Electrical Signals in Higher Plants

Barbara G. Pickard

Biology Department, Washington University, St. Louis, Missouri 63130, U.S.A.

Action potentials occur in a variety of situations in higher plants. Some such signals propagate; others evidently do not. Some have been demonstrated to play a role in sensory processes, but their functions are for the most part unknown.

Traditionally, in the minds of most biologists, one of the most striking differences between plants and animals is that animals can coordinate their activities by means of electrical excitations called action potentials, which propagate within a network of nerve cells, whereas plants have not evolved this means of coordination. Yet, almost everyone can immediately call to mind two plants in which conspicuous behavior is mediated by action potentials: the sensitive plant *Mimosa pudica*, with its leaves that collapse in response to even a very limited vibrational disturbance, and the insectivore *Dionaea muscipula*, which swiftly folds its leaves around insects that chance to walk across them. These cases have long been viewed as freaks of evolution. However, it is more plausible that they represent specializations based on an inconspicuous but generally distributed excitable mechanism or mechanisms. It is the purpose of this review to discuss three lines of evidence that action potentials may be of general occurrence in higher plants.

Spontaneous, Localized Electrical Activity

If one attaches an electrode to a leaf or stem, connects it to a suitable potentiometric amplifier and records the output, as shown in Fig. 1 with a seedling of the morning glory *Ipomoea hederacea*, within a few hours one is almost sure to find a variety of tiny voltage fluctuations which resemble action potentials. Of course, one's first concern is to clarify that the spontaneous fluctuations are not noise. Therefore, one may encase the plant and amplifier in a screen cage, protect the screen cage and recorder in a double-walled radio-frequency shielded room, filter the current which operates the recorder and lamps, and frequently check the recording system both by monitoring with the electrodes dipped in salt solution and by grounding the amplifier through a large resistance such as 10 Megohms. When, after hours of such checks, one is satisfied that the system is free of noise, one may reapply the electrodes to the plant and convince oneself that, although much of the time the plant is electrically quiet, it does indeed produce a variety of

fluctuations of voltage. These fluctuations appear to fall into three categories: repetitive spikes, solitary spikes, and general activity.

Fig. 2a illustrates the first category; it is excerpted from a train of signals which lasted over half an hour. The spikes of this sequence have rise times of less than 30 ms and recur about every 1.5 s. However, although the most pronounced feature of a train is the regularity of signals within it, great variability of signals is seen from train to train. In general, rise times range from 1 to 50 ms, and most commonly durations range from 100 to 400 ms. Separation intervals typically range
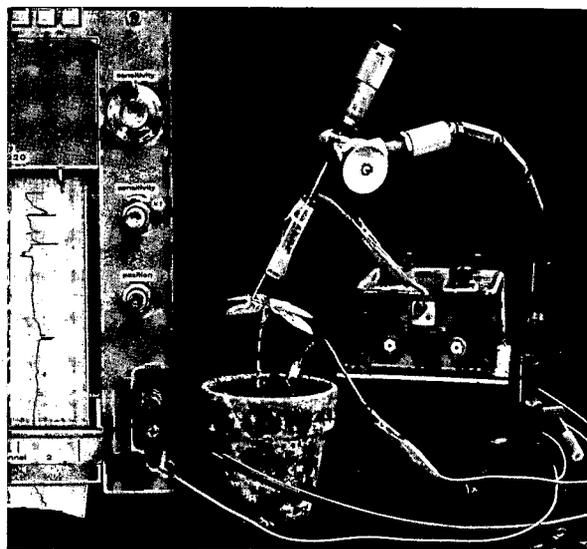

Fig. 1. A method of monitoring voltage fluctuations from a portion of a cotyledon (seedling leaf) of a young morning glory. A chlorided silver wire serves as a non-polarizable recording electrode. It is contained within a glass pipette filled with 0.1 M KCl solution; the tip of the pipette is plugged with the same solution solidified with 1 % agar. A solution-soaked cotton thread passes through the tip and rests against the surface of the plant. An amplifier of high input impedance (10^{13} Ω) receives the signal and passes it to the oscillograph. A reference electrode identical to the recording electrode is inserted in a glass pipe filled with 0.1 M KCl solidified with 1 % agar; the pipe is in turn inserted in the soil. The agar-filled pipe minimizes poisoning of the non-polarizable electrode by diffusion of substances from the soil

