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Influence of different spectral ranges of light and Ca^{2+}-channel blockers on Ca^{2+} and K^+ levels in *Phaseolus coccineus* L. pulvini

JAN BIAŁCZYK, ZBIGNIEW LECHOWSKI

Department of Plant Physiology and Development, Jagiellonian University, Al. Mickiewicza 3, 31-120 Kraków, Poland

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Abstract

The effect of different spectral ranges of light on the modification of transport processes in isolated parts of *Phaseolus coccineus* pulvini was analysed in a bath medium by determining the Ca^{2+} and K^+ contents. After 1 h incubation of separated fragments of the extensor and flexor in solutions containing deionized water, medium, or medium with verapamil or nifedipine, the investigated material was irradiated with monochromatic light of different wavelengths. The concentration of Ca^{2+}, K^+ and the pH value were determined in the medium. The obtained results suggest the occurrence of a specific coupling between the concentration of Ca^{2+} and K^+ dependend on the wavelength of the applied light and part of the pulvinus. Certain spectral ranges of light brought about opposite effects on ion transport in opposite parts of the pulvinus. Changes in the pH of mediums containing isolated parts of the pulvini part to different effects of blue, red, and far-red light on the activity of H^+-pumps located in the motor cells. The use of verapamil and nifedipine, specific Ca^{2+}-channel blockers, made it possible to demonstrate the significant effect of Ca^{2+} on the activity and functioning of K^+-channels. The two types of inhibitors decreased the influx of Ca^{2+} and K^+ to motor cells of the pulvini, however they did not limit the efflux of ions to the medium. The obtained results suggest that Ca^{2+} ions take part in transduction of the light signal. It seems probable that the action of blue light is also mediated by part of the Ca^{2+} ions.

Key words: Ca^{2+}-channel blockers, pulvini, Phaseolus coccineus

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Abbreviations: B — blue light, CCCP — carbonyl cyanide-m-chlorophenyl-hydrazone, DCCD — N, N'dicyclohexylcarbodiimid, DES — diethylsilbestrol, DMSO — dimethylsulphoxide, DW — dry weight, FR — far-red light, MES — 2-(N-morpholino) ethanesulphonic acid, PAA — phenylacetic acid, PAR — photosynthetically active radiation, PFD — photon flux density, P_{fr} — far-red light-absorbing form of phytochrome, P_r — red light-absorbing form of phytochrome, R — red light, TEA — tetraethyl-ammonium

INTRODUCTION

The action of different spectral ranges of monochromatic light significantly modifies leaf movement of nyctinastic plants. Depending on the parts of the pulvini (extensor or flexor) and phases of movement in the circadian cycle, the effects of a given spectral range may bring about different effects of a given spectral range may bring about different effects in opposite parts of the pulvini. Under natural conditions the movement of leaves leads to the state of closeness at night (the turgorescence is high in the motor cells of the flexor and low in the motor cells of the extensor) and to the state of openness in the light phase (in motor cells of the opposite parts of the pulvini the turgor values are the inverse of the former phase).

Irradiation with R stimulated the process of leaf closing while the action of B or FR initiated reactions which resulted in the opening of leaves (Satter 1979, Satter and Galston 1981, Białczyk and Lechowski 1990 a). Results of numerous studies confirmed a high level of complexity of the mechanism of this type of movement. Among closely related processes which occur cyclically and alternately in opposite parts of the pulvini the most important are: (a) changes in the activity of H^+-pumps located in the plasmalemma of motor cells (Białczyk and Lechowski 1990a, b), (b) differences in the concentrations of cations and anions which basically determine the value of the osmotic potential in effector cells (Schrempf et al. 1976, Satter 1979, Hosokawa and Kyosawa 1983), (c) the activity of the internal biological clock controlling the movement (Bünning 1973), and (d) the stationary level of natural phytohormones (Satter and Galston 1981, Białczyk and Lechowski 1987). The complex anatomical structure of the pulvinus, and particularly the occurrence of a few layers of motor cells of different size and their ability to change shape and volume in the extensor and flexor, constitute an additional difficulty in investigating the mechanism of the nyctinastic motor response of leaves (Satter 1979, Satter and Galston 1981).

The results obtained so far show that an increase or decrease in the turgor of motor cells is closely correlated with changes in the concentration of K^+ and Cl^- ions occurring in the cells (Hosokawa and Kyosawa 1983). The speed of ion transport between the opposite parts of motor cells depends on the degree of polarization and permeability of plasmatic membranes (Iglesias and Satter 1983).

