Light-triggered action potentials in plants

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Abstract

Special attention is paid in this paper to the criteria of the light-triggered action potential, namely the all-or-none law, propagation, the occurrence of refractory periods. Such action potentials have been recorded in *Acetabularia mediterranea*, *Asplenium trichomanes*, *Bryum pseudotriquetrum*, *Eremosphaera viridis* and *Conocephalum conicum*. In *Acetabularia*, action potentials are generated after sudden cessation of light stimuli of sufficient intensity. The depolarization phase of the action potential develops as a result of a transient reversal of the action of the electrogenic Cl^- pump. This is a principle of the "metabolic" action potential hypothesis proposed by Gradmann. In the gametophytes of *Asplenium trichomanes* and *Bryum pseudotriquetrum*, action potentials are triggered on illumination. Guttation starts 1.5-2 seconds after the passage of an action potential. The active water secretion facilitates fertilization. In the unicellular fresh water alga, *Eremosphaera viridis*, action potential-like responses are evoked after light termination. The process responsible for its appearance is the opening of potassium channels in the plasmalemma. The liverwort, *Conocephalum conicum*, generates action potentials in response to light, electrical, chemical and mechanical stimuli. Calcium and potassium channels as well as proton pumps are involved in electrogenesis of action impulses in the species. Excitation causes a significant increase in the respiration rate. The role of action impulses as mediators in a system of a metabolism control is discussed.

Key words: action potential, ion pump, light

INTRODUCTION

One of the basic physiological functions of cytoplasmic membranes is the perception of various kinds of stimuli. In plant cells, light constitutes perhaps

the main external factor affecting physiological processes. Changes in light intensity and its spectral range influence the state of the plasmalemma which is manifested, among others, by changes of transmembrane potential. It should be emphasized that light does not act directly on the plasmalemma. Chloroplasts are the usual reception sites of light stimuli. The exception is when light is absorbed by phytochrome (Löpert et al. 1978, Hartmann 1984) or by a blue light-absorbing system (Hayami et al. 1986). In different plant species different types of transmembrane potential changes evoked by light are observed. After illumination both hyper- and depolarization are registered. These changes may be long-lasting (Nishizaki 1963, Spanswick 1972, Prins et al. 1980), transient (Hartmann 1975, Contardi and Davis 1978), and even oscillatory (Pallaghy and Lüttge 1970, Freundling et al. 1980, Nishizaki 1987). Cessation of light usually causes changes of potential opposite to those observed on illumination (Bentrup 1974). Among the phenomena of this kind, special attention is paid to light-triggered action potentials which appear according to the all-or-none law when the stimulus exceeds a certain threshold value. Action potentials evoked in one part of a plant can spread to other parts not affected by the stimulus. This characteristic makes it possible to suppose that the action potential is an element of the control system of physiological processes.

Such classical action potentials triggered by light have been recorded so far only in a few plant species. In many other plants where electrical, mechanical and chemical stimuli can evoke action potentials, illumination causes only local potential changes, the amplitudes of which depend on the stimulus strength (Maslobrod 1972, Stolarek et al. 1980).

LIGHT-TRIGGERED ACTION POTENTIALS IN *ACETABULARIA*

Light-triggered action potentials, (AP) were first recorded in the sea alga, *Acetabularia mediterranea* (Schilde 1968). The plant reacts to a light stimulus with a transient hyperpolarization of the transmembrane potential. Cessation of the illumination causes depolarization, the magnitude of which depends on the intensity of the light stimulus applied earlier (Gradmann 1976). This subthreshold depolarization shows distinct dependence on photosynthesis (Schilde 1966, Gradmann 1978). When the light stimulus exceeds a certain value (about 100 W m^{-2}), depolarization is sufficiently large to exceed the excitability threshold and to evoke an AP. Further increase of light stimulus intensity does not change the amplitude and time course of the potential changes produced. In this way, the all-or-none law is fulfilled. Apart from that, Gradmann (1976) proposes three more criteria for classifying a phenomenon as an action potential: propagation (without decrement), the occurrence of a transient change in potential difference, and an endogenous energy supply