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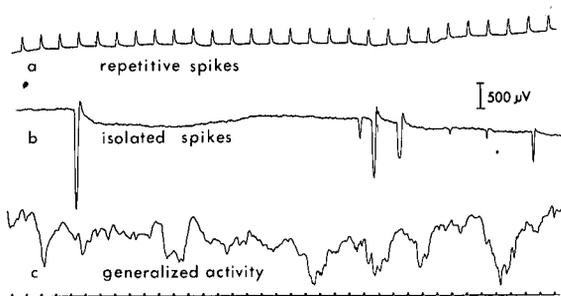
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Fig. 2. Signals obtained with a set-up such as that of Fig. 1 ([3] and unpublished recordings). Time ticks mark 5-s intervals

between 0.1 and 10 s. As detected with an extracellular electrode, the amplitudes of the fluctuations are always small—never over a few millivolts—suggesting that the signals might be emitted by only one or a small cluster of cells at a time. Moreover, simultaneous recordings from neighboring electrodes never give any evidence of propagation. Signals of this category, like the other fluctuations, can occur in either dark or light.

The second category of signals is the solitary spike, illustrated in Fig. 2 b. Solitary spikes may occur either in complete isolation or in erratic bursts. Individually occurring spikes can take any form seen in the spikes which occur in regular trains, but frequently have larger amplitude, slower time-course, and more symmetrical shape than do the repetitive spikes.

The third category of fluctuations, general activity, is characterized by such abundant and erratic fluctuations (see Fig. 2 c) that one suspects that it is simply the result of a large number of cells producing solitary spikes at frequent intervals. In the absence of exhaustive tests for biogenicity [3], one might easily mistake such general activity for electrical interference.

The tiny spontaneous signals have been reported for only a few plants—*Ficus elastica* [1, 2], *Ipomoea hederacea*, *Xanthium pennsylvanicum*, and *Pisum sativum* [3]. However, since the recent appearance of the cited publications, the fluctuations have been seen in several laboratories, with plants representing many families. Similar solitary fluctuations, incidentally, have also been described in the fungi *Phycomyces blakesleeanus* [4] and *Coprinus curtus* [5]. Thus, it is clear that the signals are of widespread distribution.

Critical tests of whether these several types of fluctuations are action potentials must of course await extensive intracellular recording. Heuristic arguments that the solitary spikes and general activity represent action potentials can be countered with the possibility that they are the incidental electrical expression of any of several kinds of physiological activity, but it is hard to imagine that the regular trains of uniform signals with rise times as brief as a millisecond could be the consequence of any type of event but membrane excitation. Recently, Jones, Novacky and Dropkin [33] have obtained intracellular recordings of trains of signals in giant transfer cells induced in the roots of *Impatiens balsamina* by a pathogenic nematode. Perhaps in the near future similar recordings will confirm that the signals occur in ordinary plant cells, and will permit investigation of the variables that trigger them.

