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Short Communication

Data On Chemical Transformations Supplying Energy to Various Types of Motivated Cells and Single-Cellular Organisms

E.I. Bon[1*], N.Ye. Maksimovich[1], U.K. Dvorina[1]

[1]Department of Pathological Physiology, Grodno State Medical University, Hrodna Region - 230009, Belarus

***Corresponding Author:** E.I. Bon, Department of Pathological Physiology, Grodno State Medical University, Hrodna Region - 230009, Belarus.

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Abstract

The study of energy supply mechanisms for cellular movement represents one of the fundamental problems in pathophysiological and biochemical research.

Following the elucidation of the role of adenosine triphosphate (ATP) in muscle contraction, the question arose whether similar principles govern the motility of other cell types, including unicellular organisms and motile cells of higher animals. The ability of various microorganisms—both saprophytic and pathogenic, including obligate and facultative anaerobes such as intestinal protozoa (Entamoeba histolytica, Balantidium coli, Trichomonas faecalis) and trypanosomes—to utilize the energy of exothermic transformations (lactic, butyric, valeric acid fermentation) for locomotion has long been recognized, yet experimental verification remained essential.

Over the past decades, the chemical dynamics of motile cells have been investigated along the lines established by muscle biochemistry, with particular attention to the role of nucleoside triphosphates in contractile processes. The development of cellular models, such as spermatozoa and trypanosomes extracted with glycerol solutions, has provided a powerful experimental framework for studying the mechanochemical coupling between ATP hydrolysis and mechanical work. The present article examines the historical and contemporary evidence supporting the unity of contractile mechanisms across diverse cell types, from amoeboid locomotion to movement via flagella and cilia, with emphasis on the role of the ATPase–ATP system in energy transduction.

Keywords: Adenosine triphosphate (ATP), Cellular motility, Anaerobic metabolism, Contractile proteins, Actomyosin, Undulipodia, Flagella, Cilia, Spermatozoa, Cellular models, Bioenergetics, Entamoeba histolytica, Trypanosomes, Fermentation, Mechanochemical coupling.

Introduction

After the mechanism of the most important biochemical transformations that supply muscle cells with the energy necessary to perform their mechanical functions had been studied primarily in muscles, the question naturally arose of the possibility of transferring these concepts to other types of cells capable of movement.

It should be noted that the ability of many microorganisms, both saprophytic and pathogenic, to use the energy of anodic processes for the purposes of movement has never been in doubt, since we were talking about organisms belonging to the group of obligate or facultative anaerobes. In addition to motile anaerobic bacteria, such microorganisms include various species of parasitic intestinal protozoa (Entamoeba histolytica, Balantidium coli, Trichomonas faecalis), many trypanosomes, etc[2,6,10,12].

The processes that supply For anaerobically living organisms, the energy required for movement is provided by the same exothermic transformations that determine the primary

type of metabolism of a given organism (lactic, valeric, butyric acid fermentation, etc.). However, this highly plausible assumption still required experimental proof in each individual case.

The study of the chemical dynamics of motile cells and motile microorganisms has developed over the past two to three decades primarily along the lines indicated by muscle biochemistry. Particular attention has been paid to clarifying the extent to which the chemical mechanisms of contraction of striated muscle fibers and more primitive motility organelles—flagella, cilia, etc.—extend. This issue is examined in more detail in specialized monographs and articles devoted to the chemical dynamics of motile cells.

Here we consider it necessary to recall that the ability to move through space using specialized organs and organelles of movement is known to be characteristic primarily of organisms belonging to the animal kingdom, although the protoplasm of plant cells also possesses some contractility and motility.

The most primitive form of protoplasmic movement is so-called amoeboid locomotion, in which the cell moves by means of pseudopodia, which simultaneously serve to capture food. These pseudopodia can be considered the results of apolar movement of protoplasmic particles, characteristic to varying degrees of any part of it. Movement by means of various types of pseudopodia is a characteristic feature of all naked protozoa. The type of pseudopodia in some cases, for example, in rhizopods, is even an important feature for the taxonomy of these organisms. Amoeboid movement can also be observed in the cells of higher animals, for example, in leukocytes, especially during the embryonic stage of development.

