to evolutionary considerations that brings the idea of plant consciousness to the fore. The very consideration of plant consciousness does not imply that plants are to be treated as proxies of animals. Nevertheless, plants represent a promising and relevant model in this endeavor.

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https://doi.org/10.1016/j.tplants.2019.12.015

References

1. Edelman, G. and Tononi, G. (2000) *A Universe of Consciousness: How Matter Becomes Imagination*, Basic Books
2. Heisenberg, M. (2014) The beauty of the network in the brain and the origin of the mind in the control of behavior. *J. Neurogenet.* 28, 389–399
3. Newport, C. *et al.* (2016) Discrimination of human faces by archerfish (*Toxotes chatareus*). *Sci. Rep.* 6, 27523
4. Leung, L.C. *et al.* (2019) Neural signatures of sleep in zebrafish. *Nature* 571, 198–204
5. Taiz, L. *et al.* (2019) Plants neither possess nor require consciousness. *Trends Plant Sci.* 24, 677–687
6. Van Duijn, M. (2017) Phylogenetic origins of biological cognition: convergent patterns in the early evolution of learning. *Interface Focus* 7, 20160158
7. Baluška, F. and Reber, A. (2019) Sentience and consciousness in single cells: how the first minds emerged in unicellular species. *BioEssays* 41, e1800229
8. Martinez-Corral, R. *et al.* (2019) Metabolic basis of brain-like electrical signalling in bacterial communities. *Philos. Trans. R. Soc. B* 374 20180382
9. Calvo, P. *et al.* (2019) Plants are intelligent, here's how. *Ann. Bot.* 124, mcz155
10. Volkov, A.G., ed (2012) *Plant Electrophysiology – Methods and Cell Electrophysiology*, Springer Verlag
11. McNamara, J.M. and Houston, A.I. (1996) State dependent life histories. *Nature* 380, 215–221
12. Yokawa, K. *et al.* (2018) Anesthetics stop diverse plant organ movements, affect endocytic vesicle recycling, ROS homeostasis, and block action potentials in Venus Flytraps. *Ann. Bot.* 122, 747–775
13. Pavlovič, A. *et al.* (2019) Anaesthesia with diethyl ether impairs jasmonate signalling in the carnivorous plant Venus flytrap (*Dionaea muscipula*). *Ann. Bot.* 124, mcz177
14. Yokawa, K. *et al.* (2019) Anesthetics, anesthesia, and plants. *Trends Plant Sci.* 24, 12–14
15. Grémiaux, A. *et al.* (2014) Plant anesthesia supports similarities between animals and plants: Claude Bernard's forgotten studies. *Plant Signal. Behav.* 9, e27886
16. Baluška, F. *et al.* (2016) Understanding of anesthesia – why consciousness is essential for life and not based on genes. *Commun. Integr. Biol.* 9, e1238118
17. Tsuchiya, H. (2017) Anesthetic agents of plant origin. *Molecules* 22, 1369
18. Mousavi, S.A.R. *et al.* (2013) Glutamate receptor-like genes mediate leaf-to-leaf wound signals. *Nature* 500, 422–426
19. Žárský, V. (2015) Signal transduction: GABA receptor found in plants. *Nat. Plants* 1, 15115