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Physiological Studies on Pea Tendrils. II. The Role of Light and ATP in Contact Coiling

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Summary. Excised pea (*Pisum sativum* L.) tendrils incubated in the light coil more than those incubated in the dark. This light effect, which displays spectral responses characteristic of chlorophyll-mediated mechanisms, is increased by at least 8 hours of prior dark incubation of plants from which the tendrils were derived. Considerable evidence indicates a major role of ATP in coiling. For example, inhibitors of ATP production decrease contact coiling. Exogenous ATP increases curvature in the dark, whereas exogenous adenosine, AMP and ADP are practically without effect. The ATP effect can be reversed by the addition of sucrose to the bathing solution. Tendrils of plants placed in the dark overnight have lower ATP levels than those held in the light. One half hour after stimulation, the endogenous ATP level of tendrils on plants kept in the light decreased fourfold. In the same period, the endogenous inorganic phosphate level increased markedly, indicating high adenosine triphosphatase activity.

Curvature is proportional to the logarithm of the molarity of applied ATP between 10^{-4} and 10^{-2} M, whereas elongation responds only to the higher dosages. It is inferred that endogenous ATP is involved as an energy source in coiling, especially in the initial phase, which involves contraction of the tendril. The existence of a higher plant analog of actomyosin, suggested by others, is supported.

The contact coiling of the tendrils of the Alaska pea (*Pisum sativum* L.) has 2 component reactions, an initial contraction followed by differential elongation of the dorsal and ventral sides (15). These reactions are separable by treatments such as variation in pH, addition of growth substances and decapitation of the tendrils. They are markedly temperature dependent. When excised tendrils are incubated in the light they display greater increments of both curvature and elongation than those incubated in the dark. This paper concerns the role of light as a source of the energy required for coiling and the intervention of ATP in this process.

Materials and Methods

The detailed procedures for the assay of contact coiling of excised tendrils and tendrils in situ have been previously described (15). Most of the experiments described in this paper were performed with excised tendrils incubated on a laboratory shaker in 10 cm petri dishes containing 10.0 ml of appropriate solution.

Ten- to 13-day-old plants were used as a source of tendrils. Some were placed in a dark room overnight (ca. 18–20 hrs) while others were kept in the light. The effect of intensity of white light on coiling was examined by covering the petri dishes containing the tendrils with various layers of cheese cloth. Light intensity was measured with a standard phototube radiation meter coupled to a multiple range precision microammeter (2). The duration of light starvation necessary to increase coiling was measured by placing light-grown plants in the dark for various times and then removing them for incubation in the light. The measurement of the coiling response to equal intensities of various narrow wavelength ranges was accomplished in a specially constructed irradiation box. This apparatus consisted of 4 chambers, each containing an air cooled 500 w projection lamp. Light from the lamp passed through a glass heat filter, a collimator and then a double wafer composed of a Bausch & Lomb interference filter and a Corning filter. Incident light intensity could be controlled both by varying the distance from the light to the tendrils and by a variable rheostat in series with the light source. Thus, 4 narrow range spectral areas could be tested at the same time. In this experiment, petri dishes of 6 cm diameter containing 5 ml of basal solution were irradiated for 2 hours. Each petri dish was shaken by hand 50

[1] Abbreviations used in this paper are: A, adenosine; CP, creatine phosphate; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethyl urea; DNP, 2,4-dinitrophenol; CCP, carbonyl cyanide phenylhydrazone.

times every one-half hour to facilitate contact coiling. In all treatments, irradiation was 100 ergs $\times$ cm^{-2} $\times$ sec^{-1}. For routine brief irradiation treatments with red or far red light, fluorescent lamps wrapped in several layers of red cellophane or photoflood infra-red lamps filtered through water plus red and blue cellophane were used (3, 4).