As for the causes of the appearance of various forms of pseudopodia on the cell surface, until recently, their formation was most often associated with a sudden decrease in surface tension in certain areas of the cell membrane—the cell pellicle—as a result of local shifts in the concentration of hydrogen ions. Other theories explained the cell's amoeboid movement by periodic changes in osmotic pressure, rapid swelling and deswelling of plasma colloids, due, for example, to the recharging of colloidal particles and so on. But even in these cases, the primary cause of the colloidal-chemical changes occurring in plasma proteins was considered to be the formation of acid- or alkaline-reacting metabolic products (for example, lactic acid, ammonia, etc.). One of us wrote the following on this subject: "All these ideas, at least in their original formulation, must now be recognized as too primitive. In light of the latest data on the mechanism of contraction of fibrillar contractile proteins of muscles, the phenomenon of contractility of protoplasm and other types of cells can hardly be reduced only to the above-mentioned colloidal or physicochemical phenomena arising as a result of a local change in the active reaction (pH). While fully recognizing the well-known significance of these factors, one can also consider that the contractility of protoplasm is due to special contractile or contractile proteins of fibrous structure, capable of suddenly changing their colloidal state (degree of hydration, and possibly micelle size) as a result of chemical interaction with certain "energy-rich" substances such as adenosine triphosphate (ATP)[1-3].

From the above text, it is quite clear that the hypothesis of the crucial role of nucleoside triphosphates in the mechanical function of motile cells arose immediately after the publication of the fundamental works establishing the role of ATP in the mechanism of muscle contraction.

A significantly more advanced form of movement, enabling the relatively rapid movement of microorganisms in space, is movement via undulipodia. These movements are produced by permanently existing organelles—plasma processes, flagella, or cilia—which are present in a specific number and arranged in a specific order in each cell. The general nature of these movements is reduced to the alternating flexion and straightening or rotation of the motor organs [4,14,20].

The formation of specialized contractile organelles with a fibrous structure at a certain stage in the phylogeny of simple organisms does not, of course, exclude the possibility of other forms of movement within the cell's protoplasm, such as the movement of vacuoles containing reserve food substances, etc [5].

Movement by undulipodia is a characteristic feature of all Flagellata and Ciliata, zoospores of algae and fungi, as well as spermatozoa of higher animals and plants, ciliated epithelial cells, and some other cells. However, it is impossible to draw a sharp distinction between the two forms of locomotion in simple organisms—amoeboid locomotion and locomotion by undulipodia—since intermediate forms of cells have been described, moving by pseudopodia, producing sudden, sometimes even synchronous, rotations or pendulum-like movements.

Without completely touching here on the fine structure of the locomotion organelles of lower organisms and their kinematics, we will nevertheless dwell in somewhat greater detail on the factors that underlie these movements.

Usually, the active contractile element of any locomotion organelle is considered not to be the relatively more rigid skeletal filament of the cilium or flagellum, which is considered to play the role of an antagonistically acting elastic extensor, but rather the liquid plasma or a special contractile fibril (myonema). Moreover, as in the case of amoeboid movement, the cause of organelle motility, as well as that of the myonema, was until recently usually attributed to a sudden change in surface tension in certain areas, the emergence of electrical charges, osmotic forces, and so on.

Regarding all of these concepts, the same observations can be made that were made during a cursory examination of the theory of amoeboid cellular movement. Undoubtedly, here too, one must not overlook the possibility of sudden changes in the colloidal state of the contractile proteins of the motile

organelle as a result of their chemical interaction with certain energy-rich substances, as occurs, for example, during the contraction of a myofibril.

Indeed a wide variety of motile organelles (flagella, cilia, etc.) possess the capacity for double refraction of light or light. "The contraction, wherever and in whatever form it occurs," writes this author, "is associated with the presence of birefringent uniaxial particles, the optical axis of which coincides with the direction of shortening."

[1]The existence of such elastic skeletal threads has now been demonstrated in many types of motile cells. Particularly interesting data on their structure have been obtained in recent years using electron.

This ability to exhibit birefringence brings the contractile substance of primitive movement organelles closer to the most studied substrate of muscle contraction—actomyosin. The latter, as is known, exhibits birefringence not only within muscle fibers, but also in vitro in solutions. In motion (the phenomenon of birefringence in flow), and partly in threads obtained by blowing protein into water.

Interestingly, the birefringence of both the anisotropic substance of myofibrils and various other contractile structures decreases sharply during contraction of the corresponding organs or organelles of movement.

