František Baluška · Stefano Mancuso · Dieter Volkmann (Eds.)

Communication in Plants

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Neuronal Aspects of Plant Life

With 82 Figures, 5 in Color

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Preface

As we enter the new millennium, plant biology is witnessing dramatic advancements in studies related to the complex behaviour of higher plants which are now beginning to reveal intelligent behaviour. Surprisingly, it is plant ecology which is leading in the revelation that plants behave as though having conscious comprehension of themselves and of their environment. Charles Darwin was the first who noted the abilities of plants to communicate with their environment and translate this information into active movements of their organs (Darwin 1880).

Plants recognize other organisms such as bacteria, fungi, other plants, insects, birds, and animals that presumably also include us, humans (Takabayashi and Dicke 1996; Paré and Tumlinson 1999; Kessler and Baldwin 2001). For instance, to accomplish their sexual reproduction, plants rely on complex interactions with insects and birds. In order to achieve this, and as Charles Darwin was one of the first to show (Darwin 1862), plants generate specially shaped sexual organs which allow insects and birds access to their flowers. Moreover, plants reward these pollinators with nectar and other compounds which are both attractive and a necessary part of the diet of these insect/bird feeders (Cozzolino and Widmer 2005). Complex interactions have been recorded between insect pheromones and plant volatile semiochemicals (Reddy and Guerrero 2004). In the case of many *Arum* spp., the insect-attracting plant volatiles with a dung-like odour are exactly those chemicals which attract insects to animal dung where they would otherwise gather and reproduce (Kite et al. 1998). These plants are thus masters of a deceptive and intelligent strategy for their own reproduction. Moreover, plants appear to possess an innate type of immunity system which closely resembles that of animals (Nürnberger et al. 2004) and, interestingly in this respect, there are also several parallels between the recognition of self and non-self in plant breeding systems and histocompatibility in animals (Nasrallah 2005). Plant roots of *Fabaceae* can recognize and 'domesticate' *Rhizobium* bacteria within nodules, and the composite bacteroids then supply the host plants with nitrogen. Less well known, perhaps, is that some plants recognize and communicate with ants (and vice versa) which protect them against herbivores, pathogens as well as competing vegetation (Brouat et al. 2001; Dejean et al. 2005). The plants, in

turn, reward the ants by secreting nectar (Heil et al. 2005) and constructing special food bodies (Solano et al. 2005). Plants actively recognize the identity of herbivores and are then able to recruit their enemies (Arimura et al. 2005). For instance, plant roots attacked by insect predators release volatiles which then attract particular species of nematodes that kill these predators (Rasmann et al. 2005). In addition, by releasing volatiles into the aerial environment, plant shoots infected by pathogens inform their neighbouring plants about immanent danger and they can then increase their immunity against these pathogens (Paré and Tumlinson 1999; Reddy and Guerrero 2004). Intriguingly, the signature of released volatiles is characteristic for herbivore damage but is different from that resulting from a general wound response (Reddy and Guerrero 2004; Arimura et al. 2005). *Nicotiana attenuata* attacked by the hornworm, *Manduca sexta*, accumulates nicotine, which poisons acetylcholine receptors, and is thus toxic to those organisms which rely on neuromuscular junctions (Baldwin 2001). Interestingly in this respect, plants express neuronal acetylcholinesterase (Sagane et al. 2005) and use acetylcholine also for their neuronal-like cell–cell communication (Momonoki et al. 1998). Furthermore, during their phylogeny, plants can also switch from an autotrophic to a heterotrophic lifestyle – a feat which, in the case of parasitic or carnivorous plants, requires the active selection of suitable host/prey organisms (Albert et al. 1992).