The effects of 0.1 mM *p*-dichlorophenyldimethylurea, 0.1 mM 2, 4-dinitrophenol and 10 μM carbonyl cyanide phenylhydrazone were tested on light starved tendrils incubated for 2 hours in the light and in the dark without sucrose in the basal medium. The effect of anaerobic incubation in nitrogen was tested in the light and in the dark on light-starved tendrils by passing a continuous stream of the gas through a manifold and thence into the reaction vessels. Each reaction vessel consisted of a 125 ml vacuum flask containing 10 tendrils in 10 ml of solution. The gas was passed in through a tube at the mouth and out through the side arm. The inlet tube terminated just above the surface of the solution, to avoid agitation of the tendrils by bubbling. The effects of adenosine, AMP, ADP and ATP were tested on light-starved tendrils shaken in the light or in the dark, with or without sucrose for 2 hours. The effect of 1 mM ATP on differential dorsi-ventral elongation of excised tendrils after 30 minute incubation in the light was determined by the previously described method (15).

Endogenous ATP was assayed by the firefly tail system which is specific for this nucleoside triphosphate (23). About 3 g of tendrils (ca. 400 tendrils) were placed in a container kept in an ice bath to prevent post-harvest coiling (15). The tendrils were weighed and then frozen. The frozen tendrils were ground with sand in ca. 15 ml of 10 % (v/v) perchloric acid and the suspension centrifuged at ca. 2200 $\times$ *g*. The supernatant fluid was neutralized with 10 N KOH and the solution centrifuged to get rid of the potassium perchlorate. The supernatant phase was dried in a flash evaporator and dissolved in 1.0 ml of distilled water, furnishing the test solution. The enzyme-substrate solution was made up of a suspension of 50 mg of an acetone powder of firefly tail (*Photenus pyralis*) extract (23) in 25 ml of cacodylate buffer (0.05 M) at pH 7.4 containing 0.02 M Mg SO_4. The reaction was monitored by the recorder in a Gilford Multiple Sample Absorbance Recorder coupled to a Beckman Model D U Spectrophotometer. The recorder was set to give a maximal deflection at 560 mμ (the wavelength of maximum emission of the reaction) (22) and the light source was turned off. Thereafter the input to the photocell was provided by the light from the reaction resulting from mixing the tendril extract with the firefly tail preparation. To monitor a reaction, 0.8 ml of the resuspended acetone powder was placed in a cuvette. The cuvette was positioned in the covered well of the spectrophotometer, which was then shielded from all light. It was important to complete the reaction mixture in total darkness because any stray light activated the recorder and tended to mask the reaction peak which occurred within 1 to 2 seconds after the addition of the test solution. 0.7 ml of the test solution was added in total darkness to complete the reaction mixture. Four standard concentrations of ATP were also tested during each experiment to give a standard curve.

Inorganic phosphate was assayed as follows. Twenty tendrils (ca. 0.1 g) were harvested, weighed and frozen. The frozen tissue was ground with sand and 5 ml of distilled water in a mortar. The resulting suspension was boiled for 10 minutes, cooled and centrifuged for 5 minutes at 2200 $\times$ *g* in a clinical centrifuge. The supernatant fluid was recovered and extracted 3 times with 3 ml of anhydrous ethyl ether to remove the last traces of chlorophyll. The aqueous fraction was made up to 10 ml, shaken with norit A activated charcoal to remove carotenoids and other colored substances, and filtered through Whatman No. 1 filter paper. Three ml of the clarified solution was added to 1 ml of the chromogenic reagent (see below) and the mixture incubated at 30° for 15 minutes. The resulting blue color was measured at 650 mμ in a Bausch and Lomb Spectronic-20 spectrophotometer using some of the undeveloped clarified solution as a reagent blank. The chromogenic reagent consisted of 5 g $FeSO_4$ and 1 g $(NH_4)_2$ MoO_4 dissolved in 100 ml of 1.0 N H_2SO_4. A standard curve was prepared using $Na_3PO_4 \cdot 12H_2O$.

Except where otherwise mentioned, all experiments were replicated at least 3 times.

Results

In many of our early experiments, the excised tendrils were incubated for 20 hours. In the experiments reported here we found that 2 hour incubations gave quantitatively smaller but qualitatively similar results. Hence, unless other incubation periods were specifically required, all experiments described had incubation times of 2 hours. In general, tendrils in situ curved most in response to a given stimulus, followed in order by excised tendrils continually shaken in 10 cm petri dishes, excised tendrils intermittently shaken in 6 cm petri dishes, excised tendrils continuously shaken in vacuum flasks and excised tendrils unshaken in petri dishes. The poor coiling in some of the vacuum flasks was probably due to the rounded bottom surface which resulted in poor turbulence, and hence little agitation of the tendrils in the solution. This diminished movement allowed less opportunity for contact between tendrils, and hence less coiling.