Thus, one can truly believe that contraction, "wherever and in whatever form it occurs," is associated not only with the presence of birefringent uniaxial particles, but also with the chemical interaction of the protein substance of these particles with energy-rich polyphosphorus compounds.

The same idea about the possibility of unity between the contractile mechanisms of muscle fiber and various types of motile cells was expressed by V. A. Engelhardt.

Experimental development of this question began almost simultaneously in 1943-1945 in several laboratories. The chosen object was the seminal cell, endowed with the capacity for extremely energetic movement, many aspects of which had already been well studied by this time.

The choice of the seminal cell as an object for studying the question of how the energy of biochemical processes is converted into mechanical work was undoubtedly successful.

It has been established that virtually all the energy released during metabolic processes in the sperm of E. esculentes is used to maintain movement. Sperm, particularly sea urchin sperm, are thus an ideal object for studying the mechanism by which chemical energy is converted into cellular work.

Of great interest has been the mechanism by which sperm utilize the energy of respiration and glycolysis to perform their motor function. As is known, according to existing concepts, during biphasic muscular work, the energy of chemical exothermic transformations is used indirectly, but through the resynthesis of adenosine triphosphate, the breakdown of which is directly linked to muscular activity. The idea of the indirect use of respiration and glycolysis energy by the sperm cell for locomotion is supported by the fact, that when respiration and glycolysis are simultaneously blocked, for example, by poisoning sperm with monobromoacetate and cyanide, the movement of the sperm cells ceases, although quickly, but not immediately. Apparently, under these conditions, spermatozoa, like muscles, have the ability to maintain movement for some time due to the energy of dephosphorylation of the ATP system.

Be that as it may, the spermatozoa's energy resources, represented by organophosphorus compounds, must be very limited. This follows from the fact that, with the simultaneous blocking of respiration and glycolysis, the ability to maintain sperm motility is ensured only for 1-3 minutes at 37°C and 5-10 minutes at 18°C [7-8,11,13].

Determination of the adenosine triphosphate content in mammalian sperm was undertaken by I. I. Ivanov and K. I. Kanygina, S. A. Burnasheva, V. A. Engelhardt, and Lardy, Hansen, and Phillips. According to I. I. Ivanov and K. I. Kanygina, the content of adenosine triphosphoric acid in bull spermatozoa obtained from the epididymis fluctuates between 12 and 30 mg of adenosine triphosphoric acid phosphorus per 100 g of Cauda epididymis content (8–20 mg% of easily hydrolyzable phosphorus). The content of adenosine triphosphoric acid decreases sharply during anaerobiosis, simultaneously with the cessation of progressive sperm motility. After the creation of aerobic conditions or with the addition of glucose, the content of adenosine triphosphoric acid in the seminal cells returns to its original value; sperm motility is simultaneously restored. Similar data were obtained by Lardy, Hansen, and Phillips, who determined that well-aerated sperm contain approximately 1 mg of readily hydrolyzable phosphorus per 1 g of dry weight of seminal cells.

The breakdown of adenosine triphosphate and loss of sperm motility under anaerobic conditions occur particularly rapidly in the presence of the glycolysis inhibitor monobromoacetate (Tables 12 and 13).

Thus, in this series of experiments, the hypothesis of the similarity in the mechanisms of energy transfer from respiration and glycolysis to the co-tractile elements of both muscle and seminal cells via the resynthesis of adenosine triphosphate was fully confirmed. Somewhat later, Mann (1945a, b) isolated adenosine triphosphoric acid as a barium salt from ram sperm and established the presence of other adenosine derivatives in mammalian spermatozoa. The N to P ratio in the isolated barium salt of adenosine triphosphoric acid corresponded to the theoretical ratio of 1:2. According to Mann, the content of adenosine triphosphoric acid in ram sperm, expressed in milligrams of amino nitrogen or easily hydrolyzable phosphorus, fluctuates within the following limits: 0.6-1.5 mg of amino nitrogen and 2.6-6.6 mg of easily hydrolyzable phosphorus per 100 ml of semen.

In the more liquid semen of bulls, the concentration of adenosine triphosphoric acid was expressed as 0.4 mg of amino nitrogen and 1.7 mg of readily hydrolyzable phosphorus, respectively.