Plants are extremely mechanosensitive. Their roots exhibit thigmotropism, which enables them to explore, with an animal-like curiosity, their environment in a continual search for water and solutes, and their shoots sometimes seek support by means of tendrils, assisted in this task by volatiles such as jasmonates. Root apices constantly monitor the numerous physical parameters of the soil and use this information in their search for better niches for survival and reproduction. In this behaviour, plant roots closely resemble fungi and, indeed, most roots enter symbiotic interactions with mycorrhizal fungi in order to increase their efficiency in obtaining critical ions such as phosphorus. In fact, roots might prove to be descendents of ancient fungi which, by entering into close association with their symbiotic photoautotrophs, have developed into heterotrophic roots – there are, after all, close resemblances between the anatomies and functions of apices of both rhizomorphs and roots (Botton and Dexheimer 1977) – while photoautotrophs have developed into the autotrophic shoots of the organisms now known as vascular plants (Atsatt 1988; Selosse and Le Tacon 1998; Heckman et al. 2001). This scenario is strongly supported by present-day pioneer colonizers such as lichens, which, just as was the case with early land plants (Yuan et al. 2005), are able to survive in even the most extreme of environmental conditions.

Literally, plants nourish the whole world. They intercept the light energy arriving on Earth from the sunbeams and transform it via energy-poor

inorganic compounds into energy-rich organic matter which then serves as the food for all heterotrophic organisms. Also, the gasoline which fuels many of Man's mechanical devices is of plant origin. Plants thus stand at the interface between a seemingly hostile and violent universe, and a fertile planet Earth teeming with life. We might postulate that if we could understand plants better, they could reveal to us something of the great mystery of life. Aristotle and his pupils were convinced that plants have complex inner life including thoughts, memories, dreams, and plans for the future. Unfortunately, our contemporary science considers plants rather as passive creatures to be exploited if discovered to be useful, and to be cleared away if not. However, their passivity – that is, their inability to change their location or to communicate via sounds – is only relative to the hyperactivity of human existence and the fleeting timescale of Man's artefacts. But the recent advances in ecology and phenomenology outlined above urge a change in this biased perception of higher plants.

We should also remember that action potentials, the very characteristic and rapidest way of neuronal communication, were discovered in plants in 1873 (Davies 2004). In those early days, the cellular basis of animal brains was not accepted and the neuronal processes in brains were just starting to be explored. Since then, a large amount of data has been accumulated on electric phenomena in plants (Meylan 1971; Davies 2004). Currently, new exciting discoveries are revealing that electrical signals modulate and control such basic physiological processes in plants as photosynthesis and phototropism (Koziolek et al. 2004; Volkov 2005). Unfortunately, the mainstream of plant biology has never completely accepted plant electrophysiology, so this field has survived in a quasi-dormant state up until now when exciting advances in plant biology are allowing the introduction of plant neurobiology as a newly emerging field of plant sciences. One foundation of this new science is the discovery that not only do plant cells express diverse neuronal molecules but that they also communicate together via plant synapses (Baluška et al. 2005).

These glimpses of the fascinating and breathtaking complexity of plants raise urgent questions which will dominate the whole field of plant biology in the next decades. In particular: Do plants have some type of neuronal system which resembles that which underlies the behaviour of animals? Conversely, if plants turn out to be 'brain-less', then the question will emerge where and how do they store and process the information which they obtain about both the abiotic and biotic environments, and how do they then use this information to optimize their future behaviour? Do plants feel (as suggested by Aristotle) and experience pain? Further: Do plants hear, and can they perceive odours? The truth is that we do not know, although their extreme sensitivity to mechanical vibrations indicates that they can perceive voices and their responses to volatile gases suggest they have a type

of olfactory response. Importantly, our lack of knowledge should not justify claims that plants do not possess these abilities and properties. In fact, their complex, rational, and surely intelligent behaviour suggests just the opposite. This is why we should be more sensitive to these issues and should commence a serious enquiry into these urgent questions, utilizing minds trained in the 'scientific method' but which can also clearly differentiate between speculation and hypothesis (Huszagh and Infante 1989).

Is it by chance that the Greek word 'neuron' refers to vegetable fibre? In fact, this happy and synchronistic coincidence might be taken to signify that the term plant neurobiology is fully justified! This book brings together all these new plant neuronal aspects and combines them with the classical plant electrophysiology. Plant neurobiology is commencing its emergence as a coherent science.

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Bonn, Bristol and Florence, July 2005

František Baluška, Peter W. Barlow, Stefano Mancuso and Dieter Volkmann

Finally, we wish to remember with affection Jolana Albrechtová (co-author of Chap. 25) who tragically died in a car accident on the 29th of November 2005 at the age of 39 years.