(independent of the energy supplied by the stimulus) for the propulsion of the phenomenon. In *A. mediterranea* the rate of AP propagation depends on the site of the stimulation and is 1.36 mm s^{-1} from the apex to the basis and 0.6 mm s^{-1} from the basis to the apex. In addition spontaneous (without any stimulus) series of action potentials whose number reaches up to 10 per hour often occur. Another typical property of AP is the occurrence of refractory periods. The absolute refractory period in *Acetabularia* is about 4 min (Gradmann 1976). Besides light, electrical stimuli (a depolarizing current) can also trigger APs. By using electrical stimuli, the dependence between stimulus strength and its duration required for evoking excitation, known as the strength-duration dependence, was determined. From this dependence the rheobase ($4.5 \mu\text{A}$) and chronaxie (27 s) can be established. Temporal summation of subthreshold electrical stimuli also occurs (Gradmann 1976).

Taking into account the ionic basis of excitation in *Acetabularia* has led Gradmann to the concept of the so-called "metabolic" action potential. In order to elucidate this problem, the electrical parameters of the *Acetabularia* membrane should be mentioned. The resting potential difference across the plasmalemma is caused by the parallel occurrence of two components: the diffusion component reflecting passive permeability mainly for K^+ and the active component connected with the electrogenic ion pump (Gradmann 1975). Under normal conditions, at the expense of ATP hydrolysis, this pump imports Cl^- into the cell against the gradient of their electrochemical potential (the equilibrium potential for Cl^- is about 0 mV). The Cl^- pump in *Acetabularia* is one of the most well understood ion pumps in plants (Saddler 1970, Mummert et al. 1981, Hansen et al. 1982, Tittor et al. 1983).

Depending on the time scale of the current impulses employed to determine the time constant, RC of the membrane, two time constants, τ_0 of the order of milliseconds and τ_∞ of the order of 10 s, were obtained. This finding necessitated the expansion of the analog circuit of the *Acetabularia* membrane

Fig. 1. The analog circuit of the *Acetabularia* membrane in the steady state. C_m — membrane capacity; D — conductance of the diffusion pathway; E_D — electromotive force of the diffusion pathway; P_1 — conductance of the carrier system of the electrogenic pump; P_2 — conductance equivalent of energy metabolism; E_p — electromotive force of the electrogenic Cl^- pump;

C_p — capacitance reflecting the ATP pool (based on Gradmann 1976 — modified)