It is easy to see that these figures are entirely consistent with the data of I. I. Ivanov and K. S. Kanygina, obtained when determining adenosine triphosphoric acid in the contents of the cauda epididymis of bull testes. In the contents of the epididymis of boar testes the concentration of adenosine triphosphoric acid ranges from 5-9 mg% of readily hydrolyzable phosphorus. S. A. Burnasheva demonstrated the possibility of immobilizing mammalian spermatozoa with magnesium salts, which inactivate the cells' adenosine triphosphatase activity, without reducing their adenosine triphosphoric acid levels. In addition, S. A. Burnasheva isolated a protein fraction from spermatozoa possessing adenosine triphosphatase activity. This fraction was named spermosin by V. A. Engelhardt.

Later, V. A. Engelhardt and S. A. Burnasheva demonstrated that the ATPase activity of spermatozoa is localized (80%) in the tail region of the sperm, i.e., directly in the contractile apparatus of the motile cell.

According to Mann, the total content of other adenosine derivatives in ram semen is approximately 3.9 mg of amino acid nitrogen per 100 ml of seminal fluid, with 3.45 mg of amino acid nitrogen contained in the formed elements of sperm—spermatozoa.

I. I. Ivanov, B. S. Kaeavina, and L. D. Fomenko isolated adenosine triphosphoric acid in the form of a barium salt from boar spermatozoa and studied its effect on muscle actomyosin. It turned out that adenosine triphosphate from seminal cells does not differ from muscle adenosine triphosphoric acid in its ability to alter the properties of actomyosin. From all of the above, it clearly followed that the ATPase-ATP system must play the same role in sperm tail movement, as well as in other types of cellular movement, as it is attributed to in the mechanism of muscle contraction.

This position was rigorously demonstrated experimentally somewhat later in the work of Hoffmann-Berling on so-called cellular models.

Hoffmann-Berling and Weber and Hoffmann-Berling proposed a method for studying the contraction of cellular protoplasm upon its interaction with ATP, using tissue culture cells extracted with 30-50% glycerol for this purpose. Living cells are known to have an elongated shape during interphase. If they are extracted with glycerol in this state, then upon the addition of ATP they contract, assuming a spherical shape. When cells are extracted after anaphase, ATP induces division, apparently due to equatorial contraction of the protoplasm. In cells extracted after early anaphase, the addition of ATP causes chromosomes to separate, sometimes to a distance comparable to that observed in living cell division.

In a later study, by the same author, it was reported that contractile protein can be extracted from sarcomatous cells and then subjected to special purification. The solubility of this protein in saline solutions depends on the ionic strength of the solution and the presence of ATP. If ATP is added to a contractile protein gel at an ionic strength of approximately 0.1, the gel contracts or, like actomyosin, undergoes superprecipitation. The protein isolated by Hoffmann-Berling exhibits significant, though less pronounced, ATPase activity than actomyosin. This activity varies depending on the concentration of Mg++ ions and the ionic strength of the solution, and is suppressed by the same poisons that inhibit actomyosin's ability to break down ATP. The viscosity of the contractile protein solution isolated by the author reversibly decreases upon the addition of ATP.

Later, B.F. Poglazov, in the laboratory of V.A. Engelhardt, discovered ATPase activity in a number of other objects, including plant ones, capable of active contraction (leaves of Mimosa pudica, Desmodium gyrans, and some acacias). However, the ATPase from mimosa leaves turned out to be a cytoplasmically soluble enzyme.

Of particular interest is that Hoffmann-Berling demonstrated the possibility of reproducing the complete contraction-relaxation cycle in cellular models (spermatozoa and trypanosomes extracted with a water-glycerol solution) simply by adding ATP to a solution containing KCl and MgCl2. Under these conditions, spermatozoa produced rapid tail movements, while trypanosomes performed wave-like movements of their undulating membranes[9,15-19].

Ciliated epithelium from the palatal mucosa of frogs, as well as rat and rabbit tracheae, extracted with 45% aqueous glycerol, also proved to be an extremely demonstrative and convenient cellular model.

The importance of cellular models in studying the mechanochemistry of contractile processes can hardly be overestimated. These models reveal a unified principle used by nature to solve a wide variety of problems associated with the need to perform various types of mechanical work. In these studies, we directly approach the decipherment of the mechanism of the biphasic activity of various movement organelles, including the alternating contraction and relaxation of muscles in highly organized animals.

Regarding the history of contractile systems not identical to actomyosin, it is necessary to recall that I. B. Zbarsky and K. A. Perevoshchikova demonstrated that ATP can induce in vitro syneresis of histone extracted from cell nuclei using the Kossel method.

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