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1 The Green Plant as an Intelligent Organism

Anthony Trewavas

Abstract Intelligence is an aspect of complex adaptive behaviour and a term not normally applied to plants. This chapter indicates a change in concept is long overdue and if poets can recognize it (above) so should scientists. Networks that control information flow are described as intelligent and such networks exist in all single living cells and in more complex multicellular organisms. Phosphoneural bacterial networks are briefly considered and these exist in a slightly different molecular but more complex form in higher plant and animal cells. Intelligent behaviour involves the whole organism and such integration involves complex communication. Evidence that plants forage and act intelligently in acquiring resources is indicated. The phenotype is actively (not passively) constructed in response to a complex changing environment by decisions that best secure the well-being of the individual plant within the life cycle goal of optimal fitness.

More and more I have come to admire resilience Not the simple resistance of a pillow whose foam Returns over and over to the same shape but the sinuous Tenacity of a tree: finding the light newly blocked on one side It turns to another. A blind intelligence true But out of such persistence arose turtles, rivers, Mitochondria figs-all this resinous un-retractable earth.

Jane Hirshfield (2005)

1.1 Introduction

Intelligence is an aspect of adaptive behaviour, even in humans. Organisms that live in challenging but variable and competitive circumstances require forms of behaviour that rise to that challenge and must be equally flexible to improve fitness. Those best able to master their environment are those most likely to succeed in the Darwinian wars. "The success of a species depends on it performing well (surviving and producing offspring, i.e. fitness) in its own particular environment. And intelligence plays a critical part in this success." Warwick 2001, p. 9). Since the life cycle is probably a primary target of natural selection (McNamara and Houston 1996; Schlichting and Pigliucci 1998), efficient acquisition of necessary food resources during growth and development is an important aspect of subsequent fitness because there is a common relation between accumulated resources and subsequent sibling number (Bazzaz 1996).

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1.1.1 The Problems of Subjective Intelligence

Before embarking on a discussion of plant intelligence it is essential to indicate what is meant by the term. The actual word is derived from the Latin *inter legere* meaning simply to choose. Dictionary definitions of intelligence use terms such as self-recognition or capacity for understanding and are couched in human terms. These definitions are perfectly adequate for public discussion that usually only involves human beings. But for biologists who wish to investigate and understand intelligence in other organisms such definitions lack useful substance.

A common problem is subjective intelligence. For example the cybernetic ist, Warwick (2001, p. 9) states that "Comparisons (of intelligence) are usually made between characteristics that humans consider important; such a stance if of course biased and subjective in terms of the groups for whom it is being used." And as he shows is easily discredited. "When we compare the important aspects of intelligence, it is those which allow one species to dominate and exert power over other species that are of prime importance" (Warwick 2001). Bearing in mind the fact that plants dominate the planet, this statement is of importance for understanding plant intelligence. A further common assumption is that only organisms with brains (primates, cetaceans, crows) can be intelligent. Vertosick (2002) describes this as simple "brain chauvinism" and Schull (1990) goes further in stating that such views ascribe nerve cells as having some sort of vitalistic quality.

1.1.2 An Ability to Integrate a Multiplicity of Information into a Response Is an Important Intelligent Capability

Plants and animals are not passive objects in the face of environmental disturbance as indicated in the poem by Hirshfield (2005). They react and positively fashion themselves according to the information (signals) being received. Behaviour is the response to signals (Silvertown and Gordon 1989). Animals move when signalled, plants change their phenotype (Trewavas 2003). After that information is processed and integrated with the internal information, a response is constructed that improves fitness, the ultimate goal.