In order more closely to approximate natural growing conditions, plants grown under continuous light were removed for various dark periods, then returned to the light before stimulation of the tendrils. Figure 1 shows that dark periods some-

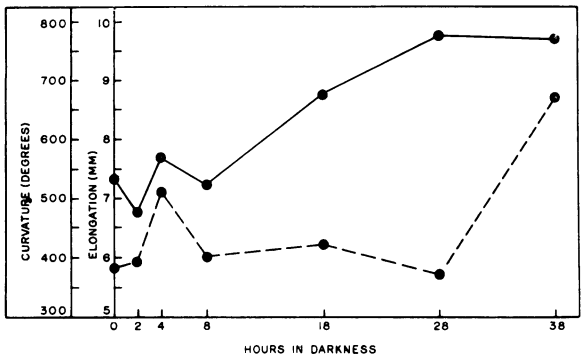

FIG. 1. Effect of duration of dark treatment on curvature (————) and elongation (- - - -) of tendrils transferred to the light and incubated there for 2 hours.

what greater than 8 hrs. increased subsequent curvature in the light, while dark pretreatments of longer than 28 hours increased tendril elongation in light. Plants which had been given such extended dark periods differed in several respects from those held in the light. The tissues (especially the new organs) were lighter green in color. In addition, the paired leaflets of the plants held in the dark were usually somewhat closed whereas those of the plants held in the light remained open. Tendril length was, however, not affected by the dark treatment.

To obtain maximum curvature responses, most of the subsequent experiments utilized tendrils from light grown plants which had been held in the dark overnight. When this was done, both curvature and elongation increased markedly upon incubation for 2 or 20 hours in the light, the response increasing with the light intensity (fig 2). Spectral response data showed optima for curvature to be in the red and blue regions of the visible spectrum. For example, the increase of curvature over the dark control of each of the following wavelengths was: 439 mμ, 23°; 482 mμ, 67°; 520 mμ, 15°; 595 mμ, 22°; 638 mμ, 166°; 680 mμ, 65°; and 735 mμ, 9°. All light treatments were at 100 ergs × cm^{-2} × sec^{-1}. The comparable curvature in white light of higher intensity was 193°.

Brief treatments with red and far red light had little or no effect on subsequent curvature or elongation whether light grown or dark treated tendrils were tested. Thus, phytochrome does not obviously control curvature in these tendrils. While a prior dark treatment of up to 28 hours increases curvature of tendrils subsequently incubated in the light, it decreases curvature in tendrils incubated in the dark. A prior dark treatment caused a decreased elongation both in the light and in the dark, while tendrils kept in continuous light elongated more in the dark than in the light.

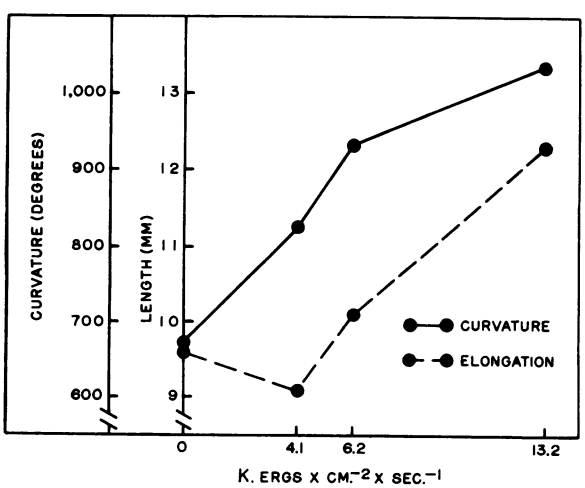

FIG. 2. Curvature (————) and elongation (- - - -) response of tendrils to various intensities of white light after 20 hours incubation. The mean tendril measurements at excision were 51.6 mm ± 1.1 mm, and 90°, ± 2°.