As was found in earlier studies, circadian changes in the concentration of K^+ and Cl^- ions in opposite parts of *Phaseolus coccineus* pulvini were accompanied by differences, also occurring cyclically, in the concentration of malic acid (Białczyk and Lechowski 1986, 1989). The concentration of malic acid in parts of *Phaseolus coccineus* pulvini also changed during irradiation with different spectral ranges of light. The action spectrum which stimulated the

process of malic acid synthesis, showed different characteristics for the extensor and flexor. For the extensor part, the main activity maxima occurred about 450 nm and 727 nm while the curve of the action spectrum of the flexor part showed one chief maximum at about 671 nm and a slight increase at about 405 nm (Białczyk and Lechowski 1990a).

The character of the curve of the action spectrum for the extensor and also the results of treating pulvini with PAA suggest that apart from the phytochrome, an unidentified photoreceptor of B occurs in this part of the pulvinus. The photoconversion of the phytochrome and changes in the P_r/P_{fr} ratio which appear in the circadian cycle, bring about opposite effects in opposite parts of the pulvinus (Satter et al. 1988, Białczyk and Lechowski 1990a).

In further experiments the use of a specific blocker of K^+-channels (TEA) and also of metabolic inhibitors (CCCP) and H^+-ATPases (DCCD and DES) made it possible to indirectly demonstrate the occurrence of K^+-channels in the pulvinus and to confirm their significant role in the transport of K^+ ions (Białczyk and Lechowski 1990b). On the basis of numerous studies it was frequently postulated that the phytochrome action was mediated by a part of the Ca^{2+} ions (Satter and Galston 1981, Satter et al. 1988, Moysset and Simon 1990). Investigations carried out on animal cells allowed a hypothesis to-be put forward that Ca^{2+} ions acts as activators of K^+-channels in membranes of animal cells (Latorre 1986, Berridge and Galione 1988). The amount of information obtained from plant cells concerning the functioning and activity of K^+-channels is much smaller than the analogical data found for animal cells (MacRobbie 1988, Thaler et al. 1989). In the present work it was attempted to elucidate the effect of Ca^{2+} ions on transport processes and activity of K^+-channels in the extensor and flexor of *Phaseolus coccineus* pulvini, as affected by different spectral ranges of light.

MATERIAL AND METHODS

PLANT MATERIAL

Seedlings of *Phaseolus coccineus* L. cv. „Piękny Jaś" were planted in garden soil of pH 6.8 for 14 days. Glow-discharge tubes („Flora" 40 W, LF-F, Polamp) were the source of light. The irradiation intensity of PAR was 90μmol $m^{-2}s^{-1}$ at the level of the first leaves with a photoperiod of 12 h light/12 h dark. The temperature were 25 ± 1°C in light and 24 ± 1°C in darkness. Average air humidity was 65 ± 5 %. Experiments were conducted on the pulvini located directly at the bases of leaf blades of the first pair of leaves. The leaves were excised 1.15 h before the end of the dark phase. Using a razor-blade, respective parts of extensor and flexor were separated from the pulvinus, as was described in previous papers (Białczyk and Lechowski 1990a, b). Before transferring

the plant material to quartz cuvettes with respective medium compositions, its fresh weight was determined each time and separated fragments were washed three times in deionized water. Separated parts of puvini (200 mg fresh weight) were placed in 2 cm^3 of either deionized water (pH 6.95) or media of the following composition: 10 mM MES buffer, 1.5 mM Ca $(NO_3)_2$, 1 mM Mg SO_4, and 5 mM KCl. The pH of the media was adjusted to 6.8 using an NaOH solution. In the case of experiments in which Ca^{2+}-channel blockers were used, the medium was used as a control while in other combinations verapamil or nifedipine at a concentration of 100 μM were added. All steps associated with preparation for the experiments were carried out in a very dim green light (0.5 μmol $m^{-2}s^{-1}$). The prepared material was incubated in darkness for 1 h in order to permit the penetration of the applied inhibitors into the isolated fragments of the pulvinus. After this period the cuvettes with the material were placed into an irradiation chamber.

