THE ROLE OF ELECTRICITY IN PLANT MOVEMENTS

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(Accepted 24 August 1980)

SUMMARY

A survey has been made of the different types of reversible movements in the plant kingdom (including those of carnivorous traps, leaves, floral parts, root tips, cytoplasmic streaming, cilia and flagella) and it is suggested that many are mediated by changes in electrical potential. Many touch-sensitive movements in higher plants are regulated by propagating electrical signals (action potentials), which relay excitation from the site of stimulation to the motor organ(s), where collapse of sensitive motor cells is brought about. The resulting change in volume of the motor cells causes movement of the entire motor organ. In some cases additional localized changes in electrical potential (receptor potentials) can be induced by external stimuli, which convert specific characteristics of the stimulus into an electrical analogue before triggering an action potential.

The role of electrical activity in other plant movements is more speculative. Action potentials do not arise in light- or endogenous rhythm-regulated movements, but changes in the membrane potential of motor cells concerned with these movements may also help to drive the ionic transport which leads to their turgor-mediated motion. The significance of electrical activity associated with intracellular movements is less certain, but may become the focus of increasing attention as the regulation of actin-directed cellular movements is further investigated. Electrical impulses comparable to those in higher plants may, however, regulate ciliary and flagellar activity in the motile gametes and spores of lower plants. Thus, it is clear that electrophysiology is an important aspect of many plant movements, and bears a remarkable similarity to excitation in animal nervous systems.

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INTRODUCTION

The investigation of electric signals in plants has been neglected by many botanists particularly in the United Kingdom. This can be traced back to the opposition of the pioneering plant physiologists of the last century to any suggestion that plants could behave like animals (Simons, 1979). As a result, there has been a historical suspicion of nerve-like behaviour in plants, little helped by the often

Abbreviations: ACh, acetylcholine; AChE, acetylcholinesterase; ATP, adenosine triphosphate; EDTA, ethylenediamine tetraacetic acid; EGTA, ethylene glycol bis (β-amino-ethyl ether)-N,N’-tetraacetic acid.

0028-646X/81/010011 +27 $02.00/0 © 1981 The New Phytologist
Table 1. Latent time period between application of stimulus and start of motile response in reversible plant movements. Note that figures only provide a rough guide, as the latent period will vary with temperature and age of material. Data from an animal is included for comparison.

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gross exaggeration in popular literature. By describing the likely functions of electrical activity in reversible plant movements (that is, movements that can be performed more than once by the same motor organ), I hope to show that the plant kingdom has successfully exploited an electrical means of communication in many varied ways. The comparison between this activity in plants and nervous activity in animals is so striking that the relevant zoological terminology is also used in plant electrophysiology (see glossary).

The role of electrical activity in plant movements has been dealt with in previous reviews by Bunning (1959), Umrah (1959), Sibaoka (1969), and Pickard (1973). These articles concentrate on seismonastic movements in higher plants, but many other types of movement are performed by a variety of species throughout the plant kingdom. The stimuli that induce these movements and the speed of movement vary considerably, and can even match some of the fastest animal movements (Table 1).

The literature cited in this review is not meant to cover the whole field of electrophysiology of plant movements, and electrical data have been kept to a minimum. Reversible hygroscopic movements (such as the twisting of the awn of *Avena fatua*) and irreversible plant movements (such as fruit dehiscence in *Ecbalium elaterium*) have been omitted, as there is no evidence linking these movements with any electrical activity.

**GLOSSARY OF NOMENCLATURE**

*Action potential.* Originally this term was applied to electrical events in nerves which cause a biological action, such as muscle contraction. There is little agreement, though, in the literature about the definition of an action potential, but the following criteria should give a general description of its properties:

(i) transient and rapid change in transmembrane potential difference (Fig. 1);
(ii) a typical voltage curve usually features a sharp spike, followed by a more gradual return to the original ‘resting’ potential (Fig. 1);
(iii) can only be triggered after a critical level of excitation has been reached – a phenomenon known as the all-or-nothing response;
(iv) if sub-threshold stimuli are delivered over limited periods, sufficient excitation can be accumulated to trigger an action potential;

![Fig. 1. Action potentials recorded from the surface of the trap of Dionaea muscipula. The recording technique of Williams and Pickard (1972) was followed, using an extracellular electrode attached to a salt bridge and cotton wick, contacting the inside surface of one trap lobe. Mechanical stimuli were delivered by bending over one trigger hair twice with a glass rod. Each stimulus caused an action potential, but the electrical disturbance following the second action potential was caused by the trap lobes moving together and jerking the electrode (recording made by K. S. Rathore and P. J. Simons).](image-url)
(v) during and immediately after the passage of an action potential, it is not possible to elicit another action potential on the same membrane site without a rest (refractory) period; (vi) can be triggered by electrical stimuli.

**Depolarization.** A decrease in electrical potential. As plant cell interiors are negative with respect to the outside medium, depolarization is generally a change to a more positive potential.

**Facilitation.** An increase in membrane potential over limited periods of time with successive stimulation.

**Hyperpolarization.** An increase in electrical potential. As plant cell interiors are negative with respect to the outside medium, hyperpolarization is generally a change to a more negative potential.

**Receptor potentials.** Transient changes in membrane potential which convert stimuli into electrical analogues. Receptor potentials always precede, and often trigger, action potentials, but they do not have the all-or-nothing, nor the propagating, properties of action potentials. The voltage curve of receptor potentials is highly variable and reflects specific properties of the stimulus.

**Synaptic gap.** These are discrete, but microscopical, junctions between nerve cells. Excitation is carried across synaptic gaps by chemical messengers – the neurotransmitters.

**Variation potentials.** First described by Houwink (1935) in the wound-induced changes in membrane potential in *Mimosa*, these are apparently confined to plants. Variation potentials develop relatively slowly over a period of minutes, rather than seconds (as in action potentials). They do not conform to the all-or-nothing property of action potentials, but are conducted away from the site of stimulation. The shape of the voltage curve is extremely variable (hence the name), often consisting of many small spikes superimposed on a slowly developing hyper- or depolarizing potential.

**Neurotransmitters.** A group of diverse chemicals concerned with transmitting excitation across synaptic gaps, muscle end-plates, or nerve-gland junctions. Neurotransmitters transfer excitation from one cell to another by binding to specific receptor sites on the plasmalemma of the receiving cell. The resulting change in membrane permeability regenerates the action potential.

**Measuring electric signals in plants**

Voltage changes in plants can be detected using an electrode placed either in a plant cell (intracellular electrode) or resting on the surface of a cell or group of cells (extracellular electrode). The electrodes can be of two types: polarizable (electrochemically irreversible) or non-polarizable (electrochemically reversible). The potential of a polarizable electrode can change with time, or when current is passed through it, whereas that of a non-polarizable electrode remains virtually constant. As a result, if measurements of potential are made over relatively long periods (of
the order of > 60 s), it is necessary to use a non-polarizable electrode to ensure
that the change in potential is caused by the plant and not by the monitoring
electrode itself. On the other hand, if signals of only brief duration (< 60 s) are
being recorded (as is the case for many action potentials), it is possible to use either
type of electrode. More detailed explanations of polarization in electrodes are given
by Albery (1975).

Another source of uncertainty arises from potential differences at boundaries,
such as that between electrode and plant. These potentials are called junction
potentials and exist even when no current is being passed through the circuit.