Propagating Action Potentials of Unknown Role

If, in response to some clearly defined stimulus, a large voltage fluctuation of reasonably rapid rise and simple shape propagates away from the site of disturbance, one has no hesitation in describing it as an action potential. It is this type of signal which mediates the familiar motile behavior of *Mimosa pudica* and *Dionaea muscipula* (for reviews see [6–10]). Such signals have also been described in the stems of a variety of "ordinary" plants, such as the pumpkin *Cucurbita pepo* (e.g. [11–14]) and the squash *C. maxima* (e.g. [15]), the bean *Phaseolus multiflorus* [13], the sunflower *Helianthus annuus* [13], the umbellifer *Heracleum sibiricum* [16], and the tropical vine *Naravelia zeylanica* (early synonym: *Clematis zeylanica*) [17]. An action potential propagating along the stem of the latter plant (see Fig. 3) is illustrated in Fig. 4; this remarkably fine recording is reproduced from a paper published in 1938 [17]. This is by no means the earliest such report; a convincing descrip-
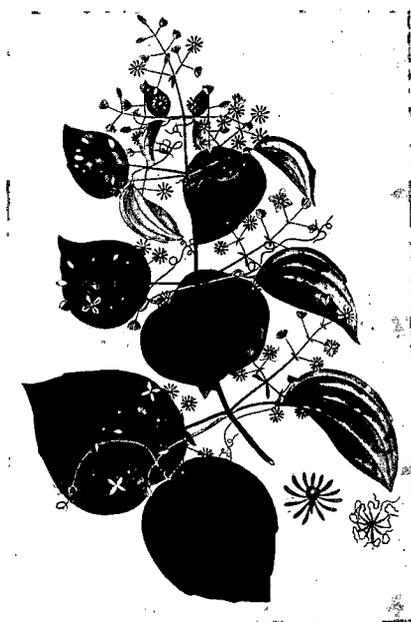

Fig. 3. Houwink's experimental plant *Naravelia zeylanica*, photographed from an early illustration (in which it was identified as *Atragene zeylanica*) [32]. When on a hot summer day one sprays the closely related, highly prized cultivars of the genus *Clematis* with drops of cold water from a garden hose, one may well elicit propagating signals such as those recorded from *Naravelia* and reproduced in Fig. 4
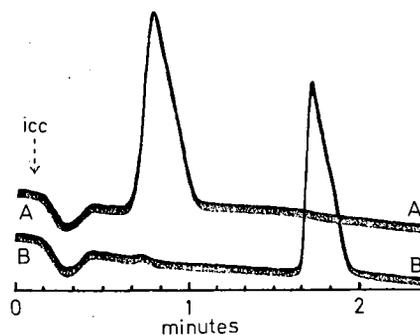

Fig. 4. A historic recording, published in 1938 by Houwink [17], of an action potential propagating in the stem of *Naravelia zeylanica* following stimulation with a drop of ice water. A and B are traces from electrodes nearer and farther from the site of stimulation, respectively

tion of propagating action potentials in *Cucurbita pepo* and other plants was published in 1928 [11], and a sketchy description of propagating action potentials in a cucurbit, a fern, mulberry, and other plants was published as early as 1907 [18]. In view of this abundant evidence, why has the concept that plants are excitable been so slow to permeate the lore of botany?

Doubtless, several factors have contributed to the neglect of this electrophysiological literature. Perhaps one of the most important problems is that several authors laid too little stress on the as yet inexplicable differences in responsiveness which are observed when plants from the same lot of seeds are grown under different temperatures, illumination, and so on. Even very suitable species for study, such as the pumpkin *Cucurbita pepo*, fail to yield action potentials except when grown under certain sets of conditions (cf. [10, 11, 19]). Then too, there is a temptation to believe that a phenomenon that cannot be reproduced at will under readily defined conditions must not be genuine. Certainly, there are many subtle ways in which artifact can invade an electrical recording.

But perhaps a more important factor lending doubt that action potentials were truly observed was the complicating occurrence of another type of propagating electrical disturbance in the same plants—a disturbance of relatively slow time-course and irregular propagation [e.g. [6, 20–22]]. It has been argued elsewhere [10] that this disturbance is the accompaniment to the movement of a wound hormone in the transpiration stream, and that under some circumstances it is accompanied by true excitation. Because this slow and irregular disturbance can be provoked in plants grown under conditions in which action potentials evidently cannot be elicited, it may well be that many careful and experienced electrophysiologists attempted to reproduce the reported experiments on excitability, but almost immediately encountered the wounding disturbance, failed to observe convincing action potentials, and concluded that the published evidence must be highly selected misrepresentations of the irregular voltage variation.