CONDITIONS OF IRRADIATION

The irradiation of separated fragments of pulvini (extensor and flexor) with different spectral ranges of light was carried out in a special irradiation chamber (Lechowski 1973, Białczyk and Lechowski 1990a). A concentrated light beam was directed from an upper cuvette on the preparation which had been placed there. Conditions of irradiation with monochromatic light and the measurement of its fluence rate at the preparation level were described in an earlier paper (Białczyk and Lechowski 1990a). In the present investigation interference filters type SIF (Zeiss, Jena, GDR) λ max: 450 nm (half band width 8 nm), 671 nm (half band width 6 nm), and 727 nm (half band width 6 nm) were used. In the particular variants of the experiment, light conditions of different wavelengths were applied with identical PFD values, reaching 10 μmol $m^{-2}s^{-1}$. As was found in the paper mentioned above, this light fluence rate was sufficient for the saturation of the motor response of *Phaseolus coccineus*.

DETERMINATION OF K^+ AND Ca^{2+} CONCENTRATIONS AND pH VALUE IN THE MEDIUM

In outer medium surrounding separate fragments of the pulvini the concentration of ionized forms of Ca^{2+} and K^+ and the pH value were measured immediatedly after placing the plant material in the medium, then after about 1 h incubation in the dark, and 3 times during the irradiation of specimens with different spectral ranges of light at 1 h intervals. The plant material was removed with pincers, then the medium was thoroughly mixed and analyses were carried out, using ionoselective electrodes installed in the following two chambers: CIBA Corning 634 Ca^{2+}/pH analyser for Ca^{2+} ions and pH, and CIBA Corning 614 Na^+/K^+ analyser for K^+ ions. The concentration of both Ca^{2+} and K^+ ions

measured in the medium fell approximatly in the middle range of the sensitivity calibration curves of the two apparatuses. The data presented in this paper are the means from 10 separate experiments.

CHEMICALS

The basis solutions were obtained by dissolving verapamil and nifedipine (10^{-2} M) in 1 % DMSO and then diluting them with the medium to the concentration of 100 μM used in the experiments. DMSO, MES, nifedipine, and verapamil were obtained from Sigma. The remaining reagents used in the experiments were purchased from Polish Chemical Reagents.

RESULTS

THE EFFECT OF LIGHT QUALITY ON Ca^{2+} AND K^+ CONTENT

After washing three times in deionized water, the separated zones of *Phaseolus coccineus* pulvini were transferred to the medium. The concentration of Ca^{2+} and K^+ ions in the outer solution, measured directly after the investigated material was placed there, were accepted as the initial, zero levels. In curves illustrating Ca^{2+} (Fig. 1A) and K^+ (Fig. 1 B) concentrations in the medium, their non-significant level during the last hour of the dark phase is indicated. Depending on the investigated part of puvinus, distinct differences were observed in the concentration of the two ions during the light phase, depending on the kind of applied light, in spite of the fact that the pattern of curves showing changes in the content of K^+ and Ca^{2+} represented similar tendencies. An increase in the content of K^+ ions in the medium (Fig. 1B) containing the extensor parts suggests a specific effect of R since the presented curves show an efflux of a significant amount of K^+ ions to the outer environment occurred. In contrast, in experiments with B and FR only a slight increase in the content of K^+ ions in the outer solution was obtained upon irradiation with either types light. In the motor response of primary leaves of *Phaseolus coccineus* during the light phase, changes in the concentration of K^+ ions are decisive for their opening. An increase in the turgor of extensor motor cells occurs in correlation with a considerable increase in the content of K^+ ions (Białczyk and Lechowski 1990a).

After a 3 h period of irradiation of flexor parts with different spectral ranges of light the pattern of changes in K^+ concentrations was different from that observed in the extensor. The characteristic increase in K^+ ions in the outer environment of preparations containing flexor parts was associated with the action of B and FR but not with R, as was in the case of the opposite parts. Under conditions of undisturbed movement of intact leaves an increase in turgor and

concentration of K^+ ions in this part of the pulvinus occurs during the light phase of the circadian cycle, stimulating the processes of leaf closing (B i a ł c z y k and L e c h o w s k i 1990a).