Both electrode polarization and junction potentials can largely be overcome
using a silver–silver chloride electrode or a calomel electrode (composed of
mercury in contact with mercurous chloride), making contact with the plant via
a salt bridge containing concentrated potassium chloride in agar jelly and held in
a glass probe. In order to complete the electrical circuit a reference electrode is
placed in solution near the plant; this electrode must also be chosen to minimize
polarization and junction potentials. Silver–silver chloride or calomel electrodes
are suitable for this purpose as well, but the stainless-steel forceps used by some
researchers as reference electrodes are unsuitable as their electrical potentials and
stability are completely unknown.

The potential differences between recording electrode and reference electrode
are extremely weak and need to be amplified before they can be recorded. A
high-impedance amplifier (10^9 to 10^{11} \text{M} \Omega) is suitable for this purpose as it draws
virtually no current from the circuit whilst amplifying the signal picked up from
the plant. Once amplified, the signal can be displayed on a chart pen-recorder or
other recording instrument.

Further descriptions of some of these recording techniques are given by many
authors, including Hope and Walker (1975), Findlay and Hope (1976), Van
Sambeek and Pickard (1976a) and Young (1973). More detailed explanations of
electrode kinetics, junction potentials and other electrochemical phenomena are
given by MacInnes (1961).

**Carnivorous plants**

Many carnivorous plants use rapid trap movements to ensnare their animal prey,
and in some species it has been shown that the movements are mediated by
electrical activity.

The leaf blade of *Drosera* is covered by numerous stalked glands (the tentacles),
which secrete a sticky digestive fluid from the gland surface at the tentacle head. An insect touching a tentacle on the leaf margin will become stuck to the digestive
fluid and be pulled in towards the centre of the leaf as the tentacle gradually bends
inwards. In the more sophisticated bilobed leaf trap of *Dionaea muscipula* (Venus’
flytrap) an arthropod may bend over one or more of the trigger hairs located there,
and if sufficient deflection occurs within an interval of 1 to 25 s, the trap lobes snap
together and enclose the prey.

Despite their different traps, the electrical activities of *Dionaea* and *Drosera* are
remarkably similar. In both species mechanical stimuli initiate local graded
receptor potentials, transducing certain physical parameters of the stimulus into
electrical analogue form. In *Dionaea* the wave form of the receptor potential has
been shown to be a function of the strength and speed of the stimulus (Jacobson,
1965), but so far this has not been quantitatively tested in *Drosera*. Given adequate
stimulation, a receptor potential generates a propagating action potential in *Dionaea* (Benolken and Jacobson, 1970) or a series of action potentials in *Drosera* (Williams and Pickard, 1972). The action potential in *Dionaea* (Fig. 1) is relayed from the stimulated trigger hair across the trap lobes (Burdon-Sanderson, 1873), whereas in *Drosera* the action potentials are contained within individual tentacles (Williams and Pickard, 1972). The frequency and number of action potentials control the rate and extent of movement in both *Dionaea* (Burdon-Sanderson and Page, 1876) and *Drosera* (Williams and Pickard, 1972). In both species the motor tissues become increasingly receptive to successive action potentials in a manner akin to facilitation in animals.

Stimuli presented over a length of time in *Dionaea* appear to be stored in a simple ‘memory’, which detects the accumulation of sufficient excitation in the trap before initiating movement. For example, two stimuli delivered at room temperature within 1 to 25 s of each other are needed to initiate closure (Sibaoka, 1966), but 14 stimuli are needed before movement begins if the stimuli are delivered once every 20 min (Brown, 1916). Since trap closure depends on the number of action potentials elicited, rather than the number of stimuli received (Jacobson, 1965), the memory is likely to involve an electrical component. In contrast, the *Drosera* trap lacks this sort of memory, as the tentacle visibly responds to all the action potentials it receives, no matter how slight the resulting movement (Williams and Pickard, 1972).

The trap of *Aldrovanda* (the Water Wheel Plant) closely resembles that of *Dionaea*, and performs similar movements in response to the same stimuli (Ashida, 1935). Mechanically induced action potentials have also been detected in *Aldrovanda* (Williams, 1976; Sibaoka, 1980), preceding the sudden loss of turgor in the inner epidermis which allows the outer epidermis to expand, thereby bringing about movement of the trap lobes (Ashida, 1934). Since the mechanism of trap closure in *Aldrovanda* and *Dionaea* is likely to be similar, it is assumed that similar turgor losses induced by action potentials also account for trap movement in *Dionaea* (Lloyd, 1942). How the action potentials trigger the losses in turgor in the motor tissues of *Dionaea, Aldrovanda* and *Drosera* still remains a mystery.

Following the rapid trap closure in *Dionaea*, the lobes tighten together, largely controlled by a chemotropic mechanism which mainly responds to nitrogenous compounds diffusing out from the prey (Robins, 1976; Lichtner and Williams, 1977). Before it is killed though, the struggling victim probably delivers many more blows to the trigger hairs, thereby promoting trap tightening (Affolter and Olivo, 1975). Action potentials resulting from these additional stimuli (but not from the chemical stimuli) have been recorded by Affolter and Olivo (1975) using a silver wire glued to the outer trap surface. Lichtner and Williams also recorded mechanically induced action potentials during trap tightening using a non-polarizable Ag/AgCl electrode connected to the trap surface (presumably the outer surface, although this was not stated), but unfortunately they do not present their recordings. These action potentials were proposed by Lichtner and Williams also to initiate secretion of the acidic fluid out of the trap lobes; however, no test was made to see whether this fluid contained digestive enzymes. Both acidic fluid and digestive enzyme secretion are largely controlled by a chemical mechanism (again, not involving action potentials), which responds to the presence and concentration of nitrogenous substances derived from the prey (Robins, 1976).

Chemical stimulation also induces slow tentacle bending, tropic leaf margin rolling and increased gland secretion in *Drosera* (Darwin, 1875). It is not known
Electricity in plant movements

If electric signals mediate gland secretion in *Drosera*, but applied electric shocks have been claimed to increase secretion (Gardiner, 1885). Common chemoreceptor mechanisms in *Dionaea* and *Drosera* have been proposed by Williams (1976), but the processes involved in exciting these receptors are obscure.

Few electrical investigations have been made on the stimulation of other carnivorous plant traps. Williams (1976) failed to detect action potentials in the tentacles of *Drosophyllum* (a genus closely related to *Drosera*), which lacks both slow and fast movements, and which does not secrete from its stalked digestive glands in response to either mechanical or chemical stimuli (Darwin, 1875).

Mechanical stimulation of the sensory hairs of the underwater bladder trap of *Utricularia* triggers an astonishingly fast opening of the trap door, leading to capture of the prey. Transient changes in the electrical potentials of bladder wall cells during trap-door opening led Sydenham and Findlay (1973) to suggest that electrical excitation may mediate the movement. Although they were unable to detect an action potential following stimulation of the sensory hairs, their microelectrode measurements were made some distance from the trap door, where the excitation would be unlikely to pass. Unfortunately, insertion of an electrode in or near the sensory hairs triggers movement before recordings can be made. There is even doubt as to whether the triggering process is a purely mechanical one (as favoured by Lloyd, 1942), or involves an excitatory step. For example, bladders cannot be fired by an electrical stimulus, which would not be expected if the process involved an electrical signal. Also, Merl (1922) failed to reduce the trap sensitivity at the low temperatures that Sydenham and Findlay later reported. Therefore, until a way is found reliably and temporarily to inhibit the opening response of the trap sufficient to insert an electrode into the bladder wall, it is unlikely that the presence of any electrical excitation will be detected.