in order to make it reflect its real electrical properties. This is shown in Fig. 1. The left side of the circuit presents the diffusion component with the electromotive force $E_d = -80$ mV, which corresponds approximately to the equilibrium potential for K^+ (-90 mV). On the right, active side there are two conducting elements, P_1 and P_2 , connected with the electrogenic Cl^- pump whose equilibrium potential is about $\lambda 200$ mV. Element P_1 reflects the conductance of the carrier system of the electrogenic pump. Element P_2 , with a parallelly connected very large capacitance C_p , of the order of 10 F m^{-2} , presents the conductance equivalent of the pump channel. The electric energy of the condenser C_p corresponds to the energy stored in the ATP pool utilized for the power supply of the pump (Gradmann 1975, 1976). Electrophysiological experiments with the application of the voltage and current clamp method have demonstrated that the active element P_2 is responsible for initiating the excitation of *Acetabularia*. The I/V characteristic of the elements P_1 and D is the same during AP s as that obtained under steady conditions. The course of events during the "metabolic" action potential is to be as follows: interruption of illumination causes a temporary insufficiency of the ATP available for the power supply of Cl^- pumps, this causes their breakdown and then reversal of their action. This may then lead to ATP synthesis. The passage of Cl^- outside the cell causes depolarization to about -50 mV which brings about the exit of K^+ as a consequence of exceeding the equilibrium potential for these ions. As a result of the efflux of K^+ from the cell, repolarization to about -90 mV occurs. Meanwhile, the ion pump regains its previous direction and begins to import Cl^- to the cell and after 30-90 seconds restores the equilibrium at a resting potential of -170 mV (Gradmann 1976). The hypothesis of a "metabolic" action potential is an attempt to extend Mitchel's (1961) chemiosmotic theory to the case of cytoplasmic membranes. The linear dependence of the half-width of AP on temperature as well as changes in the ATP level during excitation seemed to confirm this hypothesis or, at least, indicated the dependence of the AP on metabolism. The efflux of Cl^- and K^+ from *Acetabularia* cells during excitation was also observed in isotopic investigations (Gradmann et al. 1973, Mummert and Gradmann 1976). Precise analysis of the flux of Cl^- showed that at least some of these ions leave the cell in a passive manner, that is, as a result of a transient increase of the permeability of the plasmalemma for Cl^- (Gradmann and Mummert 1980). This takes place at values of membrane potential higher than -150 mV. Thus, according to a modified hypothesis, in the depolarization phase there occurs an activation of passive and active elements by means of which Cl^- flows out of the cell. Yet, purely metabolic or purely passive action potentials are also possible, depending on the kind of the stimulus which causes them (Gradmann and Mummert 1980). Changes in the ATP level during the AP mentioned above, measured in whole cells, are regarded as manifestations of the regulation process. The ATP produced and utilized in the

cytoplasm in amounts much higher than could be generated by the plasmalemma, goes to just such a pool. The capability of the Cl^- pump to reverse its action and produce ATP was demonstrated while examining changes of its level in *Acetabularia* cell fragments centrifuged from the cytoplasm. In order to enable stable operation of the pump in a reverse direction, cells prepared in such a way were placed in a medium without Cl^- . Under such conditions a triple increase in the ATP level was observed (Goldfarb et al. 1984). Yet, this should not be treated as definite proof that ATP synthesis does actually take place during the action potential. The removal of Cl^- from the external solution should hyperpolarize the resting potential below the equilibrium potential for the pump (-200 mV) and thus reverse its course, unlike that which occurs during AP when depolarization takes place.

One should hope that the near future will bring further advances in studies on an object so interesting as *Acetabularia* and will eventually enable verification of the hypothesis about the "metabolic" action potential and determination of its role in cell physiology.

ELECTROPHYSIOLOGICAL PROPERTIES OF *BRYUM* AND *ASPLENIUM*

Two other plants in which excitation occurs under the influence of light (this time with light on) are a fern *Asplenium trichomanes* and a moss *Bryum pseudotriquetrum* (Sinyukhin 1973). In both these species action potentials were recorded in gametophytes. The amplitudes of APs were 30-70 mV while the half-widths were about 5 s in *Asplenium* and about 15 s in *Bryum* (Sinyukhin 1973). These are approximate values since the microelectrodes employed for the measurement of potential difference were placed in the tissue but not inside the cells. The rate of AP propagation was similar in both species and ranged from 0.5 to 2 cm s⁻¹. The most significant aspect of the behaviour of these plants is active secretion of water on illumination. Drops of water (solution) begin to appear 1.5-2 s after generation of the AP. When it is blocked by chloroform, gutation does not take place. Active water secretion is most intensive in those external parts of cells where there are small protuberances. Gutation may also be evoked in a darkened part of the plant by initiating excitation in an uncovered part by applying light or electrical stimuli. Water secretion is a very important phenomenon for the physiology of these plants since it facilitates fertilization which may take place only in an aqueous environment.

ACTION POTENTIAL-LIKE RESPONSES IN *EREMOSPHAERA*

Action potential-like responses to light stimuli occur in the unicellular fresh water alga *Eremosphaera viridis* (Geiswald et al. 1982, Köhler et al. 1983).