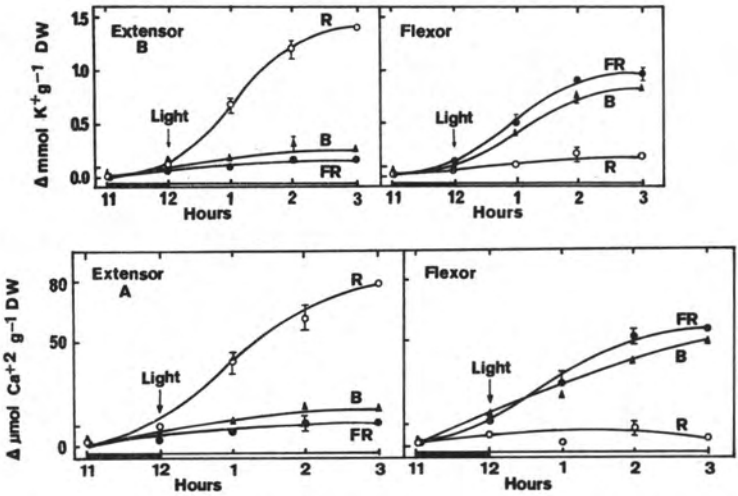

Fig. 1. Δ concentration of Ca^{2+} (A) and K^+ (B) in the medium during irradiation of extensor and flexor parts with different spectral ranges of light (SE±, n = 10)

Figure 1A presents changes in the content of Ca^{2+} ions in the medium with parts of the extensor and flexor, irradiated with different spectral ranges of light for 3 h. In spite of significant differences in the absolute values of the concentration of Ca^{2+} ions depending on the given part of the pulvinus, the obtained results show a similar pattern of R and FR action, analogous with changes in the content of K^+ ions. The analysed results suggest a similarity in the occurrence of a specific feed-back between the contents of the two kinds of ions depending on the part of the pulvinus and phases of diurnal cycle.

THE EFFECT OF LIGHT QUALITY ON pH CHANGES

Changes brought about by irradiation with different spectral ranges of light in the pH value of the outer medium containing parts of the pulvini are shown in Table 1. Three-hour irradiation of extensor parts with B or FR brought about a slight but statistically significant acidification of the outer environment. During a similar period of irradiation, R brought about the alkalization of the outer environment if the extensor parts were treated, or its acidification in the case of fragments of flexor tissue in the medium. The effects of B and FR action on the flexor parts were manifested by the alkalization of the outer medium, greater changes being observed in experiments with FR.

Table 1

Δ pH after 3 h incubation of separated parts of *Phaseolus coccineus* L. pulvini in deionized water and irradiation with different spectral ranges of light (SE±, n=10)

Spectral range	Motor tissue	
	Extensor	Flexor
B	−0.20 ± 0.02	+0.08 ± 0.01
R	+0.18 ± 0.03	−0.16 ± 0.02
FR	−0.26 ± 0.04	+0.16 ± 0.02

Tissue fresh weight was always 200 mg placed in 2 cm^3 of deionized water.

THE EFFECT OF Ca^{2+}-CHANNEL BLOCKERS

In another series of experiments, separated parts of pulvini were placed in a medium aditionally containing Ca^{2+}-channel blockers: verapamil (class: phenylalkylamine) and nifedipine (class: 1,4 dihydropyridine) at a concentration of 100 μM. After 3 h irradiation with different spectral ranges of light the concentration of Ca^{2+} and K^+ ions was determined in outer solutions containing parts of pulvini. The diagrams (Fig. 2) illustrate differences in the content of the two kinds of ions at the beginning of the irradiation period and 3 h later. Slight

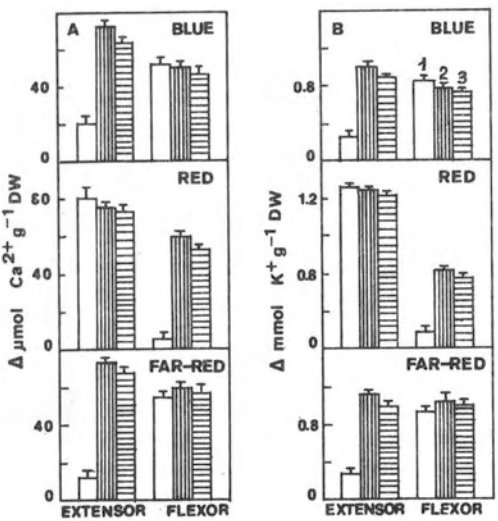

Fig. 2. Δ concentration of Ca^{2+} (A) and K^+ (B) in the medium after 3 h irradiation of isolated parts of *Phaseolus coccineus* pulvini with different spectral ranges of light. Motor tissue was incubated in: medium (1), medium with 100 μM verapamil (2), and medium with 100 μM nifedipine (3). (SE±, n = 10)

