ЖЭТФ, 2001, том 119, вып. 1, стр. 199–204

PHYSICS OF THE ATPASE MOLECULAR MOTOR

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Submitted 22 June 2000

A physical description of rotary molecular motors is given. The fundamental relations between dynamical characteristics of the motors are found and their basic macroscopic parameters are evaluated. The role of molecular chirality is explained. The membrane nano-structure and the ionic subsystem are discussed more precisely as elements of the motors. The stochastic features of the thermal noise-assisted processes occurring in the motors are manifested.

PACS: 87.16.Nn; 87.16.Dg; 64.70.Md

1. INTRODUCTION

Adenosine tri phosphate (ATP) synthase is an exceptional molecular machine acting in cell respiration in mitochondria and in photosynthesis in chloroplasts of plants and also in bacteria [1–3]. ATP synthase is called the enzyme «F_0F_1ATPase», in which the F_1 part contains the catalytic center and the F_0 part couples the F_1 part to the membrane. It was shown that a stream of hydrogen ions across the membrane drives the ATP formation and the coupling of ATP synthase to the hydrogen ion transport occurs via the F_0 part. ATP functions as a carrier of energy in all living organisms, it captures the chemical energy released by the combustion of nutrients and transfers it to reactions that require energy. ATP consists of the nucleoside adenosine linked to three phosphate groups. On removal of the outermost phosphate group, adenosine di phosphate (ADP) is formed and the energy released can be used in other reactions. Conversely, with the help of energy, an inorganic phosphate group can be bound to ADP and form ATP.

To understand in detail how the F_0F_1ATPase functions, a detailed chemical and structural knowledge of an enzyme was obtained [2]. The three-dimensional structure of ATP synthase was clarified. The F_1 part consists of five sub-units α, β, γ, δ, and ε. While there are three α and three β units, there is only one unit of γ, δ, and ε. The ATP synthesis occurs on the β units. The sub-units γ, δ, and ε are not symmetrical, they are in fact chiral [4, 5], a feature of importance for our understanding of how ATP synthase functions.

Much attention has been given to the F_1 part. It was found that the step requiring energy is not the synthesis of ATP from ADP and inorganic phosphate, but the binding of ADP and the phosphate to the enzyme, which produces the ATP where the energy surplus is stored. The γ, δ, and ε sub-units rotate in a cylinder formed of the alternating α and β sub-units. This rotation induces structural changes in β that lead to differences in the binding ability during a cycle; in addition, this rotation is driven by the ion flow through the membrane. The γ sub-unit behaves as an asymmetrical axle. It has unique contacts with the β sub-units and forces their active surfaces to assume different three-dimensional structures. The rotation of the γ sub-unit was demonstrated experimentally [6].

2. GENERALIZED FORCES AND CURRENTS IN THE ISOTHERMAL CHIRAL ROTARY MOTOR

This molecular motor is isothermal, which means that its internal states are locally in equilibrium at a constant temperature T. We believe that a certain general physical approach to the description of these motors is possible, similarly to how this was recently done for linear molecular motors [7]. The action of the motor is induced by generalized forces that are the electric field $\mathbf{E}$ acting in the membrane, the mechanical motion velocity $\mathbf{N}$ relevant to the motor, and the chemical potential difference Δ that measures the free energy change per consumed «fuel» molecule. $\Delta = 0$ at chemical equilibrium. Δ is positive for the ATP hydrolysis process when ATP is in excess and is negative when ADP is in excess. The action of the forces $\mathbf{E}$, $\mathbf{N}$, and Δ leads to the electric current, rotation, and fuel consumption characterized by the generalized «currents»: the electric current density $\mathbf{j}$, the mechanical force $\mathbf{g}$ applied to the motor, and the average consumption rate of fuel molecules u, i. e., in our case, the average number of ATP molecules bound and hydrolyzed per unit time (or the average number of ADP molecules bound to the enzyme and used for the ATP synthesis). The mechanical force $\mathbf{g}$ includes the viscous friction force relevant to the motor in which the mechanical motion occurs.