In this plant typical *APs* were not observed, if only because of the lack of an excitability threshold. Hence, instead of the term action potential, such terms as “chemically induced action potential” or “control-loop action potential”, *CAP* (Köhler et al. 1986) or “transient potential”, *TP* (Thaler et al. 1987) are proposed. The phenomena occurring involving the plasmalemma of *Eremosphaera* share however many properties with classical action potentials. Similarly as in *Acetabularia*, in *Eremosphaera* excitation takes place as a consequence of cessation of illumination. It may also be induced by a hyperpolarizing current, 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU), 1,3 dicyclohexylcarbodiimide (DCCD), or a sudden temperature drop (Köhler et al. 1983). This indicates the evident dependence of *CAPs* on cell metabolism. The excitation is accompanied by a drastic fall in membrane resistance. Blocking of the response to the stimuli by tetraethylammonium (TEA), an inhibitor of K^+ channels, points to the decisive participation of the channels in the generation of *CAPs*. It was also noticed by changing the concentration of K^+ in the medium that the *CAP* peak corresponded to the equilibrium potential for potassium, E_K . The dependence of the magnitude of the resting potential of *Eremosphaera* on K^+ concentration outside the cell is shown in Fig. 2. The values of equilibrium potentials for K^+ (dashed line) were calculated from the Nernst equation. As can be seen, at K^+ concentration ranging from 10^{-1} M to 10^{-3} M *CAPs* occur in a form of transient depolarization of more or less constant amplitudes. Between 10^{-3} M and 10^{-4} M, the *CAP* amplitude gradually drops to zero and, what is particularly interesting, further decrease in K^+ concentration causes a reversal of the response phase towards hyperpolarization and a gradual rise of the amp-

Fig. 2. The dependence of changes in the transmembrane potential of *Eremosphaera viridis* on the concentration of potassium ions in the external medium. The dashed line connects the values of equilibrium potentials for potassium and the maxima of action potential-like responses to light turned off (based on Köhler et al. 1983 — modified)

litudes. Interpretation of the behaviour of the *E. viridis* membrane is as follows. At K^+ concentrations above 10^{-4} M the resting potential is equal to the diffusion potential for K^+ , Na^+ , Cl^- , and H^+ (Köhler et al. 1985). At K^+ concentrations above 10^{-3} M the value of the resting potential is partly established by the electrogenic pump. As a result of its operation, potassium ions are removed outside the cell (Köhler et al. 1983). The interruption of illumination causes a transient opening of K^+ channels. The factor which is supposed to be responsible for this is a drop in cytoplasmic pH after illumination cessation as demonstrated by means of pH-sensitive microelectrodes (Köhler et al. 1986). It is probable that calcium ions could mediate between cytoplasm acidification and K^+ channel opening. Indirect evidence is provided by the fact that the low concentration of Ba^{2+} which may play a role of activator of Ca^{2+} channels (Carafoli 1987), in the presence of Ca^{2+} causes an evident rise in excitability until the appearance of a series of CAPs (Thaler et al. 1987). However, it should also be demonstrated that the drop in cytoplasmic pH stimulates the opening of Ca^{2+} channels; otherwise, one may consider two independent systems of K^+ channel activation. The physiological function of the CAP in *Eremosphaera viridis* would consist in the regulation of cytoplasmic pH. The quoted authors propose the so-called "battery" model according to which the regulation of the H^+ concentration in the cell takes place by means of an anion/proton co-transporter. The opening of K^+ channels is to constitute a low-impedance battery for its power supply (Köhler et al. 1986).