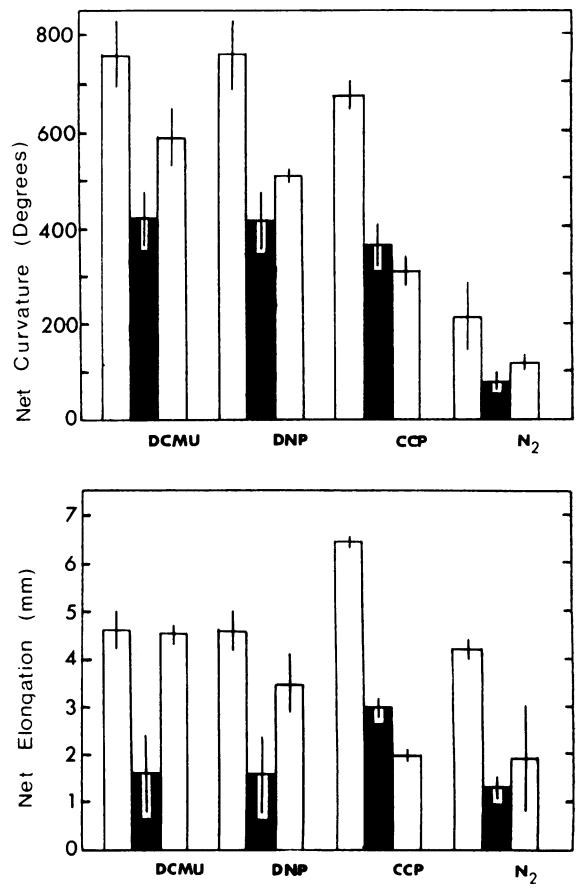

FIG. 3. Effect of electron transport inhibitors and anaerobiosis on curvature and elongation of tendrils incubated in white light for 2 hours. Open bars indicate incubation in the light; black bars indicate incubation in the dark. Lines on bars indicate magnitude of the standard error.

In the light, DCMU had a slight inhibitory effect on curvature but none on elongation (fig 3).

DNP partially decreased both curvature and elongation in the light. CCP completely stopped the curvature and elongation due to light. Incubation under anaerobic conditions in a stream of N_2 decreased curvature in the light to about 55 % of the control, and elongation to about 45 % of the control. When comparable experiments were performed in the dark, N_2 significantly reduced curvature to about 33 % of the dark control and elongation to about 35 % of the dark control. However, neither DCMU, DNP nor CCP, significantly affected curvature or elongation in the dark.

We have previously noted (15) that 0.1 M sucrose included in the bathing solution decreases curvature and elongation in the light. This is shown again in figure 4. In the dark, sucrose had little effect on curvature, but did increase elongation. These effects of sucrose, together with the effects of the inhibitors of oxidative and photosynthetic phosphorylation suggested that endogenous levels of energy-rich phosphates might be the determining factor in both curvature and growth. To test this, exogenous ATP, ADP, AMP and adenosine were added to the medium in the dark and the curvature and elongation compared with light controls. The data are presented in figure 4. It is apparent that

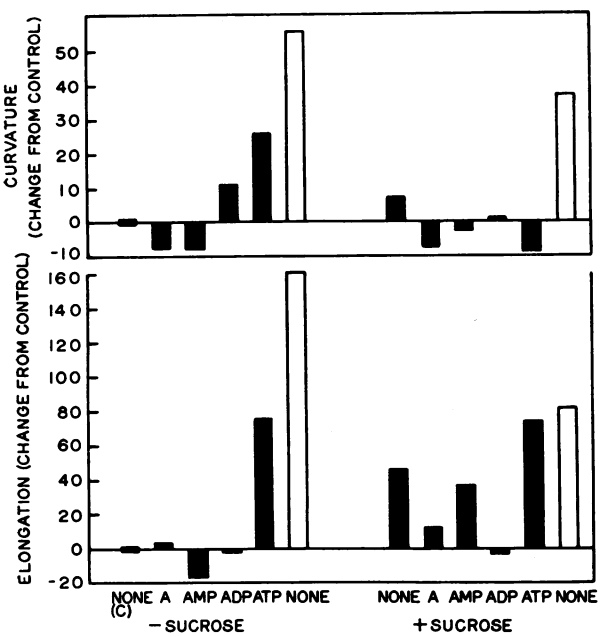

FIG. 4. Interactions of 0.1 M sucrose with mM adenosine (A), AMP, ADP and ATP in coiling of tendrils incubated for 2 hours. Curvature and elongation in the ordinates are expressed as percent change from the control. The open bars indicate incubation in the light whereas the black bars indicate incubation in the dark. The mean tendril measurements at excision were 58.9 mm ± a standard error of 0.7 mm, and 74° ± a standard error of 4°. All data are given relative to the dark controls lacking sucrose. The measurements of these controls were 1.6 mm and 414°.