The dependences $\mathbf{j}(\mathbf{E},\mathbf{N},\Delta)$, $\mathbf{g}(\mathbf{E},\mathbf{N},\Delta)$, and $u(\mathbf{E},\mathbf{N},\Delta)$ are in general nonlinear, because the motor operates far from the equilibrium ($\Delta > k_BT$). But it is useful to consider the linear regime ($\Delta < k_BT$), where we can write the relations

$$\mathbf{j} = \sigma\mathbf{E} + v\mathbf{n}\times\mathbf{N} + \mathbf{e}\Delta, \tag{1a}$$

$$u = -\mathbf{e}\cdot\mathbf{E} - \mathbf{v}\cdot\mathbf{N} + \lambda\Delta, \tag{1b}$$

$$\mathbf{g} = v\mathbf{n}\times\mathbf{E} + \eta\mathbf{N} + \mathbf{v}\Delta. \tag{1c}$$

Relations (1) insure that the dissipation rate $\dot{S}$ is positive,

$$\dot{S} = \mathbf{j}\cdot\mathbf{E} + u\Delta + \mathbf{g}\cdot\mathbf{N} = \sigma E^2 + \lambda\Delta^2 + \eta N^2, \tag{2}$$

where the electric conductivity σ, the viscosity η, and a coefficient λ are positive. The appearance of the coefficient v in Eqs. (1) is directly related to the asymmetry (chirality) of the moving part—the γ sub-unit—of the motor; v is a pseudo-scalar when the product $\mathbf{n}\times\mathbf{N}$ is a pseudo-vector and $v\ \mathbf{n}\times\mathbf{N}$ is a vector. The component $\mathbf{n}_\perp$ of the director $\mathbf{n} = \mathbf{n}_\parallel + \mathbf{n}_\perp$ describes the inclination of the γ sub-unit axis $\mathbf{n}$ at a small angle Θ from the normal $\mathbf{z}$ to the membrane surface,

$$n_x^2 + n_y^2 = \Theta^2, \quad \mathbf{n}^2 = 1, \quad n_z^2 \approx 1. \tag{3}$$

We have the vector $\mathbf{N} = d\mathbf{n}/dt = \mathbf{\Omega}\times\mathbf{n}$, where the pseudo-vector $\mathbf{\Omega}$ is the angular velocity of the axle,

$$\begin{gathered} \Omega_z \neq 0, \quad \Omega_x = \Omega_y = 0, \\ N_x = -n_y\Omega_z, \quad N_y = n_x\Omega_z, \quad N_z = 0. \end{gathered} \tag{4}$$

It is seen from Eqs. (1) and (4) that the polar vector $\mathbf{v}$ must be perpendicular to $\mathbf{n}$ and parallel to $\mathbf{N}$ if $\mathbf{vN} \neq 0$. The formalism in Eqs. (1)–(4) based on describing the motor by a director $\mathbf{n}$ is quite similar to the approach developed for liquid crystals [8].

The kinetic coefficient $\mathbf{e}$ is a polar vector. It describes the interaction whereby the fuel consumption induces the electric current and mechanical motion. Without the tilting at a finite angle Θ, this interaction disappears. We, thus, assume $\mathbf{e}$ to be related physically to some polar interactions, for example between dipoles (electric and/or steric) $\mathbf{p}_\beta$ characterizing the deformation of the β-units and the polarization $\mathbf{P}_\gamma$ characterizing the inclined γ-unit. Because of chirality, the two-dimensional vector $\mathbf{P}_y$ is related to $\mathbf{n}$ by

$$\mathbf{P}_\gamma = \mu\xi, \quad \xi_x = n_z n_y, \quad \xi_y = -n_z n_x, \tag{5a}$$

$$\begin{gathered} P_{\gamma x} = \mu n_z n_y, \quad P_{\gamma y} = -\mu n_z n_x, \\ \mathbf{P}_y \times \mathbf{n}_\perp \approx \mu\Theta^2, \end{gathered} \tag{5b}$$

where μ is the «piezomodulus» depending on the enzyme chirality. Equations (5) are similar to the formalism developed for the description of chiral smectic-C liquid crystals [9]. Thus, the vector $\mathbf{e}$ can be represented as

$$\mathbf{e} = c\mathbf{P}_\beta \times \boldsymbol{\xi}, \tag{6}$$

which vanishes in the absence of the γ-unit tilting.