CONOCEPHALUM CONICUM RESPONSE TO LIGHT

Finally, there is a somewhat longer discussion of the electrophysiological properties of the liverwort *Conocephalum conicum*, which is very easily excited by light as well as electrical, mechanical and chemical stimuli (Paszewski et al. 1982, Dziubińska et al. 1983, Trębacz and Zawadzki 1985, Trębacz et al. 1988b). The reaction of *C. conicum* to light of gradually increasing intensity (Fig. 3) is similar to that in *Acetabularia*, though in *C. conicum* the response to the light switched on and off has a reverse polarization than in *Acetabularia*. The all-or-none law is fulfilled and the light stimulus is required only to initiate the AP, which then develops in an unchanged form without the participation of the stimulus — Fig. 3e (Trębacz and Zawadzki 1985). Action potentials are propagated at a rate of $0.4\text{--}1.5\text{ cm s}^{-1}$, *in situ* (Zawadzki and Trębacz 1985). Refractory periods occur. A light stimulus applied during a refractory period after an AP produced by an electrical stimulus does not lead to excitation and only a generator potential (GP) is then produced. In contrast, an AP cannot be induced by an electrical pulse during the refractory period after an excitation evoked by a light stimulus. The

Fig. 3. Responses of *Conocephalum conicum* cells to light stimuli of rising intensity. Downward arrows denote the moment light is turned off while upward arrows — light turned on. The intensities of white light stimuli were: a — 18, b — 37, c — 80, d — 310, e — 310 W m^{-2} (light was turned off when the excitability threshold was exceeded)

duration of the refractory period depends on the intensity of the light and electrical stimuli (Fig. 4). These data indicate that we do not encounter two types of APs but one and the same phenomenon which may be triggered in various ways.

Fig. 4. The dependence between stimulus strength and duration of the refractory period in *Conocephalum conicum*. The ordinate: stimulus strength — on the left side a light stimulus expressed in $W m^{-2}$, and on the right side an electrical stimuli expressed as multiples of the rheobase. The abscissa: time period between successive stimulations. Crosses refer to light stimuli, circles — electrical stimuli

In *C. conicum* a temporal summation of subthreshold light stimuli and light and electrical stimuli occurs (Trębacz and Zawadzki 1985). The GPs, which mediate between light stimulus perception and excitation, are connected with the process of photosynthesis. The latter has been demonstrated by determining their action spectrum (Trębacz et al. 1989a) and by applying DCMU, an inhibitor of the photosynthetic electron transfer chain. This substance caused a total disappearance of GPs and hence, the disappearance of the response to light (Zawadzki et al. 1984, Trębacz and Zawadzki 1985). At that time, neither the excitability threshold nor the duration of the refractory period of APs induced by electrical stimuli underwent any significant changes (Trębacz and Zawadzki 1985). Particularly excitable plants spontaneously generate long-lasting series of APs, while in other plants they may be evoked by cutting or by chemical stimuli (Paszewski et al. 1982, Trębacz et al. 1989b).

Introductory investigations of the ionic mechanism of APs in *Conocephalum* showed that, similarly to *Eremosphaera*, excitation may be completely blocked

by TEA. Then only *GPs* induced by light were unchanged. The findings indicate, on one hand, the participation of K^+ channels in generation of action impulses, while on the other hand — independence of generator potentials of the degree of membrane permeability for K^+ . The application of $LaCl_3$ and $MnCl_2$, inhibitors of Ca^{2+} channels, also caused a gradual decrease of excitability until its total disappearance. During the inhibition process the amplitude and half-width of *APs* gradually decreased. As in the case of TEA, the magnitude and rate of *GP* rise did not undergo any change (Trębacz et al. 1989b). This may imply that the blocking of the entry of Ca^{2+} into the cell, which normally takes place in the excitation process (Williamson and Ashley 1982, Kikuyama and Tazawa 1983, Shiina and Tazawa 1987a), could cause a closure of Cl^- channels which in turn would make the flow of the current into the cell impossible (Lunevsky et al. 1983, Tsutsui et al. 1986, Berestovsky et al. 1987, Shiina and Tazawa 1987b).