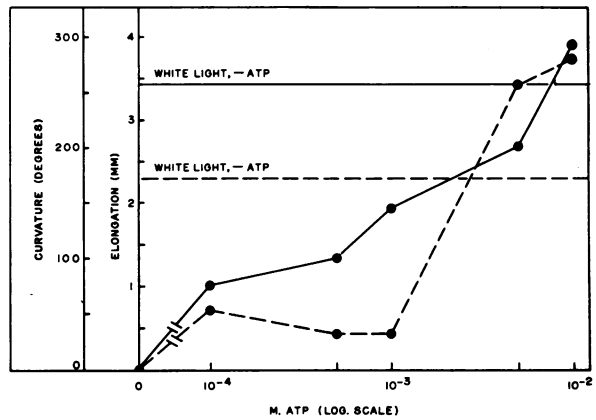

FIG. 5. Elongation (- - -) and curvature (———) response of tendrils to various concentrations of ATP. Each point on the curves is given relative to the control which contained no ATP. The net changes in these controls were 2.6 mm and 291°. Except for the light controls, incubation was for 2 hours in the dark. The mean tendril measurements at excision were 50.3 mm ± 1.4 mm, and 86° ± 6°.

ATP increases both growth and curvature in the absence of sucrose and elongation in the presence of sucrose. None of the other addenda was as effective. The effect of ATP on curvature is approximately proportional to the logarithm of the applied concentration (fig 5). Elongation responds similarly at higher concentrations of ATP but is not affected at concentrations much lower than 5 mM. The ventral surface of light grown tendrils, when treated with mM ATP in the light, contracted considerably more than the controls which were not given ATP. The length data were as follows: ventral surfaces of the controls contracted 0.05 mm, from 4.59 mm to 4.54 mm. The ventral surface of tendrils treated with ATP contracted 0.24 mm, from 4.68 mm to 4.44 mm.

To check on the specificity of ATP in producing these effects, tendrils were treated in the dark with mM nucleoside triphosphates and creatine phosphate. When curvature in the dark, minus any addendum, was adjusted to a base of zero, curvature in the light, similarly treated, was 99°. The tendrils

Table I. *Effect of Darkness and Coiling on ATP Levels in Tendrils*

Each datum is followed by its standard error.

Treatment	Mean degrees curvature	mμmoles ATP per g fr wt
Overnight in darkness, unstimulated	69 ± 6	480 ± 134
Kept in light, unstimulated	74 ± 2	690 ± 168
Kept in light, stimulated and contracted*	350 ± 6	170 ± 124

* Stimulated and allowed to coil in situ for 30 min.

treated with various addenda in the dark curved as follows: ATP, 120; CTP, 73; ITP, 64; CP, 24; GTP, 4; and UTP, −57 degrees.

Table I shows that an overnight dark treatment caused almost a 30 % decrease in the endogenous ATP content of the tendrils, compared with a light control. The contraction phase of the coiling event caused a 75 % decrease in ATP level within 30 minutes. In the same period, the endogenous inorganic phosphate of stimulated tendrils increased markedly and appeared to reach a peak at about 20 minutes (table II).

Table II. *Effect of Coiling on Inorganic Phosphate (P_i) Levels in Tendrils Incubated in the Light*
Each datum is followed by its standard error.

Treatment	Mean degrees curvature	mμmoles P_i per g fr wt
Unstimulated tendrils	66 ± 20	320 ± 17
Contracted for 10 min*	191 ± 2	360 ± 59
Contracted for 20 min*	267 ± 6	510 ± 59
Contracted for 30 min*	342 ± 8	440 ± 69

* Stimulated and allowed to coil in situ.

