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Letters

Plant neurobiology: no brain, no gain?

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The past three years have witnessed the birth and propagation of a provocative idea in the plant sciences. Its proponents have suggested that higher plants have nerves, synapses, the equivalent of a brain localized somewhere in the roots, and an intelligence. The idea has attracted a number of adherents, to the extent that meetings have now been held in different host countries to address the topic, and an international society devoted to 'plant neurobiology' has been founded. We are concerned with the rationale behind this concept. We maintain that plant neurobiology does not add to our

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understanding of plant physiology, plant cell biology or signaling.

We begin by stating simply that there is no evidence for structures such as neurons, synapses or a brain in plants. The fact that the term 'neuron' is derived from a Greek word describing a 'vegetable fiber' is not a compelling argument to reclaim this term for plant biology. Let us consider the erroneous arguments that have been put forward to support the concept of plant 'neurons'. By this logic, cells that contribute to auxin transport are equated to chains of neurons, and it is argued that auxin transport occurs via a concerted vesicle-based trafficking mechanism of 'neurotransmitter-like cell–cell transport' [1,2]. There are two immediate difficulties with this reasoning. (i) Neurotransmitters are not transported from cell to cell over long distances. (ii) The evidence that auxin is sequestered within exocytic vesicles is weak [3]. This notion is difficult to reconcile with the acknowledged distribution and function of the PIN and AUX families of auxin transporters, which locate to different polar domains of the plasma membrane [4] and cycle to and from endosomal compartments to the plasma membrane under the control of auxin [5]. Together with the P-glycoprotein subfamily of ABC auxin transport proteins [6], which appear to function coordinately with PIN efflux carrier proteins [7], these transport activities are sufficient to account for the known rates of polar auxin transport, and do not sit comfortably with the idea of vesicle-mediated traffic of auxin, even over sub-cellular distances.

Another fundamental stumbling block regarding the concept of plant neurobiology is the common occurrence of plasmodesmata in plants. Their existence 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 – leading Eric Brenner *et al.* [2] to argue that 'these cytoplasmic connections have a poorly described role in electrical coupling between adjacent polarized plant cells'. In fact, huge numbers of plasmodesmata occur between cells that contribute to polar auxin transport, but their existence has been neglected within the plant hormone research field. Given the existence of plasmodesmata, there is no *a priori* reason why plant hormones should not be transported symplastically through the cytosol. Indeed, the presence of influx and efflux transporters for auxin at the plasma membrane suggests that auxin is present in the cytosol. So either auxin is effectively excluded at plasmodesmata, or it does not enter the cytosol until it reaches cells of the extension zone where it is taken up and then released to exert its effects. Clearly, there are still many unknowns surrounding auxin transport, and the role (if any) of plasmodesmata in this process remains as enigmatic as it was almost 15 years ago [8]. It could be argued that auxin is taken up in vesicles via endocytosis and moves by vesicular traffic to the opposing plasma membrane where it is released by exocytosis, and that this process is continually repeated along the axis of transport. However, this model should not be confused with events in nerves and at the synapse.

So, are we better informed scientifically about these unknowns, or better guided towards their resolution, by the plant neurobiology concept? Plant cells do share features in common with all biological cells, including neurons. To name just a few: plant cells show action potentials, their membranes harbor voltage-gated ion channels, and there is evidence of neurotransmitter-like substances. Equally, in a broader sense, signal transduction and transmission over distance is a property of plants and animals. Although at the molecular level the same general principles apply and some important parallels can be drawn between the two major organismal groups, this does not imply *a priori* that comparable structures for signal propagation exist at the cellular, tissue and organ levels. A careful analysis of our current knowledge of plant and animal physiology, cell biology and signaling provides no evidence of such structures.

New concepts and fields of research develop from the synthesis of creative thinking and cautious scientific analysis. True success is measured by the ability to foster new experimental approaches that are founded on the solid grounding of previous studies. What long-term scientific benefits will the plant science research community gain from the concept of 'plant neurobiology'? We suggest these will be limited until plant neurobiology is no longer founded on superficial analogies and questionable extrapolations. We recognize the importance of a vigorous and healthy dialog and accept that, as a catch-phrase, 'plant neurobiology' has served a purpose as an initial forum for discussions on the mechanisms involved in plant signaling. We now urge the proponents of plant neurobiology to reevaluate critically the concept and to develop an intellectually rigorous foundation for it.

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