The sensitive three-celled ring trap of the carnivorous fungus *Dactylella* also responds to mechanical stimuli, rapidly inflating one or more of the trap cells so as to squeeze its prey tight. It is not known how the trap senses or responds so rapidly to its prey, but it may be worth considering the possibility of electrical excitation in future studies, since an electric shock has been reported to induce trap closure (Winkel, cited by Muller, 1958).

Thus, *Dionaea* and *Drosera* are the only carnivorous plants in which both receptor and action potentials have been recorded. Receptor potentials serve to recognize suitable prey – only arthropods of suitable size can sufficiently stimulate the trap to induce the necessary receptor potential required to trigger an action potential. In *Drosera* the prey can be detained for some time by the sticky gland secretions, and the slower electrical signals reflect the slow rate of tentacle movement. In contrast, *Dionaea* relies almost entirely on speed alone to capture its victims, and its electrical signals are correspondingly faster than those in *Drosera*. By storing information on the action potentials in a primitive ‘memory’, *Dionaea* is also able to ignore single, chance stimuli, which might otherwise trigger trap closure and so waste considerable metabolic energy.

**Mimosa**

The compound leaf of *Mimosa* is sensitive to a variety of stimuli – including electrical, mechanical, chemical, thermal, wounding and light – which induce rapid movements of the leaflets, pinna-raches or petiole. These movements are performed by motor organs termed pulvini, which subtend the junctions of the
petiole and stem (the primary, or main, pulvini), petiole and pinna-raches (the secondary pulvini), and pinna rachis and leaflets (the tertiary pulvini, termed pulvinules). Unless otherwise stated, *Mimosa* will refer to *Mimosa pudica*, although many other mimosas are seismonastic to some extent and will presumably share similar electrical behaviour.

There has been no report of a receptor potential initiated by a mechanical stimulus in *Mimosa*, but local changes in potential resembling receptor potentials were detected by Sibaoka (1954) following electrical stimulation of the petiole, although he did not describe these as receptor potentials. Once a critical threshold in the intensity of the receptor potential had been reached, an action potential was fired. Action potentials are also elicited by mechanical, chemical, thermal and wounding stimuli, and are rapidly conducted to the pulvini, where they initiate movement (Bose, 1907; Houwink, 1935). Action potentials arriving at the main pulvini fire a separate pulvinal action potential, which is only conducted through the lower half of the pulvinus, where sudden loss of turgor in the motor cells is elicited (Oda and Abe, 1972).

In addition, a wound stimulus also initiates a variation potential, which is thought to arise from the release of an unidentified hormone (the so-called Ricca's factor) into the transpiration stream (Houwink, 1935). The variation potential triggers an action potential in advance of its own passage, although only the variation potential is capable of passing through the entire pulvinus, regenerating an action potential on the other side of the pulvinus. In this way a wound stimulus can be carried throughout the entire shoot (Houwink, 1935; Sibaoka, 1953). Wound-induced variation and action potentials have also been detected in *Mimosa spagazzinii* (Umrath, 1928) and *M. invisa* (Umrath, 1931).

The main pulvinus starts to bend 70 to 120 ms following the onset of the pulvinal action potential (Oda and Abe, 1972), but the exact mechanism coupling the electrical excitation to motor cell movement is poorly understood. Three separate mechanisms have been proposed to account for the seismonastic response in *Mimosa*, and are briefly described here. Further details on the physiology of *Mimosa* leaf movements are given by Sibaoka (1969), Sanberg (1976) and Roblin (1979).

(1) Intercellular fluxes of K⁺ have been demonstrated in the main pulvini using cytochemical (Toriyama, 1955), X-ray fluorescence and radioactive label (⁴²K⁺) (Allen, 1969) techniques. Migration of K⁺ occurs predominantly out of the motor cells in the lower half of the pulvinus, resulting in an efflux (presumably osmotic) of water (Allen, 1969). Campbell et al. (1980) have recently used X-ray microanalysis and ion microscopy to examine pulvinules frozen at minus 150°C in order to fix the motor tissues during movement and to avoid redistribution of diffusible ions after the movement has occurred. They found that motor cells contained large amounts of K⁺ in their tannin vacuoles and that leaf movements were accompanied by lateral migration of K⁺ between opposing sides of the pulvinule. Toriyama (1962) found that K⁺ salts previously located inside vascular bundle parenchyma tissues were expelled into adjoining intercellular spaces and/or sieve tubes, following the passage of an action potential. Since these parenchyma tissues have also been shown to conduct the action potential in the petiole (Sibaoka, 1962), K⁺ efflux is likely to be involved in the action potential process. If the pulvinal action potential also involves K⁺ migration, it is tempting to speculate that generation of the action potential may directly alter the osmotic potential of the motor cells so as to cause the observed changes in turgor. However, the following evidence
suggests that the pulvinar action potential is not directly responsible for the ion fluxes associated with the turgor loss, for the following reasons.

(a) The flux of ions required to generate a pulvinar action potential is unlikely to be sufficient to account for the magnitude of the turgor loss. This can be best illustrated in the giant internodal cells of Chara, in which the passage of an action potential results in comparable fluxes of K\(^+\) and Cl\(^-\) (Hope and Walker, 1975). Only a slight loss of turgor accompanies the action potential (a pressure loss of 1 to 3 kPa was detected by Barry, 1970), although the magnitude and duration of the action potential (and hence the associated ionic fluxes) is far greater than in Mimosa action potentials.

(b) The K\(^+\) efflux continues long after the action potential has passed (Allen, 1969).

(c) The refractory period for the movement is over 30 s longer than the refractory period for the pulvinar action potential (Oda and Abe, 1972). Thus, recovery processes for the action potential and for the movement do not completely match up.

(d) The secondary pulvinus fails to respond to action potentials that pass through it (Simons, unpublished) even though there is no apparent cytological explanation for this (Fleurat-Lessard and Bonnaemain, 1978). Secondary pulvini do, however, perform nyctinastic ('sleep') movements, as do the pulvinules.

(2) Numerous small vacuoles have been observed to contract in the excitable cells of the upper half of the pulvinule (Weintraub, 1951). The contractile vacuoles are believed to expel water rapidly from motor-cell protoplasts (Weintraub, 1951), perhaps in a manner akin to the contractile vacuoles in protozoans and many unicellular algae (in which such vacuoles play an important part in osmoregulation). In at least one protozoan, Amoeba proteus, episodes of membrane depolarization are associated with emptying of the contractile vacuoles (Josefsson, 1966) and electrical stimulation of the contractile vacuoles of Paramecium caudatum accelerates their activity (Czarska, 1964), indicating that electrical events may control the activity of these vacuoles.