Discussion

In nature, the pea plant is exposed to alternate periods of light and dark, and the contact coiling capacity of the tendrils shows an adaptation to this regime. A dark period given to light-grown plants seems to have little effect on the habital growth of tendrils, although it does affect their chlorophyll and ATP content. Incubation of the tendril in the light subsequent to the dark period results in an increase in contact coiling. From figure 1 it appears that the minimum dark period required to produce this effect is approximately 8 hours. There appears to be an increasing effect with increasing dark period, at least up to 38 hours, and there is no indication of either an optimum or of circadian rhythms.

Red and blue light are both effective in increasing curvature whereas violet, green, and far red light are less effective. Based on these facts the light effect might be attributed either to chlorophyll or phytochrome, both of which are known to mediate the light-induced movements of plant parts (6, 17, 24). The rates of circumnutation of dark grown pea (8) and laminar unfolding in wheat (24) are greatly increased by red light, and these effects are reversible by far red light. On the other hand, Kuiper concludes that the maintainance of stomatal opening depends on photosynthesis (17) although he conducted no red-far red reversibility studies to rule out the possibility of partial phytochrome involvement. Two facts indicate that phytochrome does not play a role in the light effects on pea tendril coiling; first, low energies of light are ineffective, and second the reaction is not red-far red reversible. Thus, photosynthesis, or at least some chlorophyll-mediated mechanism is probably involved. However, the reduction of CO_2 and ultimate production of sugar does not seem to be the major chemical process involved because the presence of sucrose in the bathing solution causes little change in coiling in the dark and actually decreases it in the light. One must therefore look to the possibility that other products of photosynthesis such as ATP are directly involved in the movement. In this connection, it should be noted that Kuiper (17) concluded that stomatal movement was mediated by photosynthetic ATP production. The postulated light-induced phosphorylation is apparently not entirely due to photosynthesis, since N_2 partially inhibited coiling in the light. It may be due, in part, to light-increased oxidative phosphorylation, since respiration of bean leaves has been shown to increase as a result of exposure to light (21). Of the 3 organic inhibitors used, the greatest inhibition of curvature in the light was caused by 0.1 mM DNP, which reportedly inhibits oxidative phosphorylation (9), but not photophosphorylation (1) and CCP, an inhibitor of both types of phosphorylation (10, 11). This might be taken to indicate that respiratory energy is responsible for curvature. However, these compounds have no effect on curvature in the dark. Thus one might assume that photorespiration, which apparently differs from dark respiration (7) is in part responsible for the light effect on coiling. N_2 only partially inhibits light induced coiling; thus some of the coiling increment due to light must be due to an N_2-stable mechanism. Since DCMU, which is a photosynthetic poison, partially inhibits the light induced coiling, and since photosynthetic phosphorylation can occur in N_2, we conclude that there is a photosynthetic component in light-induced contact coiling. These facts might help to explain the increased curvature found to occur at 482 mμ, since photorespiration in an achlorophyllous strain of *Chlorella vulgaris* is stimulated by blue-green light (16). Therefore both photosynthesis and photorespiration seem to be involved in the light induced increment of contact coiling.

We have shown previously that the first event in contact coiling involves contraction (15). During this phase, which persists for 30 to 120 minutes in excised tendrils, the ventral side of the tendril contracts, while the dorsal side elongates. Then follows a phase during which the dorsal side elongates at a greater rate than the ventral side. An increase in rate of the contraction phase should still be reflected by greater curvature after 2 hours, although its effect would be diluted by a further lapse of time. Thus, even if the exogenous ATP increased only the duration of the contraction phase and did not enhance coiling during the elongation phase, it could account for the measurable increase in coiling. It would seem that the primary effect of ATP is, in fact on contraction, because such

an effect has been observed and because curvature increases over a wide range of ATP concentrations, whereas elongation is affected only by the higher ATP levels (fig 5).

ATP has been implicated as the energy source in various types of contractile systems, such as the amoeboid movement of the slime mold *Physarum polyccphalum* (18), cilia of *Vorticella* (13), and, of course, muscle fibers (20). Thus it is not surprising that the pea tendrils, which contract during the first phase of contact coiling, are controlled by a similar mechanism. Such a view is supported by the recent discovery of a contractile adenosine triphosphatase system in the leaves of higher plants (25). It is interesting to note that Hasselbach (12) in a study of the effect of various nucleoside triphosphates on muscle fiber contraction, found the relative activity to be 100 for ATP, 80 for CTP, 30 for ITP, and 15 for GTP. If ATP is set to a value of 100 in our experiments, the comparable values for curvature induction for the other compounds are: CTP, 61; ITP, 53; and GTP, 3. Such similarities in 2 such disparate contractile systems suggest that the details of the energetics of contraction may be alike.