changes of the ionic concentration were brought about by the action of various spectral light ranges and of the inhibitors. However, they distinctly characterize differences in the effect of various spectral ranges and also the specificity of action of verapamil and nifedipine on the process of ion transport. The diagrams evidence changes in the concentration of ions in outer solutions depending on the parts of the pulvini and suggest that the action of these inhibitors controls the influx of ions to motor cells. On the other hand, their effect on the process of ion transport from a cell to the outer environment is insignificant. Analysis of the obtained results also shows that verapamil is more active than nifedipine in inhibiting the transport of ions to motor cells. In experiments with higher concentrations of the two inhibitors (1 mM) in the incubating medium the obtained changes in Ca^{2+} and K^+ concentration were similar to those described above (data not shown).

The results presented in this paper seem to suggest that in the case of verapamil or nifedipine treatment changes in the concentration of Ca^{2+} and K^+ ions observed in the outer medium modify the functioning of Ca^{2+}-channels. On the other hand, in comparing changes in the concentration of Ca^{2+} and K^+ in the outer medium, containing the given parts of the pulvini treated with Ca^{2+}-channel blockers, with a respective control, a stimulating effect of Ca^{2+} ions on the functioning of K^+-channels is motor cells is suggested.

DISCUSSION

Ion channels constitute a basic element in the structural system of plasmatic membranes. The effect of changes in their potential on the rate and effectiveness of ion transport has been confirmed in experiments carried out both on animal and plant cells. Investigations on the functioning of Ca^{2+}-channels have been carried out mainly on animal tissues, however, numerous observations on the role of Ca^{2+} as a second messenger in mediating between such reactions as seismonastic and nyctinastic movement or geotropic reactions, have also been recently obtained on plant material (Otsiogo-Oyabi and Roblin 1984, Poovaiah and Reddy 1987, Moran et al. 1988). Bisson (1984) and Amstrong and Matteson (1986) postulated that high concentrations of Ca^{2+} bring about the closing of K^+-channels through direct interaction with channel proteins. Tsien et al. (1987) assumed that concentration of Ca^{2+} to a micromolar level resulted in loss of selectivity in the functioning of Ca^{2+}-channels. The existence of coupling between the concentration of Ca^{2+} and the degree of opening of K^+-channels was also demonstrated in the algae, *Eremosphaera viridis* (Thaler et al. 1989) A-23187 calcium ionophore treatment. The above data suggest that a slight increase in the cytoplasmic Ca^{2+} level activated the opening of K^+-channels which remained open for a period of a few minutes. A further incrase in the Ca^{2+} concentration of 10^{-5}M brings about the closing of K^+-channels and the initiation of a Ca^{+2}-dependent on the transport

system of ATPases, which induces a decrease in the cytoplasmic Ca^{2+} level (Giannini et al. 1987).

In a previous study the occurrence of K^+-channels in parts of *Phaseolus coccineus* pulvini was documented. Their activity depends upon movements, being also closely related with the activity of electrogenic ion pumps (Białczyk and Lechowski 1990b). The present results suggest a different effect of the investigated spectral ranges on the Ca^{2+} and K^+ transport processes in motor cells. In the case of two parts of the pulvinus the nature of the changes in the ion levels seems to confirm a significant effect of Ca^{2+} on the activity and functioning of K^+-channels. The conversion of the changed concentrations of Ca^{2+} in the medium (Fig. 1A) to DW of tissue, demonstrates micromolar variation in this content. Small changes in the concentration of Ca^{2+} show that the role of calcium consists in mediating the transduction of the light signal. However, differences in the concentration of Ca^{2+} have a significant effect on the K^+ level in the extensor and flexor parts (Fig. 1B).

The results of experiments in which two parts of the pulvini were irradiated with B, R, and FR ranges, showed that in the light phase of the diurnal cycle, R reversed the direction of Ca^{2+} and K^+ transport. Under these light conditions the efflux of these ions took place in the extensor parts. A similar effect of B and FR was found in the flexor. In this case the observed changes are probably due to the mediation of Ca^{2+} transport by phytochrome photoconversion and creation of a new P_r/P_{fr} ratio (Lee and Satter 1988, Satter et al. 1988, Białczyk and Lechowski 1990a).