(3) Ca\(^{2+}\)-release from the membrane of a tannin vacuole into the central vacuole in the contracting motor cells of the main pulvinus has been claimed to contribute towards movement (Toriyama and Jaffe, 1972). Microfibrils in the central vacuole are believed to contract during the collapse of the motor cell (Toriyama and Satô, 1969), and it was suggested that the liberation of Ca\(^{2+}\) into the central vacuole may bind to, and activate, these microfibrils (Toriyama and Jaffe, 1972). Toriyama and Jaffe also suggested that Ca\(^{2+}\)-migration may facilitate the K\(^+\)-efflux from the cell. However, the material used by them had been treated with aqueous fixatives during cytochemical staining for calcium, so that artificial redistribution of Ca\(^{2+}\) may have occurred, and the significance of their findings is therefore not conclusive. Light-microscope and ion-microscope studies performed by Campbell, Sitka and Morrison (1979) on unstimulated main pulvini have located relatively large amounts of Ca\(^{2+}\) and K\(^+\) in the tannin vacuoles, plastids and cell walls of motor cells located in the outer zone of the cortex of the pulvinus. In contrast, cortical cells surrounding the central vascular strand (the inner zone) generally lack tannin vacuoles but contain a matrix material (microfibrils?) in their central vacuoles. Whether cells in this inner zone can be considered motor cells is not clear, but Campbell et al. (1979) found that their Ca\(^{2+}\) and K\(^+\) contents were segregated – Ca\(^{2+}\) was largely confined to the cell walls, whereas K\(^+\) was mainly detected in the
protoplasts. Ion microscopy has not been used yet to detect any changes in ion distribution following stimulation of the main pulvinus. The participation of Ca$^{2+}$ in the seismonastic reaction has been suggested by the inhibition of movement by a calcium chelating agent, 10$^{-6}$ M EDTA (Campbell and Thomson, 1977) (although Vanden Driessche, 1963, only obtained 'partial insensitivity' to mechanical stimuli using 10$^{-5}$ M EDTA), or by the calcium transport inhibitor, 10$^{-5}$ M lanthanum (Campbell and Thomson, 1977). However, in all these ion inhibitor studies it is difficult to known whether the observed effects are due to inhibition of the motor mechanism and/or the electrical excitability (and also whether the inhibiting agent is not affecting another, but completely separate, process). Apart from ion microscopy, movement of Ca$^{2+}$ during the seismonastic reaction might be established in future studies using electron microprobe analysis, aequorin microluminescence (as used by Ridgway and Durham, 1976, with slime moulds), chlorotetracyclic microfluorescence (as used by Reiss and Herth, 1978, on pollen tubes), or $^{45}$Ca autoradiography.

Much remains to be understood about the physiology of seismonasty in *Mimosa* and the role that electrical activity plays in it. Future studies might be expected to differentiate between cells of the outer and inner cortex of the main pulvinus since the microscopy studies of Campbell's group indicate that these two types of cell may differ in function.

Seismonastic leaf movements also occur in several other members of the Mimosaceae and also of the Caesalpininaeae, Fabaceae and Oxalidaceae, although their sensitivity and range of leaf movement varies considerably. Action potentials associated with seismonasty have been recorded in *Neptunia plena* (Umrath, 1928), *Biophytum sensitivum* (Bose, 1907; Umrath, 1928; Guhathakurta and Dutt, 1963) and a species of *Biophytum* originally identified as *B. somnulentum* (Sibaoka, 1973), but which was later established as *B. dendroides* by J. F. Veldkamp (Sibaoka, pers. comm.). In these species pulvinule movements are elicited by action potentials, but the larger pulvini at the base of their pinna-raches remain stationary (although they can perform nyctinastic movements).

Sibaoka (1973) also recorded local changes in potential in *Biophytum dendroides* in response to electrical stimulation, and these can be identified as receptor potentials. The intensity of the receptor potentials reflected the intensity of the stimuli, and when stimulation exceeded a threshold an action potential was triggered. This pattern of excitation is similar to that in *Mimosa*, indicating that a common receptor mechanism may exist in other seismonastic leaf movements.

Seismonasty (and its associated electric signals) has been claimed to protect young leaves from possible insect attack by scaring or shaking off intruders, as in *Mimosa pudica* (Pickard, 1973). However, it is difficult to imagine an insect being evicted from the leaves of say, *Oxalis acetosella*, which requires repeated shaking before its leaves begin even slowly to drop (Stiles, 1936). The function of seismonasty in some species is therefore curious.

**Leaf Movements Regulated by Light and Endogenous Rhythms**

Many leaf movements result from co-ordinated changes in motor cell turgor on opposite sides of a pulvinus. Changes in turgor in *Albizzia julibrissin* (Satter and Galston, 1971), *Samanea saman* (Satter et al., 1974) and *Trifolium repens* (Scott, Gulline and Robinson, 1977) are caused by the osmotic passage of water following large fluxes of K$^+$ in or out of pulvinar motor cells. Similar K$^+$-directed water
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Movement has been found during the tropic sun-tracking and cupping movements of *Lupinus arizonicus* (Wainwright, 1977). The displacement of charge caused by the movement of K\(^+\) is largely balanced by Cl\(^-\)-migration in the same direction in *Albizia* (Schrempf, Satter and Galston, 1976) and in *Samanea* (Satter et al., 1977). Although ion pumping is thought to account for the K\(^+\)-flux during rhythmic and phytochrome-mediated nyctinastic closure in *Albizia* (Satter and Galston, 1973), the forces regulating the ion pumps and the transport of K\(^+\) during other phases of leaflet movement, are obscure. Lanthanum inhibits nyctinastic leaflet closure of *Mimosa* leaves (Campbell and Thomson, 1977), sun-tracking and cupping leaf movements in *Lupinus* (Wainwright, 1977) and nyctinastic and endogenous rhythm (but not phytochrome-promoted) leaflet movements of *Albizia* (Campbell, 1979). Thus, Ca\(^{2+}\) transport may play an important role in many leaf movements, but movement of Ca\(^{2+}\) was not detected during movement of *Albizia* pulvini using electron microprobe analysis (Satter, Marinoff and Galston, 1970).

The older literature indicates that changes in potential measured on the outside of a pulvinus precede the movement of the pulvinus (for example, Yamaguti, 1932). It has since been demonstrated that intracellular potentials of motor cells on opposite sides of the pulvinus of *Samanea* (Racusen and Satter, 1975) and *Trifolium* (Scott et al., 1977) oscillate rhythmically during leaf movements regulated by endogenous rhythms. The change in electrical potential of *Samanea* flexor motor cells (those that contract during leaflet closure) matches the leaflet movement, increasing in polarity during leaflet opening and depolarizing during closure (Racusen and Satter, 1975). Flexor motor cells (those that expand during leaflet closure) also respond rapidly to switches between white light and darkness, and between red and far red light (Racusen and Satter, 1975). The electrical potential of the extensor motor cells (those that expand during leaflet opening) are about 8 h out of phase with the rhythm in flexor cell potential, increasing in potential just before opening is detectable. Changes in electrical potential may help to drive K\(^+\) ions into or out of the motor cells, but the extent of electrical control over K\(^+\) movement is not certain. Studies on the photochrome-mediated closure of *Samanea* leaflets indicate that K\(^+\) flux is much slower than the change in potential (Racusen and Satter, 1975), suggesting that other events, possibly electrical, precede and cause the K\(^+\) flux. It would be interesting to see whether leaflet movements can be altered in any way using electrical methods, such as voltage clamping, in order to test for the significance of the electrical potential of the motor cells in pulvinar movements.

One possible mechanism for driving rhythmic changes in electrical potential in pulvini has been proposed by Racusen and Galston (1977), who found that depolarization of motor cells by applied sucrose was strongly dependent on the pH of the bathing medium. The magnitude of the sucrose-induced depolarization varied in a circadian manner, and it was suggested that sucrose may be co-transported across motor cell plasmalemmae with protons. The resulting change in membrane potential may contribute towards the rhythmic changes in pulvinar potential, but this needs further verification.