The polar vector $\mathbf{v}$, by the same physical reasons, is assumed to be related to the director $\mathbf{n}$ and the polarization vectors $\mathbf{P}_\gamma$ and $\mathbf{p}_\beta$. But the relation $\mathbf{v} = b\mathbf{P}_\gamma$, for example, is forbidden because in this case, a part of the dissipation rate is the scalar product

$$\Delta\mathbf{v}\cdot\mathbf{N} = -b\mu n_z\Omega_z\Theta^2\Delta$$

that depends on the direction of $\mathbf{n}$, but the physical quantities must not depend on the direction of $\mathbf{n}$ (they depend on even combinations of the n components). At the same time, the components of $\mathbf{v}$ must be proportional to the components of the director $\mathbf{n}$, with $\mathbf{v}$ being parallel to $\mathbf{N}$ in accordance with Eqs. (1). It is possible to write a unique combination (at small tilt angles) for the vector $\mathbf{v}$,

$$\mathbf{v} = b\mu[\mathbf{n}\times\mathbf{e}] = -b\mu\xi(\mathbf{n}_\perp\cdot\mathbf{p}_\beta) = -b\mathbf{P}_\gamma(\mathbf{n}_\perp\cdot\mathbf{p}_\beta). \tag{7}$$

The products $\mathbf{v}\cdot\mathbf{N}$ and $\mathbf{v}\times\mathbf{n}$ then become

$$\mathbf{v}\cdot\mathbf{N} = b\mu n_z\Omega_z\Theta^2(\mathbf{n}_\perp\cdot\mathbf{p}_\beta), \tag{8}$$

$$[\mathbf{v}\times\mathbf{n}]_i = b\mu(\mathbf{n}_\perp\cdot\mathbf{p}_\beta)(n_z^2 - \delta_{iz})n_i. \tag{9}$$

These expressions depend only on even combinations of the $\mathbf{n}$ components. The products $\mathbf{n}_\perp\cdot\mathbf{p}_\beta$ and $\mathbf{p}_\beta\times\xi$

must be constant parameters of the system under consideration. This is possible under the assumptions made above: the dipoles $\mathbf{p}_\beta$, the pseudo-vector ξ, and the director component $\mathbf{n}_\perp$ are in the membrane plane, $\mathbf{n}_\perp$ and $\mathbf{p}_\beta$ are collinear, and $\mathbf{n}_\perp$ and ξ are orthogonal to each other during the interactions of the rotating γ-unit with different β-units. It then follows that $\mathbf{n}_\perp \cdot \mathbf{p}_\beta = \Theta p_\beta$. Thus, these products are constant parameters of the membrane system and are proportional to the tilt angle Θ and the dipole moment p_β.

We note that the tilt angle Θ and the dipole moment p_β describing the inclination of the γ-unit and deformations of β-units respectively, must depend on the energy transferred to these sub-units during the motor work. These quantities vanish in the absence of this energy transfer. The energy transfer can occur due to chemical reactions, ionic currents, and mechanical movements. The constants b and c in relations (6) and (7) must in general describe some energy transfer mechanisms, which are unknown in detail unfortunately. Because these constants involved in $\mathbf{e}$ and $\mathbf{v}$ are related to the same physical process, we can expect them to be related to each other by other parameters of the motor, such as the electric conductivity, chirality etc.; in other words, the motor is assumed to work as a self-consistent system in which all kinds of motion start and stop simultaneously.