While the wound potential is of interest in its own right, it is of more immediate interest that at least two stimuli which elicit action potentials do not, under ordinary circumstances, appear to elicit wound potentials [10]. These are application of concentrated salt solution and sudden, localized cooling. Pooling information from reports of signals elicited by these two stimuli, one can learn that velocity of propagation typically ranges from about 1 to 30 mm s^{-1}, and that propagation may occur either up or down the stem. The rise time of a signal commonly falls between 1 and 5 s, though sometimes outside this range, and duration (for convenience considered to be the time between attainment of and return to half-maximal amplitude) typically varies from 1 to 30 s. Evidently, as in the case of the sensitive plant *Mimosa pudica* [20, 23, 24], the conductive cells are located in the phloem [16, 17, 25]. The distance of propagation is variable; sometimes signals have been reported to move through the entire shoot of a large plant (e.g. [23]), but in other cases the action potentials cannot pass beyond a node [17] or pass nodes only infrequently [10].

While chilling and application of saline are convenient means of eliciting action potentials, there is no evidence that these particular stimuli normally play a critical role in the life of the plant. Rather, it seems likely that excitable membranes of plants resemble those of animals in that a large number of miscellaneous variables can trigger response under artificial conditions. The twin questions of whether the action potentials are normal responses to internal or external variables which the plant encounters in its natural habitat, and of what consequences the action potentials might have for the tissue through which they propagate, remain for future exploration.

Action Potentials in Diverse Sensory Systems

The renowned propagating action potentials of *Mimosa pudica* and *Dionaea muscipula* obviously serve a sensory function. There are numerous other less familiar sensory systems which utilize excitable membranes; ealier literature has been well discussed by Sibaoka [8]. Three examples, two from the more recent literature, will now be discussed in order to illustrate the variety of sensory responses which involve action potentials and as a further indication of the very general distribution of excitability in the higher plants.

The first example is the mechanism employed by the insectivore *Drosera intermedia* (and many other species of *Drosera*) to deal with its prey [26, 27]. The leaf of *Drosera* is provided with an array of tentacles with glandular heads which secrete large drops of slimey mucilaginous material (Fig. 5). If an insect alights on the leaf, it is apt to become stuck and thrash about in an attempt to escape. As its wings and feet flail the glandular heads of the tall outer tentacles, each responds with a decrease in the potential which can be monitored with an electrode recording from the slime with respect to a suitable ground (Fig. 6). If the decrease, which is termed a receptor potential, exceeds a certain value, action potentials are initiated at the junction of the head and its stalk, and these propagate to the base of the stalk at approximately 10 mm s^{-1}. When they reach the base, they trigger a bending of the tentacle, and the bending
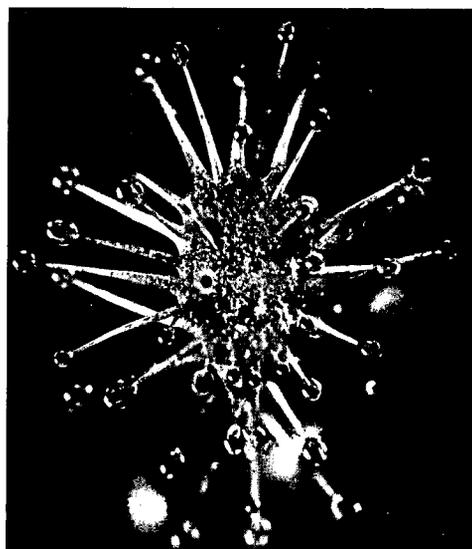

Fig. 5. A leaf of the insectivore *Drosera intermedia;* note the excitable tentacles with which it enfolds its prey
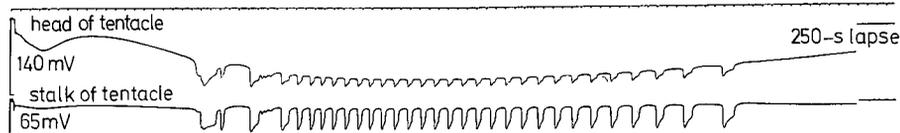
Fig. 6. Paired extracellular recordings from the head and stalk of a *Drosera* tentacle [26]. Stimulation was accomplished by rubbing the surface of the head with a wet cotton thread. The relatively slow and irregular voltage drop recorded from the head is the receptor potential, which elicits the action potentials seen superimposed on the receptor potential and seen propagating down the stalk. Ticks indicate 5-s intervals

results in the conveyance of the entangled insect toward the shorter tentacles in the center of the leaf. The central tentacles secrete digestive fluid into the aggregate of slime which by now surrounds the insect, and within a day or so an indigestible exoskeleton is the only visible hint of the insect's fate.