The co-ordination of ionic fluxes throughout the pulvinus is also unclear. For instance, stimulation of *Samanea* pulvini with light fails to elicit action potentials (Racusen and Satter, 1975), but in *Mimosa* stimulation of a localized area of a pulvinule with a narrow beam of light induces a bending response throughout the entire pulvinule (Watanabe and Sibaoka, 1973). An external stimulus can therefore...
be conducted through the motor tissues of the pulvinus, but the nature of this conduction is unknown. Similarly, the mechanism co-ordinating complementary changes in ion fluxes on opposite sides of a pulvinus is also unknown, although recent evidence using X-ray microanalysis of frozen pulvini of Samanea has shown that the apoplast of the motor tissue is an important pathway for the lateral migration of K⁺ and Cl⁻ across the pulvinus (Satter, Campbell and Garber, 1980).

**Tanada effect**

Tanada (1968) first described phytochrome-mediated adhesion of mung bean root tips to charged glass surfaces. He found that the red-light-induced adherence of root tips required a specific composition of the solution bathing the root tips, and a phosphate pretreatment of a glass beaker. The adhesion of the root tips is associated with a sudden change in surface charge of the epidermal cells of the root cap (Racusen and Etherton, 1975), although measurements of the electrical potential on the root surface have shown only small (about 1 mV) changes in potential (Jaffe, 1968). In addition, phytochrome-mediated adhesion is also associated with an increase in acetylcholine content (Jaffe, 1970), H⁺ release into the bathing solution, increased O₂ consumption and increased ATP consumption (Yunghans and Jaffe, 1972). These findings suggest a causal sequence of events which may have some features in common with nerve excitation, although there is no conclusive evidence to support this notion.

It would be interesting to see whether the light-induced adhesion of Spirogyra filamentous cells to glass, as reported by Nagata (1977), is also mediated by electrical events similar to those in mung bean root tips. In this connection Fujii, Shimmen and Tazawa (1978) have reported light-induced changes in membrane potential in Spirogyra filamentous cells.

**Floral parts**

Certain members of the following families perform rapid and reversible floral movements in response to mechanical stimulation, in order to promote pollination: stamen filament movements in the Berberidaceae, Cactaceae, Cistaceae, Compositae, Cucurbitaceae, Malvaceae, Portulaceae, and Tiliaceae; stigma movements in the Bignoniaceae, Lentibulaceae, Liliaceae, Martyniaceae and Scrophulariaceae; style movements in the Compositae and Mimulaceae; fused stamen/style movements in the Stylidiaceae; corolla tube contraction in the Gentianaceae; labellum movements in the Orchidaceae.

Few electrical investigations have been made on these motor responses, but in those cases that have been investigated, electrical changes have been found to precede movement. The contractile stamen filaments of Sparmannia africana and Berberis vulgaris generate a localized action potential at their bases when they are mechanically or electrically stimulated (Bunning, 1934). The bending movement closely follows the passage of an action potential, and as movement has not been observed without recording a preceding action potential, it seems reasonable to assume that the action potential is a requirement for movement. Repeated action potentials do not elicit further movement until the motor tissue has completed their own refractory period (Umrath, 1937). There is also a significant lag phase between the passage of an action potential and movement in both Sparmannia (Bunning, 1934) and Berberis (Bunning, 1959). Thus the mechanism coupling the action
potential to movement is not likely to be a simple one and is not yet understood. Electrical shocks also induce stamen contraction in *Centauraea* (Burdon-Sanderson, 1911; Stern, 1924) and *Mahonia* (Millet and Thibert, 1976), and action potentials associated with stamen bending have recently been detected in *Mahonia* (Millet, pers. comm.). Sinyukhin and Britikov (1967a, b) have also measured localized action potentials following mechanical stimulation of the stigmatic lobes of *Incarvillea*, prior to the lobes shutting together.

The mechanism controlling the changes in motor cell turgor of a motile floral organ has recently been investigated by Findlay and Pallagby (1978) in the extraordinarily rapid bending of the fused stilar-stamen column of *Stylidium graminifolium*. Stimulation of the region around the base of the column causes a rapid loss of K\(^+\) and Cl\(^-\) from the motor cells, sufficient to account for the corresponding water loss. There has been no published account of electrical activity associated with this movement, but electrical shocks also initiate movement (Kabasch, 1861; Findlay and Findlay, 1975), although this alone cannot be taken as proof of mediation by endogenous electrical signals. On the basis of investigations on *Berberis*, *Sparmannia*, *Mahonia* and *Incarvillea* it is likely that many, if not all, seismonastic floral movements are mediated by electrical impulses, but so far this prospect has not been fully explored.

**STOMATA**

Active uptake of K\(^+\) into guard cells is now accepted as providing the necessary osmoticum required for guard cell expansion (and hence opening of the stomatal pore), while loss of K\(^+\) accounts for the loss of guard cell turgor (pore closure). It has been suggested that the movement of K\(^+\) is balanced by a concomitant transport of anions (particularly Cl\(^-\)) in the same direction and of cations in the opposite direction, or synthesis of malate anions in the guard cells (see Hsiao, 1976; Raschke, 1976). However, the mechanism driving the transmembrane K\(^+\) flux is far from clear.

Relatively few electrophysiological studies have been carried out on stomata, probably because the thickness of the cell wall presents a formidable obstacle to successful microelectrode impalement. Penny and Bowling (1974) found no difference in electrical potential between guard cells, subsidiary cells and surrounding epidermal cells during equilibrium states, and Pallagby (1968) could not detect changes in guard cell potential with changes in light intensity or in the presence of bicarbonate ions. However, substantial and rapid changes in guard cell membrane potential following switches between light and darkness have been reported for *Tradescantia* (Gunar, Zlotnikova and Panichkin, 1975) and *Allium* (Zeiger *et al*., 1977; Moody and Zeiger, 1978). Zeiger’s group considered that the rapidity of the electrical response (having no detectable latency period) was probably caused by an electrogenic proton pump at the plasmalemma, although the mechanism triggering this pump is not known.

The role of the membrane potential in guard cell movement is still highly speculative. Zeiger *et al*., (1977) and Dittrich, Mayer and Meusel (1979) consider that the increase in membrane potential can drive the movement of potassium ions into the guard cells. However, Raschke and Humble (1973) found that increasing the level of K\(^+\) in the solution bathing epidermal strips of *Vicia* increased the amount of H\(^+\) released. Fusicoccin-induced acceleration of K\(^+\) uptake is also correlated with an increase in H\(^+\) expulsion (Raschke, 1976); these results suggest
that K⁺ exchanges for H⁺ at the guard cell plasmalemma instead of (or in addition to) the proposed proton pumping. Nevertheless, rapid electrical responses at the guard cell plasmalemma may be involved with transducing the environmental signals which trigger the subsequent ion fluxes.

Other electrical investigations of stomata have relied on application of electrical shocks to the leaf epidermis. Darwin and Action (1894) were the first to report the induction of stomatal closure by electrical shocks in Allium, and similar results have been obtained by other workers (Köketsu, 1923; Umrath, 1959; Pallaghy, 1968), but it is not known whether these shocks mimic natural processes involved in guard cell movement, or whether they introduce artificial excitation.

The nature of the communication between stomatal complexes has been poorly studied. A local reduction in light intensity on one part of a leaf can induce a decrease in stomatal aperture in another part, even when separated by an area under high light intensity (Heath and Russell, 1954). The intercellular spaces of the leaves were continuously swept with CO₂-free air so as to eliminate the possibility of stimulus transmission by reductions in CO₂ levels, and Heath and Russell proposed that either a chemical or electrical messenger could account for this phenomenon. Unfortunately, the speed of stimulus conduction was not reported, but propagating transient photo-induced changes in potential have been detected in many photosynthetic tissues and are able to travel through darkened or non-green cells (for example, Waller, 1925; Brinkmann and Lütte, 1974). It would be interesting to know whether these photo-induced electrical fluctuations could induce changes in guard cell potential, possibly leading to stomatal pore movement.