Further information about the excitation mechanism in *Conocephalum* was provided by the application of phosphorylation uncouplers (DNP, CCCP, NH_4Cl), inhibitors (DCCD), and activators (IAA) of a proton pump. 2,4

Fig. 5. Changes in the transmembrane potential in *Conocephalum conicum* after DNP treatment. Bold arrows mark electrical stimuli, thin downward and upward arrows — light turned on and off, respectively. The vertical line reaching zero, in the right part of the Figure — microelectrode withdrawal from the cell

Dinitrophenol (DNP) caused a quick depolarization of the transmembrane potential (Fig. 5) which was accompanied by a vanishing series of *APs*. After the establishment of the potential difference on a new constant level no stimulus succeeded in exciting the plant. Responses to carbonyl cyanide-*m*-chlorophenylhydrazone (CCCP) and NH_4Cl were similar although these substances caused an evident increase in the amplitudes of light induced *GPs*. The response to ammonium chloride was clearly weakened by an increased concentration of K^+ in the external medium. DCCD, a lipophilic inhibitor of the proton pump, caused a slow depolarization of the transmembrane potential. Under its effect the response to electrical stimuli disappeared, while *GPs* underwent a considerable reduction. Indole-3-acetic acid (IAA), a substance activating the proton pump (Polevoy and Salamatova 1975, Spanswick 1981, Stolarek and Karcz 1987), in *Conocephalum conicum* caused a quick hyperpolarization of the resting potential by 30-35 mV. Excitability induced by electrical stimuli increased (about two-fold). Still, the characteristics of the response to light stimuli were the same as in the control. These results indicate the participation of the proton pump in the electrogenesis of action potentials in *Conocephalum conicum* (Trębacz et al. 1989b).

The effect of the factors connected with metabolism on the excitation process is also confirmed by the following observations. Interruption of illumination during the *AP* causes a return to the resting potential much quicker than normally (Fig. 6). Light turned off in the depolarization phase causes narrowing of the peak but has no effect on its amplitude. DCMU inhibits the effects of illumination onset and termination on the half-width of *APs* which implies a connection of this effect with photosynthesis. Both at constant illumination and in darkness, the shape of the records of *APs* is the same. It was also noticed that if the plant is stimulated slowly with a linearly rising light stimulus then the accommodation effect occurs. The plant is not

Fig. 6. Changes in the time periods of action potentials in *Conocephalum conicum* caused by light turned on and off. Upward arrows denote light switched on, downward arrows — light switched off. Vertical, parallel sections mark 5 min. intervals

excited even if the final intensity of the light stimulus exceeds by several times the value of the excitability threshold. In the case of slowly rising electrical stimuli accommodation does not take place. The transmembrane potential changes in both cases are shown in Fig. 7.

Fig. 7. Responses of *Conocephalum conicum* to quickly and slowly rising electrical stimuli (the upper record) and light stimuli (the lower record). On the left — action potentials triggered by threshold stimuli. On the right — responses to slowly rising stimuli. Excitation appeared on the electrical stimulus reaching the value of 0.95 of the rheobase. The light stimulus failed to excite the cell although it reached a value exceeding the threshold by five times

This observation indicates that in the plasmalemma of *C. conicum* two types of structures which may lead to excitation function parallelly and differ from each other in the dynamics of their response to slowly rising stimuli. One structure may consist of voltage gated ionic channels. One may therefore ask why the cells are not excited by a slowly rising light stimulus, in spite of considerable depolarization. It may be assumed that inhibition of voltage gated channels by a factor liberated during illumination, e.g. protons, occurs. The other type of structures could comprise electrogenic proton pumps. Changes in the amounts of H^+ ions pumped at light turned on and off is one of the factors influencing pump activity and, hence, the magnitude of the potential difference (Felle and Bertl 1986). Rapid changes in pH at sudden illumination or darkening may produce much greater changes in the trans-

membrane potential because of the inertia of the pump. Then co-operation with voltage-controlled channels whose opening would ensure the course of the response to the stimulus according to the all-or-none law, may take place. The lack of such possible co-operation would explain the fact that in many plants generating typical action potentials in response to electrical stimuli, light produces only transient depolarization whose magnitude depends on stimulus intensity and which disappears as the distance from the stimulation site increases.