The most impressive aspect of electrical coordination by the *Drosera* tentacle is its complexity. The amplitude and duration of the receptor potential are known to control the frequency and number of action potentials which travel down the stalk, and these parameters in turn control the rate and extent of inflection of the tentacle. This example serves to indicate, then, that plants are indeed capable of developing reasonably elaborate electrical mechanisms of regulating their activities.

A second suggestive example is the occurrence of putative action potentials following frictional stimulation of the dark-grown seedling of the garden pea *Pisum sativum*. As the newly germinated shoot of a pea pushes upward through the overlying soil, it modulates its diameter according to the frictional resistance it encounters. The immediate cause of the modulation is the graded release of the gaseous hormone ethylene [28]. In extracellular recordings from the epidermis of the shoot, electrical quiet prevails in the absence of mechanical stimulation [29]. Within some seconds after the surface of the shoot is rubbed with a tiny rod, however, nonpropagating deflections with a rise time of about 0.2 s begin to appear. These soon become very numerous, and may continue to occur for several hours. The deflections have not been positively identified, but there is a strong possibility that they are action potentials. It is also possible, on the other hand, that they represent the release of vesicles or some similar membrane event. Among the reasons for interest in these elicited putative action potentials is their similarity to the isolated spikes which occur simultaneously in the photosynthetic pea shoot [3], and the possibility that they occur in a wide selection of plants (cf. [28]).

A third example is the pollen-triggered propagation of a single action potential down the style of the lily *Lilium martagon* reported by Sinyukhin and Britikov [30]. By means of extracellular electrodes recording from the stigma and from two positions along the length of the style, these authors claim that within a few minutes after pollen is deposited on the stigma, its potential shifts negatively. Following this shift, an action potential propagates from the tip to the base of the style, signaling an increase in ovarian respiration. Similar events were reported for two species of *Incarvillea*. It is independently known that pollen can trigger preparations for fertilization within the ovule long before arrival of the pollen tube with its contained

male nuclei (e.g. [31]); perhaps at least some such changes are mediated by an action potential rather than by a hormone as has been previously supposed.

Clearly, this system deserves much more extensive investigation. With relatively well defined stimulus and response, it should be easy to study. Though the precise role of the electrical message is not clear, it cannot be doubted that if reproducible it must be of great importance to the plant. The diversity of floral morphology and physiology should offer wide scope for comparative studies. All in all, it is surprising that no further reports on this topic seem to have been published.

Prospect

Although in many cases it is not yet demonstrated that the action potentials in plants have a function, in several situations a coordinating role is clear. It would be surprising indeed if in general action potentials should prove to be events without meaning to the plant. Rather, one may hope that the study of electrical signals will provide new insights about the integrative behavior of plants.

The expanding number of situations in which action potentials are known or thought to occur in plants indicates that at the level of membrane behavior plants and animals have more in common than has generally been assumed. Since the study of electrical signaling is so much more advanced for animals than for plants, it is obvious that the methods and models of zoologists will speed the progress of botanical electrophysiologists. On the other hand, it may well be that botanists will soon have something to offer their zoological colleagues in return. The cells of plants, unlike nerve cells, are not morphologically specialized for excitation and conduction; important knowledge could come from the comparative study of such relatively simple systems. Moreover, the study of hormonal secretion induced by nervous activity has often been held back by the small size and inaccessibility of the cells involved. In plants, which may in some instances have relatively large and accessible excitable cells, we may look for new opportunities to study the interface between electrical and chemical mechanisms of control.

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