Wounding leaves results in the conduction of a stimulus which induces partial stomatal closure (Scarth, 1932; Williams, 1948). It is strange, though, that the slow conduction of the stimulus (about 0.1 mm s⁻¹) measured by Williams in Pelargonium zonale did not match the transport of Ricca’s factor (about 3 to 4 mm s⁻¹) that Van Sambeek and Pickard (1976b) found was released when leaves of several species of higher plants were wounded, and which led to the propagation of both variation and action potentials. This discrepancy may be partly explained by the lag period (about 1 to 5 min) between receipt of the wound-induced excitation and the start of stomatal movement, that Williams recorded using a pressure sensing porometer. Van Sambeek and Pickard (1976c) also found that arrival of a variation potential at a leaf distant from the one wounded was soon followed by increased respiration, decreased photosynthetic CO₂ uptake and decreased transpiration. Whether the decrease in transpiration was directly caused by the variation potential or by the increase in ambient CO₂ concentration, was not ascertained. Since applications of Ricca’s factor induces stomatal closure in a variety of species (Umrath, 1966) and depolarization of individual leaf cells (Cheeseman and Pickard, 1977), electrical events may play a part in the stomatal response to wounding.

There have also been reports of seismonastic reactions in stomata (for example, Knight, 1916), and although this response may be partly due to bursts of CO₂ released as a result of mechanical stimulation (Williams, 1949), studies using different wind velocities have indicated that stomata are at least partially sensitive to mechanical stimuli (Martin and Clements, 1935). Possible electrical activity associated with the stomatal response to mechanical stimulation has not been investigated so far.
The relationship between cytoplasmic streaming and associated electrical activity is still very confused. Studies of cytoplasmic streaming in plants have concentrated on slime moulds and the internodal cells of the characean algae; the mechanics and biochemistry of the motive forces that drive streaming in these organisms have been recently reviewed (R. D. Allen and N. S. Allen, 1978; N. S. Allen and R. D. Allen, 1978; Vanden Driessche, 1979). In slime mould plasmodia cytoplasmic streaming back and forth along protoplasmic strands is responsible for the slow movement of the plasmodia, and occurs as a result of strands of endoplasm being squeezed by alternating contractions of Ca^{2+}-sensitive actomyosin fibres at the two ends of the strands (Nachmias and Asch, 1974; Fleischer and Wohlfarth-Botterman, 1975). Cytoplasmic streaming of plasmodia is highly sensitive to applied calcium ions and ceases at concentrations < 10^{-6} M (Hatano, 1970). The membrane potentials of the two ends of the endoplasmic strand of *Physarum polycephalum* have been recorded using external electrodes and found to oscillate with approximately the same frequency as the streaming rhythm (Iwamura, 1949; Kamiya and Abe, 1950; Ridgway and Durham, 1976). In addition, Ridgway and Durham (1976) detected oscillations in endogenous Ca^{2+} concentrations using an aequorin-luminescence technique, which matched the frequency of the electrical rhythm. As maximum Ca^{2+} concentrations precede maximum recordings of hyperpolarizations in the amoeba *Chaos chaos*, Nuccitelli, Poo and Jaffe (1977) suggested that current enters during the rise in Ca^{2+} due to a local Ca^{2+} leak at the plasmalemma, and that a similar sequence of events may occur in *Physarum*. Cobbold (1980) though, has recently found from calibrated aequorin measurements on the amoeba *Chaos carolinense* that cytoplasmic movement occurs without changes in the free Ca^{2+} concentration of the cytoplasm, and suggested that previous proposals of calcium control of motility in other types of cells based on aequorin studies are now in doubt.

However, a causal link between electrical events and Ca^{2+} transport is far from certain. Kamiya and Abe (1950) found that the electrical rhythm of *Physarum* plasmodia lagged behind the streaming rhythm. The electrical oscillations also remained unaltered whether the cytoplasm was allowed to flow freely, brought to a standstill, or even reversed by means of pressure applied across the ends of the strand. This evidence suggested that streaming and the electrical potential were independent of each other, but Kishimoto (1958) found that the electrical rhythm could be affected by applied pressures and argued that Kamiya and Abe’s results were largely invalidated. Nevertheless, Kamiya and Abe also found that a potential difference of between 0.01 to 4 V applied for a short period across a plasmodium did not produce any noticeable effects on the pattern of streaming. In addition, Iwamura (1949) found that the electrical rhythm was disrupted by applying 1 M NaOH or HCl, but streaming was unaffected. These two observations seem to indicate that the electrical potential does not directly control protoplasmic streaming. Whether streaming causes the rhythm in potential is not known for slime moulds, but comparable oscillations in electrical activity continue in *Nitella* when streaming is inhibited by application of cytochalasin B (Ogata and Kishimoto, 1976). If this is also true of slime moulds, then streaming and membrane potential are likely to be governed by a common, but separate mechanism.

Further evidence against electrical mediation of streaming in slime moulds comes from studies on the chemotaxis of plasmodia. Once a critical threshold of
a particular chemical has been exceeded, a receptor potential is triggered and is shortly followed by a change in the rate and direction of streaming, resulting in a chemotactic response (either towards or away from the chemical stimulus) (Ueda et al., 1975). It is puzzling, though, that no matter whether the chemical stimulus induces repulsion or attraction of the plasmodium, it always triggers a depolarizing receptor potential. In addition, increasing the concentration of the chemical stimulus beyond the receptor potential threshold increases the magnitude of the potential, but not the magnitude of the streaming response (Ueda et al., 1975). The chemically induced change in membrane potential may therefore serve no function in chemotaxis, and may only be the insignificant byproduct of another process. For example, the co-transport of a sugar molecule with a proton may depolarize the plasmalemma (as has been shown in another fungus, Neurospora – see Slayman and Slayman, 1974).

In contrast, evidence in favour of a causal sequence of events linking changes in membrane potential to streaming has been found from studies of streaming in the giant characean internodal cells. Electrical or mechanical stimuli can trigger an action potential which is then conducted along the plasmalemma, and sometimes passing beyond into neighbouring cells. The start of an action potential always precedes the stoppage of streaming, which usually occurs at the peak of the action potential (Tazawa and Kishimoto, 1968). Pickard (1969), though, was able to induce stoppage of streaming in Nitella without triggering an action potential, by clamping the voltage of the vacuolar potential and steadily depolarizing the potential over relatively long (1000 s) periods. Depolarization of the vacuole beyond a critical voltage induced an abrupt halt in streaming, and Pickard reasoned that changes in the plasmalemma conductance to ions accompanying the passage of an action potential was responsible for the stoppage in unclamped cells. Barry (1968) had previously reached a similar conclusion, as bathing Nitella cells in Ca$^{2+}$, Sr$^{2+}$, Mg$^{2+}$ and Ba$^{2+}$ chlorides resulted in increased action potentials in the above order, but only action potentials triggered in Ca$^{2+}$ or Sr$^{2+}$ media were capable of stopping streaming. So it appears that the action potential in some way opens up a passage in the plasmalemma to allow entry of Ca$^{2+}$, where it somehow reacts with an actomyosin contraction system (see N. S. Allen and R. D. Allen, 1978; Vanden Driessche, 1978).