Green plants respond to numerous environmental biotic factors such as food resources (light, minerals, water) mechanical stimuli, humidity, soil structure, temperature and gases (Trewavas 2000; Turkington and Aarsen 1984). In each case the strength, direction, specific characteristics (e.g.

light wavelength) and intensity can be separately discriminated (Ballare 1994, 1999), and further complexity is added by virtue of the availability of resources being present either in fluctuating quantities varying from seconds to months, gradients with fluctuating intensity or a mosaic in the soil of vastly different concentrations (Bell and Lechowicz 1994; Farley and Fitter 1999; Grime 1994; Kuppers 1994; Pearcy et al. 1994; Robertson and Gross 1994) and others. Biotic signals are also sensed and acted upon and these include space; presence, absence and identity of neighbours (Tremmel and Bazzaz 1993); disturbance; competition (Darwinkel 1978; Goldberg and Barton 1992; Tremmel and Bazzaz 1995), predation and disease (Callaway et al. 2003; Turkington and Aarsen 1984). We understand little of the nature of the signals involved. Growth of individuals and neighbours continually and specifically changes the information spectrum.

There is no unique separate response to each signal in this complex but merely a response issued from an integration of all environmental and internal information. In the case of green plants, the visible response to signals is phenotypic plasticity (Bradshaw 1965; Schlichting and Pigliucci 1998; Sultan 2000). During information processing all signals meet somewhere in the cellular and tissue reactions that specify changes in form.

In seeking to understand the biological origins of human intelligence, Stenhouse (1974) described intelligence as adaptively variable behaviour during the lifetime of the individual in an attempt to discriminate intelligent behaviour from autonomic, that is unvarying, responses. Given the plethora of signals that plants integrate into a response, autonomic responses do not occur. Signal perception is instead ranked according to assessments of strength and exposure. But autonomic responses can be rejected; the numbers of different environments that any wild plant experiences must be almost infinite in number. Only complex computation can fashion the optimal fitness response.

1.1.3 Experimental Circumstances Can Be Misleading

When one factor is experimentally varied at a time in an attempt to simplify the complexity that wild plants normally experience, all those factors that do not vary are still sensed and integrated with the modified variable. For example, exposing a dicot seedling root to a gravitational signal leads to the textbook response of a resumption of vertical growth. But gradients of humidity, minerals, light, temperature imposed in a different direction or touch can override the gravity signal (Eapen et al. 2003; Massa and Gilroy 2003). Further complexity can result from an individuality in response to any one imposed signal (Trewavas 1998). Again for example with

gravity, the growth trajectories with which each root approaches the vertical can be individual (Bennett-Clerk and Ball 1951, referenced in Trewavas 2003).

The common use of statistics to obliterate individual variation leads to assumptions that the response to signals is always replicable. If the same signal and response are chosen, the same genotype, the environmental conditions are identical and the results are averaged statistically, this is no doubt true (but then the same can be said of an IQ test for human beings). No such simplicity of circumstance is available to an individual wild plant, which in meeting an almost infinite variety of environmental states must construct individual responses to improve its own fitness. No genome could contain the information that would provide an autonomic response to every environmental state. And even cloned individuals do not exhibit identical responses.

However, it is not just abiotic factors that are critical. Natural selection operates on individuals and Darwin (1859) considered that there is "a deeply seated error of considering the physical conditions of a country as the most important for its inhabitants whereas it cannot be disputed that the nature of other inhabitants with which each one has to compete is generally a far more important element of success." Considering the number of different species and individuals that co-exist, each one variable in phenotype and characteristics, any individual plant faces complexity not simplicity. Instead we are left only with the possibility of non-heritable (epigenetic) means whereby optimal fitness is achieved. Plants adequately meet the Stenhouse (1974) definition of intelligence.

1.2 Intelligent Behaviour of Single Cells

1.2.1 Molecular Networks in Single Eucaryote Cells

Cells are organized structures and vital properties result from the connections between the molecular constituents of which they are composed (Kitano 2002; Trewavas 1998). Numerous molecular connections integrate into a higher emergent organized order that we recognize as living. It is now known (1) that various steps in metabolism act like many Boolean computer logic gates such as AND, OR and NOR (Bray 1995) and are termed chemical neurons (Arkin and Ross 1994; Hjelmfelt and Ross 1992; Okamoto et al. 1987), (2) that these chemical neurons can act as pattern-recognition systems (Hjelmfeldt et al. 1993), (3) that proteins can act as computational elements (Bray 1995), and (4) that protein phosphorylation using about