



FIG. 1. C, control; P, short-day treatment prolonged until the time of ear emergence.

were arranged so that all were completed on the same day (Aug. 7) and the seedlings were transplanted on that day. After the short-day treatment was over, the seedlings were kept in the pot culture house under environmental conditions identical with those of the control plants which were sown and transplanted on the very same day as the plants from treated seeds. In another set, after 6 wk of short days in the seed bed, the short days were continued till ear emergence was noted in all the plants. Data for ear emergence of the main shoot are graphically represented in Fig. 1. A study of this figure shows that there is a gradual delay in the time of ear emergence as the duration of short-day treatments is increased in the seed bed and thereafter. In the experimental set where the short days were prolonged until heading, the delay was very marked. The photoperiodic behavior of these 3 medium-early varieties is somewhat akin to that of the 4 early varieties T.136, T.N.22, T.N.27, and Ch.10 of U.P. (2). Similar results were obtained by Sircar and Ghosh (3) in Charnock and Panbira, 2 summer varieties of rice of Bengal, by the application of 8-hr short days. Sircar and Parija (4), however, have not obtained any delaying effect in Jhanji 34 and Bhutmari 36, 2 other summer varieties of Bengal, by giving similar treatments. Kar (5), after giving long and short days for only 15 days to 2 summer and 8 winter varieties of rice of Bengal, made a general statement that in different varieties of paddy, high temperature associated with short day lengths was inductive to earliness and that low temperature or longer day lengths produced retardation. In the light of the present investigation, Kar's statement needs modification. In these 3 medium-early varieties of rice of U.P., short days did not induce earliness but rather they greatly prolonged the time of ear emergence. The photoperiodic behavior of medium-early varieties stands quite in contrast to those of late or winter varieties of rice where considerable earliness is obtained by application of the same short-day photoperiod (6). The response to photoperiod in rice is thus greatly varietal and is largely controlled by the agricultural characteristic of the predominant groups. While studying the

effect of long days on these medium-early varieties it was also seen that 24-hr long days for 3-6 wk in the seed bed brought about a delaying effect on ear emergence. On the basis of their flowering behavior as related to length of day, these medium-early varieties may be classified as intermediates, as they flower within a definite range of length of day, producing flowers less readily when the days are either sufficiently shortened on the one hand or sufficiently lengthened on the other (7, 8).

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## The Effect of Adenosinetriphosphate on the Cilia of the Pharyngeal Mucosa of the Frog

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At the present time it is generally agreed that adenosinetriphosphate (ATP) participates widely in the chemical to mechanical energy-converting systems of living organisms. Particularly in the case of muscle, the role of this compound has been studied extensively (1, 2). Bacterial flagellar proteins have been observed to contract when treated with ATP, and bacterial motility is increased specifically by this substance (3). Moreover, the rates of cytoplasmic streaming and amoeboid movement rise after injection of ATP solutions into the tail region of *Amoeba discoides* (4). In the present report, data summarized show that the movement of cilia of the pharyngeal mucosa of the frog is strikingly accelerated in the presence of ATP. Thus, the evidence suggests that ciliary activity may be included among the various types of cellular movement related to this ubiquitous compound.

Ciliary activity was measured in terms of the rate of transport of a standard object across the ciliated pharyngeal mucosa of the frog (*Rana pipiens*), using a technique generally similar to the method employed by Stewart (5). In each of 29 experiments, the pharyngeal mucosa of a pithed frog was dissected free of underlying tissues and pinned with slight traction to a weighted cork. The preparation was immersed in 20-200 ml aliquots of specified test solutions in a paraffin-lined or glass container. The time required for the transport of a piece of aluminum foil (weight = 0.1 mg; area ca. 1 mm<sup>2</sup>) along a 1-cm distance in a hori-

TABLE 1  
EFFECT OF ATP ( $1.5 \times 10^{-4}$  M) ON THE RATE OF  
TRANSPORT OF A TEST OBJECT ACROSS  
THE CILIATED MUCOSA