Our accumulated evidence indicates that ATP is the native source of chemical energy for contact coiling. This evidence includes the fact that the endogenous ATP level decreases and the P_i level increases during coiling, strongly suggesting that adenosine triphosphatase activity is involved in coiling. It should be noted that the demonstrated decrease in ATP (table I) exceeds by far the demonstrated increase in P_i. This inequality may be due to regulatory mechanisms involved in rapid incorporation of P_i into a variety of compounds. This occurs, for example, in striated muscle contraction, where ATP is cleaved and the resulting P_i rapidly incorporated into glyceric acid 1, 3-diphosphate and recycled via creatine-phosphate during relaxation to regenerate ATP (20). In such a system, one might expect an initial large increase in P_i, which rapidly diminishes with time. This explanation seems to fit the kind of results which we have obtained. Twenty minutes after stimulation, the endogenous P_i had increased by about 190 $m\mu$ moles/gm fr wt. One half hour after stimulation, the endogenous ATP had decreased by approximately 520 $m\mu$ moles/gm fr wt and the increase in P_i had dropped to 120 $m\mu$ moles/gm fr wt. It would be very desirable to measure ATP levels 10 and 20 minutes after stimulation, but the time required to harvest the necessary 400 tendrils precludes such observations at present. This experiment awaits a more sensitive means of measuring ATP concentration, making feasible a smaller, more rapid harvest. Such an apparatus has recently been made available to us.

The inhibition of both coiling and the ATP effect by sucrose is difficult to understand and the mechanism of this inhibition is unclear. It is interesting to note, however, that sucrose has been found to antagonize certain effects of auxin on ion uptake (14) and that auxin increases both coiling (15) and ATP production (19).

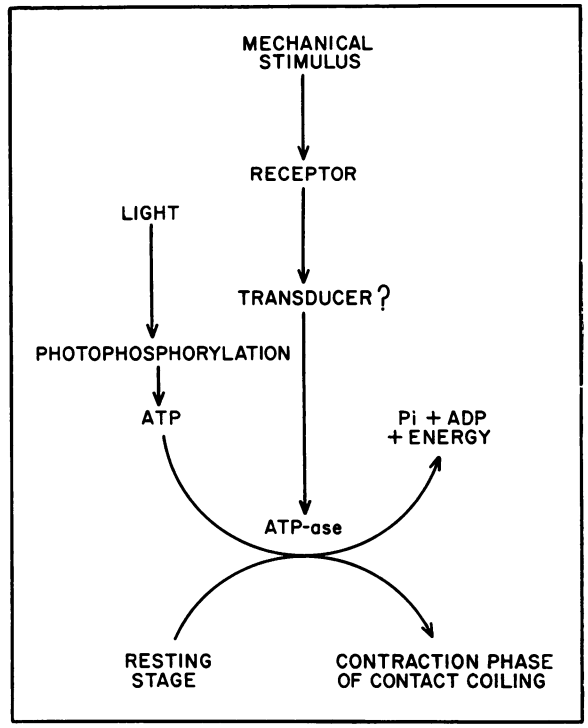

FIG. 6. Possible sequence of events leading to contact coiling.

It is possible to construct a model for the contraction phase of contact coiling which seems harmonious with all the available facts (fig 6). In the resting stage, ATP exists at a certain level. Withdrawing light or otherwise inhibiting phosphorylation decreases this level and hence the ability of the tendril to coil. Upon stimulation of the irritable portion of the ventral surface of the tendril, ATP is cleaved, P_i liberated, and the energy used in contraction. During the early stages of contraction, P_i is released in excess; later some acceptor substance scavenges this excess phosphate.

Whether or not the original ATP level is eventually regenerated cannot be determined from the data presented here. In a tendril whose support was removed after simulation, Darwin (5) found a return to the resting stage and a renewed capability for contact coiling. In such a tendril, regeneration of ATP probably does occur.

Acknowledgments

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