Update TRENDS in Plant Science Vol.xxx No.x

Full text provided by www.sciencedirect.com ScienceDirect

Letters Response

# Response to Alpi *et al.*: Plant neurobiology: the gain is more than the name

**Eric D. Brenner[1], Rainer Stahlberg[2], Stefano Mancuso[3,4], František Baluška[4,5,6] and Elizabeth Van Volkenburgh[2]**

[1] Genomics, New York Botanical Garden, NY 10458, USA
[2] Department of Biology, University of Washington, Seattle, WA 98195, USA
[3] Department of Horticulture, University of Florence, Viale delle Idee 30, 50019 Sesto Fiorentino (FI), Italy
[4] International Plant Neurobiology Laboratory, Viale delle idee 30, 50019 Florence, Italy; Kirschallee 1, 53115 Bonn, Germany
[5] Institite of Cellular and Molecular Botany, Rheinische Friedrich-Wilhelms-University of Bonn, Kirschallee 1, 53115 Bonn, Germany
[6] Institute of Botany, Slovak Academy of Sciences, Dubravska cesta 14, SK-84223, Bratislava, Slovak Republic

The past three years have seen three thought-provoking and well attended symposia, the founding of a new society, the Society of Plant Neurobiology (SPN), and the promising start of a new journal, *Plant Signaling and Behavior*. Although most participants within the Plant Neurobiology framework are finding plenty of stimulating, inspirational and controversial material, other colleagues have some concern about the scientific validity and rationale behind 'plant neurobiology'. Vigilance is a justifiable concern of the scientific community. In their critique of Plant Neurobiology, Amedeo Alpi *et al.* [1] ask the question "What long-term scientific benefits will the plant science research community gain from the concept of 'plant neurobiology'?", which they believe is '...based on superficial analogies and questionable extrapolations...' such as nerves, brain synapses, intelligent responses being expatriated from the field of animal neurobiology to explain some of the complex behavior of plants.

Most of our statements and publications should have made clear that plant neurobiology is pursuing a framework of ideas that were introduced by outstanding representatives of the plant sciences such as Wilhelm Pfeffer [2,3], Charles Darwin [4], Julius von Sachs [5], Georg Haberlandt [6] and Erwin Bünning [7]. No one proposes that we literally look for a walnut-shaped little brain in the root or shoot tip or some myelinated superconducting nerve cells in plants. Neither did Haberlandt [6] when he compared long-distance signalling in *Mimosa* with that in animals, nor Darwin when he considered the Venus' flytrap as the most animal-like plant [8] or conjectured that the root tip fulfills complex tasks like a brain [4].

We are less concerned with names than with the phenomena that have been overlooked in plant science, which, in our opinion, need to be addressed to truly understand plant operation, particularly in an era of outstanding new technologies. We begin with the fact that action potentials were observed in plants more than 100 years ago but we still don't know their means of propagation and biological purpose and the molecular components that maintain and respond to plant action potentials have still to be determined. We have known since Pfeffer, Haberlandt and Jagadish Chandra Bose that action potentials are conducted in the vascular bundles (see Ref. [9] for reference). If one wants to figure out how a sunflower plant is able to propagate an action potential over a distance of 0.3 m (a length of more than one thousand cells), then with what related phenomenon should we start our comparisons if not those of animals? We need to ascertain the role of action potentials in plants. Preliminary data suggest that action potentials are implicated in ionic homeostasis, phloem transport, protein expression, respiration, pollination and organ movements (for most recent papers see Refs [10,11] and for reviews see Refs [12,13]). Although we know a lot about potassium channels in plants, we have no idea what their roles are in propagating plant action potentials. So far, we have placed only a few tiles in the complex mosaic.

Plant Neurobiology creates an important and yet unfilled niche for plant biology. Already, the field has evolved considerably since its inception. The interdisciplinary nature of the three international symposia did more than just challenge (and in some cases reject) the use of neurobiological terms and our understanding of plant behavior: it generated ideas about how to understand the broader picture of plant signaling. Together we move towards a more integrated view, seeking the means by which plants communicate within and among themselves as well as with other organisms, and whether this is a centralized or decentralized (or somewhere in between) process within the plant.