Solution in which tissue was immersed	Number of experiments	Rate of transport mm/10 sec	Rate of transport relative (initial control = 100)
Initial control Ringer's solution (pH = 7.14)	9	$4.3 \pm 1.4$	100
Ringer's with ATP ( $1.5 \times 10^{-4}$ M) (pH = 7.18)	9	$8.1 \pm 1.7$	$196 \pm 40$
Final control Ringer's solution (pH = 7.14)	9	$3.9 \pm 1.4$	$91 \pm 13$

zontal plane was measured, and the rate of transport (mm/10 sec) was calculated. The detailed procedure was as follows: 6 rate determinations were made in the control solution (buffered amphibian Ringer's solution). The mucosa was then transferred to an experimental solution containing ATP and 6 determinations were again made. Finally, the ciliated tissue was placed in a fresh aliquot of control Ringer's solution, and the rate was measured as before. A 1-min equilibration period was allowed, after transfer of the tissue to the new immersion medium, before measurements were made. All solutions were at room temperature (ca. 22–26° C). The concentrations of solutes in the amphibian Ringer's solution were 0.124 M for NaCl, 1.1 mM for  $\text{CaCl}_2$ , 1.9 mM for KCl, 2.4 mM for  $\text{NaHCO}_3$ , 0.7 mM for  $\text{NaH}_2\text{PO}_4$ , and 1.11 mM for glucose.<sup>1</sup> ATP—in the form of the sodium salt,  $\text{Na}_4(\text{ATP}) \cdot 3\text{H}_2\text{O}$ —was present in concentrations of  $1.5 \times 10^{-5}$  M,  $1.5 \times 10^{-4}$  M, or  $1.5 \times 10^{-3}$  M. In some experiments, the effect of ATP hydrolyzed according to the method of Lohmann (6) was tested.

In every instance in which ATP was present in the Ringer's solution, ciliary activity increased markedly. The data summarized in Table 1 show that the rate was approximately doubled in  $1.5 \times 10^{-4}$  M ATP. The effect was reversible, for, when the mucosa was transferred to a fresh lot of control Ringer's solution, the activity was noted to fall to a level close to the control rate (Table 1). The time required for these alterations was brief, since the changes had become fully established by the end of the standard 1-min equilibration time. A maximal response was seen with ATP concentrations as low as  $1.5 \times 10^{-5}$  M, and a 100-fold increase

<sup>1</sup> It may be noted that this solution contained glucose as substrate and no magnesium ions. In further experiments a modified Krebs-Ringer phosphate solution (242 mOs/l) was used which contained  $\text{MgSO}_4$  at a concentration of 1.14 mM and had no substrate. Since the results of these experiments were closely similar to the results discussed above, it was concluded that neither the absence of  $\text{Mg}^{++}$  nor the presence of glucose was a significant factor in determining the effect of ATP on ciliary activity.

in ATP concentration did not result in an appreciable further increase in rate (Table 2). In specimens in which initial activity in Ringer's solution was irregular, it became stabilized in the presence of ATP. Moreover, in one experiment where no ciliary activity could be detected under control conditions, the addition of ATP was followed immediately by the onset of ciliary movement. Solutions containing a hydrolyzate of ATP were without any effect on the rate of ciliary activity (Table 2).

TABLE 2  
EFFECT OF VARIOUS SOLUTIONS ON THE RATE OF  
TRANSPORT OF A TEST OBJECT ACROSS  
THE CILIATED MUCOSA

Solution tested	Number of experiments	Rate of transport mm/10 sec	Relative rate of transport (initial control = 100)
Control Ringer's solution (pH = 7.14)	27	$4.3 \pm 1.3$	100
Ringer's with ATP $1.5 \times 10^{-5}$ M	5	$9.3 \pm 1.1$	$210 \pm 31$
Ringer's with ATP $1.5 \times 10^{-4}$ M (pH = 7.18)	9	$8.1 \pm 1.7$	$196 \pm 40$
Ringer's with ATP $1.5 \times 10^{-3}$ M	5	$10.1 \pm 2.5$	$292 \pm 100$
Ringer's with hydrolyzate of ATP $1.5 \times 10^{-4}$ M (pH = 7.12)	4	$3.0 \pm 0.7$	$94 \pm 11$

The accelerating action of ATP on the ciliary movement of the frog's pharyngeal mucosa may be described, in summary, as highly consistent, rapid, reversible, and demonstrable in the presence of relatively low concentrations of ATP. The effect appears to be specific in that hydrolysis of the substance abolishes completely its effect on the test system. The mechanism of action of ATP on ciliary movement is still unclear, however, for the compound may affect the ciliary contractile elements directly or indirectly (through concomitant alterations in the cell membrane). In spite of their obvious significance in general physiology and in medicine, problems of ciliary activity have been somewhat neglected of late. They warrant careful reinvestigation in the light of recent developments in the field of cell physiology and biochemistry.

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