How membrane permeability to specific ions is suddenly increased at a critical threshold of electrical excitation is not known, but is reminiscent of smooth muscle contraction in which actomyosin contraction is also triggered by a critical membrane voltage in an all-or-nothing fashion. However, contractions in both muscle cells and in slime moulds are activated by Ca$^{2+}$ concentrations > $10^{-7}$ M, whereas similar Ca$^{2+}$ concentrations in characean cells inhibit streaming (and also autonomous chloroplast movements) (Hayama, Shimmen and Tazawa, 1979). Cytoplasmic streaming also continues unabated in cells treated with the Ca$^{2+}$-chelating agent EGTA, even following excitation (Tazawa, Kikuyama and Shimmen, 1976). So it appears that a critical Ca$^{2+}$ concentration can turn off the motive force in characean cytoplasmic streaming and that electrical events are unlikely to play a part in internally regulated streaming, but are involved in the perception of at least some external stimuli.

Fibrils similar to those responsible for streaming in the characean cells and slime mould plasmodia have also been observed in higher plants (O'Brien and McCulley, 1970), and which may also contain actin (see Hepler and Palevitz, 1974). Little is known about the control of streaming in higher plants, but electric shocks have
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been found to stop streaming in the leaf cells of *Elodea* and young staminal hairs of *Tradescantia* (see Pfeffer, 1906; Kamiya, 1959). It is not known whether endogenous electrical activity also affects streaming, but the controlling mechanism is likely to be similar to that in characean cells. For example, Forde and Steer (1976) demonstrated that streaming in *Elodea canadensis* was inhibited by the same agents that inhibit characean streaming, namely cytochalasin B (an inhibitor of actin activity), or $10^{-5} \text{ M Ca}^{2+}$, whilst $10^{-3} \text{ M EDTA}$ or $\text{Mg}^{2+}$ (concentration not given) stimulated streaming (as in *Chara* – see Williamson, 1975).

**TACTIC MOVEMENTS**

The complete mechanisms of ciliary and flagellar beating is not understood but Naitoh and Eckert (1974) have established that both orientation and frequency of ciliary beating in the protozoan *Paramecium* are controlled by electrical impulses carried along the plasmalemma. Adverse external stimuli (such as mechanical knocks) cause increased membrane permeability in the region stimulated. As a result, an ionic current is generated that creates a depolarizing receptor potential, which is then conducted electrotonically along the membrane (without the need for an all-or-nothing action potential). $\text{Ca}^{2+}$-specific ion channels in the membrane are sensitive to changes in the membrane potential and depolarization results in a rapid and large influx of $\text{Ca}^{2+}$. The subsequent rise in intracellular concentration activates an ATP-dependent motor process bringing about reversal of ciliary beating, which results in the tactic movement of the organism away from the stimulus. The rise in internal $\text{Ca}^{2+}$ concentration finally induces a transient increase in $\text{K}^{+}$ conductance, resulting in a return of the membrane potential to its original ‘resting’ level, so terminating the $\text{Ca}^{2+}$-mediated ciliary reversal.

A second mechanism is involved in controlling the frequency of ciliary beating in *Paramecium*. Hyperpolarizing currents, or depolarizing currents greater than several mV, increase the beating frequency, whereas milder depolarizing currents inactivate or slow cilia. The beating frequency is closely related to intracellular $\text{Ca}^{2+}$ (and possibly $\text{Mg}^{2+}$) concentrations, so that the frequency may also be coupled to the membrane potential through $\text{Ca}^{2+}$ (and possibly $\text{Mg}^{2+}$) fluxes (Eckert, Naitoh and Machemer, 1976).

Similar electrical events may also control flagellar movements and recent evidence from a number of studies on unicellular plant cells supports this view. $\text{Ca}^{2+}$ has been shown to play an important part in the phototaxis of *Chlamydomonas*, by acting as the agent coupling flagellar reversal to photostimulation in a manner akin to the role of calcium in coupling ciliary reversal to membrane stimulation in *Paramecium* (Schmidt and Eckert, 1976). Applied electric fields inhibit the phototactic response of *Chlamydomonas* (Marbach and Mayer, 1971), and flagellar movements in *Euglena* in an electric field mimics the photophotic response of the flagellum (Bancroft, 1913). Injection of a hyperpolarizing current into *Euglena* results in a reduced or inactivated flagellar activity, whereas injection of a depolarizing current increases flagellar beating (Nichols and Rikmenspoel, 1977). Similarly, an applied hyperpolarizing current inhibits the flagellar activity of bull spermatozoa (O'Day, Rikmenspoel and Lindemann, 1976). In contrast, an injection of hyperpolarizing current into *Paramecium* results in increased ciliary beating in the forward swimming position (Eckert and Machemer, 1975).

More direct evidence for electrical control of flagellar activity comes from extracellular electrode recordings made on *Haematococcus pluvialis* by Litvin,
Sineschekov and Sineschekov (1978). These workers found that many of the factors that affect phototaxis (such as duration and intensity of a light stimulus) induced changes in membrane potential. Furthermore, the action spectrum of the photo-induced changes in potential resemble the action spectrum of the phototactic response. These findings indicate that electrical events are probably involved in the control of flagellar activity. It would be interesting to see if the membrane potentials of unicellular plant cells respond to chemical and mechanical stimuli in the same electrical fashion as in Paramecium (Naitoh and Eckert, 1969; Eckert, 1972), so allowing a direct comparison of the mechanisms controlling flagellar and ciliary activity in these organisms.

Tactic movements are also performed by organisms lacking cilia and flagella. Slime mould taxis has already been dealt with. The filamentous blue-green alga Phormidium uncinatum performs phototactic movements - a switch from light to darkness generally causes the filaments to reverse their previous path of movement (Häder, 1978b). Both intra- and extracellular electrode recordings have detected photo-induced changes in electrical potential, with lag phases roughly corresponding to the lag phase of the phototactic reaction (Häder, 1978a). In addition, the phototactic reaction is inhibited by applied electric fields (Häder, 1977). These findings indicate that electrical events are involved in the phototactic movement of the filaments, but unfortunately it is not clear what part they play. They may, for instance, involve perception of the stimulus, or conduction of the excitation to the motor region, or be a part of the motor reaction itself.

Concluding remarks

Many of the events leading to seismonastic movements are likely to be shared by a variety of higher plants - such as Dionaea, Aldrovanda, Mimosa, Biophytum and Stylidium - and probably occur in many other species as well (Fig. 2). The electrical characteristics of this sequence are surprisingly similar to those of animal nervous systems (Fig. 3), albeit on a simpler and slower scale (Table 2). In both animals and plants a receptor potential perceives a stimulus, firing an action potential after sufficient stimulation which then carries the excitation signal to the organs/tissues concerned with the response. It appears from work on the Dionaea 'memory', and the behaviour of Mimosa pulvini, that the mechanism coupling the action potential to changes in motor cell turgor in plants is not simply due to the ionic movements accompanying the action potential. Rather, it would appear that some other event is involved in triggering the motor cell response, perhaps the release of an excitatory chemical such as a neurotransmitter, or an 'excitatory ion' such as Ca$^{2+}$. Neurotransmitter-like substances are present in the pulvini of Mimosa (Trabucchi, 1948) and several other plant species (Applewhite, 1973), but the literature on this subject is too large to cover here. What is not certain is whether these chemicals play any part in plant movements, and combined biochemical and electrophysiological investigations will be needed to test this possibility. There is, however, a danger in drawing too many parallels with excitation in animals, as both ACh and AChE have been detected in relatively high concentrations in non-motile plant tissues, particularly actively growing tissues (see Fluck and Jaffe, 1976), in which their significance is also obscure. The role of Ricca's factor in plant movements is also of considerable interest, as this agent or group of agents has not only been shown to generate the variation potentials which lead to pulvinar movements in Mimosa, but also to induce
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**Fig. 2.** A generalized sequence of events leading to seismonomastic movements in higher plants. The scheme represents common features from a variety of species, and does not include unusual events peculiar to a particular species.