There is no doubt that animal and plant biologists have borrowed terms from each other throughout the evolution of their fields – often amid much controversy at the time. For example, Robert Hook originally discovered cells in plant tissues in 1665 and this cellular analogy proved useful for animal tissues much later [14]. Moreover, plant physiology faced a rather difficult and long introduction into plant sciences. Julius von Sachs, at the young age of 25, had his 'habilitation' in the emerging field of plant physiology. When he submitted his thesis at the Charles

DOI of original article: 10.1016/j.tplants.2007.03.002.
Available online xxxxxx
*Corresponding authors:* Brenner, E.D. (ebrenner@nybg.org);
Baluška, F. (baluska@uni-bonn.de); Van Volkenburgh, E. (lizvanv@u.washington.edu).
Available online xxxxxx.

  doi:10.1016/j.tplants.2007.06.005

Please cite this article in press as: Brenner, E.D. et al., Response to Alpi *et al.*: Plant neurobiology: the gain is more than the name, Trends Plant Sci. (2007), doi:10.1016/j.tplants.2007.06.005

University (then known as Carl-Ferdinands Universität) in Prague [15], it was returned to him with a comment that plant physiology does not exist (p. 469 in Ref. [16]). It was only the influence of Jan Evangelista Purkyne that convinced his colleagues to accept this thesis. However, the birth of plant physiology was a controversial event and it was not until 1926 that the journal *Plant Physiology* was founded.

From the critique by Alpi *et al*. [1] we recognize that we need to engage many more scientists in the plant signaling community. Alpi *et al*. focus their criticism on the possibility that auxin has 'neurotransmitter-like' characteristics in plants. Both groups agree that auxin is tranported cell-to-cell via a variety of transporters. However, outstanding questions remain as to whether intercellular movement of auxin passes through the symplast and/or the apoplast. If apoplastic, does this intercellular movement occur via plasma membrane-localized transporters and/or via a vesicle-mediated system, or both? Alternatively, auxin might be transported via the symplast through plasmodesmata, as Alpi *et al*. speculate. The role of plasmodesmata in the long-distance transport of auxin is poorly described, and is an exciting area that needs more consideration. An even larger question at hand is how electrical cell–cell coupling is regulated. We differ with Alpi *et al*. who maintain that the '...occurance of plasmodesmata...poses a problem for signaling from an electrophysiological point of view – extensive electrical coupling would preclude the need for any cell-to-cell transport of a 'neurotransmitter-like' compound...'. However, we believe that too little is known regarding plant signaling, particularly in the apoplast and/or the symplast, to exclude a role of cell-to-cell transport of a 'neurotransmitter-like' compound as a mediator of intercellular-electrochemical signals.

We welcome a healthy discussion, pros and cons, during this exciting introduction of the plant neurobiology concept and we seek the development of an intellectually rigorous foundation.

## References

1 Alpi, A. *et al.* (2007) Plant neurobiology: no brain, no gain? *Trends Plant Sci.* 12, 135–136
2 Pfeffer, W. (1873) *Physiologische Untersuchungen,* Engelmann-Verlag
3 Pfeffer, W. (1906) *The Physiology of Plants: A Treatise upon the Metabolism and Sources of Energy in Plants,* Clarendon Press
4 Darwin, C. (1880) *The Power of Movements in Plants,* John Murray
5 Sachs, J. (1882) *Lectures on the Physiology of Plants,* Clarendon Press
6 Haberlandt, G. (1890) *Das reizleitende Gewebesystem der Sinnpflanze,* Engelmann-Verlag
7 Bünning, E. (1977) Fifty years of research in the wake of Wilhelm Pfeffer. *Ann. Rev. Plant Physiol.* 28, 1–22
8 Darwin, C. (1875) *Insectivorous plants,* John Murray
9 Stahlberg, R. (2006) Historical overview on plant neurobiology. *Plant Signal. Behav.* 1, 6–8
10 Felle, H.H. and Zimmermann, M.R. (2007) Systemic signalling in barley through action potentials. *Planta* 226, 203–214
11 Grams, T.E. *et al.* (2007) Distinct roles of electric and hydraulic signals on the reaction of leaf gas exchange upon re-irrigation in *Zea mays* L. *Plant Cell Environ.* 30, 79–84
12 Brenner, E. *et al.* (2006) Plant Neurobiology: an integrated view of plant signaling. *Trends in Plant Science* 11, 413–419
13 Fromm, J. and Lautner, S. (2007) Electrical signals and their physiological significance in plants. *Plant Cell Environ.* 30, 249–257
14 Harris, H. (1999) *The Birth of the Cell,* Yale University Press
15 Gimmler, H. *et al.* (2003) *Julius von Sachs in Briefen und Dokumenten, Teil 1: 1832–1868,* Druck Schmitt & Meyer GmbH
16 Němec, B. (2002) *Vzpomínky (Memoirs of Bohumil Němec),* ACAS, Prague



Please cite this article in press as: Brenner, E.D. et al., Response to Alpi *et al*.: Plant neurobiology: the gain is more than the name, Trends Plant Sci. (2007), doi:10.1016/j.tplants.2007.06.005