In the described processes of directional transport of ions, an important role is played by the activity of H^+-pumps located in the plasmalemma of motor cells. In the extensor part the action of B or FR stimulates their activity (Iglesias and Satter 1983, Lee and Satter 1989). R has a similar effect in the flexor part. The processes of activated release of H^+ from motor cells are accompanied by the reverse direction of K^+ transport (Satter et al. 1988). Changes in pH values of the medium (Table 1), depending on the action of different spectral ranges of light, reflect different activity of H^+-pumps in motor cells of the extensor and flexor zones. The slight alkalization of the medium due to B irradiation of the flexor part (about + 0.08 unit) requires a separate discussion. On the basis of previous results (Białczyk and Lechowski 1990a) we assumed that apart from the phytochrome an unidentified B sensor pigment occurred in the extensor. The results of the present work may suggest that its action is also mediated by Ca^{2+}. In this part of the pulvinus B, like darkness brings about the destruction of P_{fr}. After 3 h irradiation of the flexor with B, lower pH values in relation to FR may be attributed to: (a) a partial absorption of B by the phytochrome, or (b) the excitation of chlorophyll and fluorescent emission of R, which to a certain degree may carry out photoconversion of P_r to P_{fr}.

The effect of verapamil and nifedipine, specific Ca^{2+}-channel blockers, is

expressed by the limited influx of Ca^{2+} and K^+. The changes found in the Ca^{2+} and K^+ concentration in the medium are brought about by specific and characteristic action of the given spectral range, depending on the part of the pulvinus. As our results presented in Fig. 2 (compare the effect of R on extensor parts and of B and FR on flexor parts) show, the two inhibitors applied to the medium do not control the efflux of ions. A similar one-way character of action of the inhibitors on Ca^{2+}-channels was also postulated on the basis of their influence on light-induced cytoplasm movement of *Villisneria gigantea* protoplasts (Takagi and Nagai 1988). Variable and frequently contradictory results concerning the Ca^{2+}-channel blockers applied to plant tissues, have been obtained (Okazaki et al. 1987, Shina and Tazawa 1987). Current hypotheses do not have a sufficiently firm basis for resolving the questions arising concerning the functioning of Ca^{2+}-channels. Our present results permit us to postulate that the processes of K^+ transport and functioning of K^+-channels in *Phaseolus* pulvini depend to a significant degree on changes occurring at the level of cytoplasmic calcium in motor cells.

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Wpływ różnych zakresów spektralnych światła i blokerów Ca^{2+}-kanałów na koncentrację Ca^{2+} i K^+ w poduszeczkach liściowych Phaseolus coccineus L.

Streszczenie

Wpływ różnych zakresów spektralnych światła na modyfikację procesów transportowych badano w separowanych partiach poduszeczki liściowej *Phaseolus coccineus*. Po 1 h inkubacji separowanych partii prostownika i zwieracza w roztworach zawierających odpowiednio: wodę dejonizowaną, pożywkę, pożywkę z werapamilem lub nifedipiną, badany materiał poddawano 3 h napromieniowaniu światłem monochromatycznym o różnych długościach fali. W roztworach zewnętrznych oznaczano koncentrację jonów Ca^{2+}, K^+ i pH. Uzyskane wyniki wykazują występowanie specyficznego sprzężenia między koncentracją Ca^{2+} i K^+ w zależności od rodzaju stosowanego światła i partii poduszeczki liściowej. Określone zakresy spektralne światła wywołują przeciwstawne efekty w transporcie jonów w opozycyjnych partiach poduszeczki. Zmiany pH roztworów zewnętrznych zawierających separowane partie prostownika i zwieracza świadczą o różnym oddziaływaniu światła niebieskiego, czerwieni i dalekiej czerwieni na aktywność zlokalizowanych w komórkach motorycznych H^+-pomp. Zastosowanie specyficznych inhibitorów Ca^{2+}-kanałów: werapamilu i nifedypiny umożliwiło wykazanie istotnego wpływu jonów Ca^{2+} na aktywność i funkcjonowanie K^+-kanałów. Obydwa rodzaje inhibitorów hamują transport Ca^{2+} i K^+ do komórek motorycznych poduszeczki, nie wywierają natomiast wpływu na ich transport do środowiska zewnętrznego. Z prezentowanych obecnie wyników można wnioskować, że jony Ca^{2+} pośredniczą w transdukcji bodźca świetlnego.