Stomatal closure in a variety of species (Umrath, 1966) and stamen bending in *Berberis* (Umrath, 1943). Considerable progress has now been made in characterizing Ricca's factor obtained from *Mimosa*, and which has been found to include gentisic acid among other agents (Schildknecht, 1978), so that it should now be possible to investigate its physiological properties more thoroughly.

K⁺ and Cl⁻ fluxes are apparently common to all reversible turgor-mediated movements that are sensitive to mechanical stimulation. Circumstantial evidence has indicated that Ca²⁺ may also participate in these movements, perhaps by altering membrane properties so as to trigger the large fluxes of K⁺ and Cl⁻. The driving forces for these ionic movements are poorly understood, although it is known that considerable ATP hydrolysis accompanies many turgor-mediated movements, such as leaflet opening in *Albizzia* (Satter and Galston, 1973), *Dionaea* trap closure (Jaffe, 1973) and *Mimosa* pulvinus bending (Lyubimova et al., 1964). Electrogenic ion pump activity has been implicated in these movements (as in rhythmic and nyctinastic leaf movements—see Galston and Satter, 1976), but changes in membrane potential are likely to drive at least some of the ionic transport, perhaps by regulating the activity of the ion pumps, as has been indicated by studies on *Nitella* (Spanswick, 1972) and *Haliclyctus* (Graves and Gutknecht, 1977). Control of ionic movement across the plasmalemma by electrical potential is believed to play an important part in the transmission of action...
Fig. 3. Sequence of salient events occurring during sensory excitation in higher animals.

potentials in excitable cells in animals – a phenomenon known as ‘voltage-gating’ (see Armstrong, 1975; Ulbricht, 1977).

The conflicting evidence concerning electrical control of Ca\(^{2+}\)-mediated cytoplasmic streaming activity in slime moulds and characean algae indicates that too close an analogy with the sequence of events leading to actomyosin contraction in animal muscles cannot be made (see, for example, Wilkie, 1968). Yet understanding the mechanisms controlling actin or actomyosin contraction in plant cells has important implications, since actin has been linked with chromosome movement (and hence cell division) in *Haemanthus katherinae* (Forer and Jackson, 1976), as well as the movement of chloroplasts (Wagner, Haupt and Laux, 1972; Schonbohm, 1973) and possibly even vesicles (see Quatrano, 1978).

The control of ciliary beating in *Paramecium* by electrical activity lends strong support to similar control of unicellular plant ciliary and flagellar activity. If this is so, then electrically regulated movements will be widespread throughout the plant kingdom, since male gametes of all but the gymnosperms and angiosperms are propelled by either cilia or flagellae. In addition, electrical impulses also trigger the bioluminescence flash and tentacle contraction in the dinoflagellate *Noctiluca militaris* in response to mechanical stimuli (Eckert, 1965a, b; Eckert and Sibaoka, 1967; Sibaoka and Eckert, 1967).

In contrast to the vascular cryptogams, rapid and reversible movements are relatively rare in higher plants, and as a result the electrophysiology of their movements has tended to be of only minority interest. Yet, despite the speculative nature of much of this review, it is clear that electrical activity plays an important part in many plant movements and has helped to prompt investigations into electrical activity in other aspects of plant physiology. Action potentials in higher
Electricity in plant movements

Table 2. Conduction velocities of electrical excitations mediating reversible plant movements. Note that considerable variation in these velocities will occur due to temperature, humidity, intensity of stimulus and age of specimens, and that data given here are meant to indicate the order of velocities involved. Two examples from excitation in animals have been included for comparison.

<table>
<thead>
<tr>
<th>Species</th>
<th>Organ</th>
<th>Stimulus</th>
<th>Excitation velocity (mm s⁻¹)</th>
<th>Key reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aldrovanda vesiculosa</td>
<td>Trap lobe</td>
<td>Electrical</td>
<td>40-120</td>
<td>Sibaoka, 1980</td>
</tr>
<tr>
<td>Biophytum dendroides</td>
<td>Pinna-rachis</td>
<td>Electrical</td>
<td>3-5</td>
<td>Guhathakurta &amp; Dutt, 1963</td>
</tr>
<tr>
<td>Chara braunii</td>
<td>Internode</td>
<td>Electrical</td>
<td>10-18</td>
<td>Sibaoka, 1958</td>
</tr>
<tr>
<td>Dionaea muscipula</td>
<td>Trap lobe</td>
<td>Electrical</td>
<td>60-170</td>
<td>Sibaoka, 1966</td>
</tr>
<tr>
<td>Drosera intermedia</td>
<td>Tentacle stalk</td>
<td>Electrical</td>
<td>c. 10</td>
<td>Williams &amp; Pickard, 1972</td>
</tr>
<tr>
<td>Incarvillea grandiflora</td>
<td>Stigmatic lobe</td>
<td>Mechanical</td>
<td>18</td>
<td>Sinyukhin &amp; Britikov, 1965a, b</td>
</tr>
<tr>
<td>Mimosa pudica</td>
<td>Petiole</td>
<td>Electrical</td>
<td>6-44</td>
<td>Sibaoka, 1950b</td>
</tr>
<tr>
<td>M. pudica</td>
<td>Stem</td>
<td>Electrical</td>
<td>40-50</td>
<td>Umrath, 1937</td>
</tr>
<tr>
<td>M. pudica</td>
<td>Stem</td>
<td>Wound (cut or burn)</td>
<td>20-30</td>
<td>Sibaoka, 1950a</td>
</tr>
<tr>
<td>M. pudica</td>
<td>Stem</td>
<td>Severe wound (cut or burn)</td>
<td>100-400</td>
<td>Sibaoka, 1954</td>
</tr>
<tr>
<td>M. invisa</td>
<td>Pinna-rachis</td>
<td>Wound (cut)</td>
<td>7-5</td>
<td>Umrath, 1959</td>
</tr>
<tr>
<td>Neptunia plena</td>
<td>Petiole</td>
<td>Electrical</td>
<td>9-12</td>
<td>Umrath, 1928</td>
</tr>
<tr>
<td>Nitella flexilis</td>
<td>Internode</td>
<td>Electrical</td>
<td>40-48</td>
<td>Sibaoka, 1958</td>
</tr>
<tr>
<td>Animals</td>
<td>Column</td>
<td>Electrical</td>
<td>121-146</td>
<td>Parker, 1918</td>
</tr>
<tr>
<td>Anemone</td>
<td>Dorsal spino-</td>
<td>Electrical</td>
<td>85,000-165,000</td>
<td>Grundfest &amp; Campbell, 1942</td>
</tr>
<tr>
<td>Felix (cat)</td>
<td>cerebellar</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Plants have been admirably reviewed by Pickard (1973), but the possible functions of electric signals in systems lacking motile properties is largely a mystery. On the other hand, electrical activity is believed to play an important part in cell development (see Jaffe and Nuccitelli, 1977). Clearly, many perplexing problems in plant electrophysiology remain to be solved.

Note added in proof


Acknowledgements

I am grateful to Dr M. J. Earnshaw for critical reading of the manuscript, Dr M. Spiro for technical advice and help in translation, Mr N. Billingham for advice on animal biochemistry, and Mr and Mrs A. M. Setchell for technical assistance.


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