Besides the mechanism of excitation, the most significant problem concerns the physiological function of action impulses. After stimulation causing generation of the *AP* in *Conocephalum* a considerable increase (30-70%) in the rate of respiration occurs, starting about 5 seconds after *AP* initiation in a rhythm similar to the changes of the transmembrane potential (Dziubińska et al. 1989). If the stimulation is accompanied by a series of *APs*, e.g. after cutting the thallus, then one observes as many acts of respiration rate increases as there have been excitations. In plants subjected to the action of TEA, i.e. with a blocked ability of *AP* generation, an increase in the respiration rate does not take place, regardless of the stimulus intensity.

As can be seen, the main function of excitation is the mobilization of energy which is a manifestation of the operation of a metabolism control mechanism. Action potentials are a convenient basis of such a mechanism because of their ability to propagate and the possibility of frequency coding of information about the stimulus strength (Paszewski et al. 1982). At least two factors could mediate between *APs* and respiration. One of them could be the activation of the key enzymes of glycolysis by changes in cytoplasmic pH. Changes in pH were recorded during excitation in *Nitellopsis obtusa* (Gyenes et al. 1981) and in *Dionaea muscipula* (Williams and Bennet 1982). The entry of Ca^{2+} into the cell during an *AP* connected with the activation of calmodulin may offer another possibility (Beilby and MacRobbie 1984, Tsutsui et al. 1987).

The body of facts and hypotheses presented in this paper indicate still one more function of photosynthetically active light, the function of a stimulus activating a control system of life processes connected with cytoplasmic membranes.

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Potencjały czynnościowe u roślin wywoływane światłem

Streszczenie

Scharakteryzowano potencjały czynnościowe u roślin wywoływane bodźcami świetlnymi. Zwrócono uwagę na spełnianie kryteriów potencjałów czynnościowych, takich jak: prawo wszystko-albo-nic, rozprzestrzenianie, występowanie okresów refrakcji. Potencjały takie rejestrowane były u: *Acetabularia mediterranea*, *Asplenium trichomanes*, *Bryum pseudotriquetrum*, *Eremosphaera viridis* i *Conocephalum conicum*. U *Acetabularia* potencjały czynnościowe rejestrowane są po gwałtownym wyłączeniu bodźców świetlnych o dostatecznej sile. Faza depolaryzacji potencjału czynnościowego rozwija się w wyniku odwrócenia funkcjonowania elektrogenicznej pompy chlorowej. Jest to zasadą hipotezy "metabolicznego" potencjału czynnościowego zaproponowanej przez Gradmanna. W gametofitach *Asplenium trichomanes* i *Bryum pseudotriquetrum* potencjały czynnościowe są wywoływane przez oświetlenie. 1.5-2 Sekund po przejściu potencjału czynnościowego rozpoczyna się gutacja. Aktywna sekrecja wody umożliwia zapłodnienie. U jednokomórkowego glonu słodkowodnego *Eremosphaera viridis* odpowiedzi typu potencjał czynnościowy są otrzymywane po zaciemnieniu. Procesem odpowiedzialnym za tę reakcję jest otwieranie kanałów potasowych w plazmolemie. Wątrobowiec *Conocephalum conicum* generuje potencjały czynnościowe w odpowiedzi na bodźce świetlne, elektryczne, chemiczne i mechaniczne. Kanały wapniowe i potasowe, jak również pompy protonowe są zaangażowane w elektrogenizację impulsów czynnościowych. Pobudzenie powoduje znaczny wzrost tempa oddychania. Rola potencjałów czynnościowych jako pośredników w systemie kontroli metabolizmu jest dyskutowana.