3. NON-PASSIVE REGIMES OF THE MOTOR WORK

The molecular motor stops in the absence of the γ-unit tilting, because both the $\mathbf{j} \cdot \mathbf{E}$ and $u\Delta$ terms are positive and $\mathbf{g} \cdot \mathbf{N} = 0$, i. e., there is no energy output from the enzyme: all work performed at the enzyme is dissipated in the thermal bath. When $\Delta = 0$ and $\Theta = 0$, we have the density current $\mathbf{j} = \sigma \mathbf{E}$ if the electric field is present inside the membrane. But without the energy output from the thermal bath, this current decreases with time and vanishes at the equilibrium conditions because of a re-distribution of ions. We assume that $\mathbf{E} = 0$ if the difference Δ is zero.

If $\mathbf{g} \cdot \mathbf{N}$ is negative, mechanical work is performed by the motor. If $u\Delta$ is negative, chemical energy is generated by the motor. If $\mathbf{j} \cdot \mathbf{E}$ is negative, the motor produces electric energy. Thus, the enzyme can work in various non-passive regimes.

1) $u\Delta > 0, \mathbf{g} \cdot \mathbf{N} < 0, \mathbf{j} \cdot \mathbf{E} > 0$. The motor takes the energy from the heat bath, for instance it uses the hydrolysis of ATP in excess (i. e., $u > 0$ and $\Delta > 0$) and from the work produced by the electric current to generate mechanical rotation.

2) $u\Delta < 0, \mathbf{g} \cdot \mathbf{N} > 0, \mathbf{j} \cdot \mathbf{E} > 0$. The system binds ADP and the phosphate to the enzyme and releases ATP already in excess (i. e., $u < 0$ and $\Delta > 0$) from the mechanical and electrical input.

3) $u\Delta > 0, \mathbf{g} \cdot \mathbf{N} < 0, \mathbf{j} \cdot \mathbf{E} > 0$. The motor uses ADP in excess (i. e., $u < 0$ and $\Delta < 0$) and the electric current to generate mechanical work.

4) $u\Delta < 0, \mathbf{g} \cdot \mathbf{N} > 0, \mathbf{j} \cdot \mathbf{E} > 0$. The system produces ADP already in excess (i. e., $u > 0$ and $\Delta < 0$) from the mechanical and electrical input.

5) $u\Delta > 0, \mathbf{g} \cdot \mathbf{N} < 0, \mathbf{j} \cdot \mathbf{E} < 0$. The motor a) uses the hydrolysis of ATP in excess (i. e., $u > 0$ and $\Delta > 0$) or b) uses ADP in excess for the synthesis of ATP (i. e., $u < 0$ and $\Delta < 0$) to generate mechanical rotation and electric current.

6) $u\Delta < 0, \mathbf{g} \cdot \mathbf{N} > 0, \mathbf{j} \cdot \mathbf{E} < 0$. The system a) produces ADP already in excess (i. e., $u > 0$ and $\Delta < 0$) or b) produces ATP already in excess (i. e., $u < 0$ and $\Delta > 0$) and also the electric current from the mechanical input.

7) $u\Delta > 0, \mathbf{g} \cdot \mathbf{N} > 0, \mathbf{j} \cdot \mathbf{E} < 0$. The motor a) uses the hydrolysis of ATP in excess (i. e., $u > 0$ and $\Delta > 0$) or b) uses ADP in excess (i. e., $u < 0$ and $\Delta < 0$) and also the mechanical input to generate electric current.

8) $u\Delta < 0, \mathbf{g} \cdot \mathbf{N} < 0, \mathbf{j} \cdot \mathbf{E} > 0$. The motor a) releases ATP already in excess (i. e., $u < 0$ and $\Delta > 0$) or b) produces ADP already in excess (i. e., $u > 0$ and $\Delta < 0$) and generates mechanical rotation from the electric input.

Thus, 12 regimes are available in this motor. The rotation of the axle (at $\Theta \neq 0$) with a constant angular velocity $\Omega_z = \dot{\phi}$ occurs when the viscous-driven torque and the field-driven torque compensate each other (neglecting some elastic forces), i. e., when $\mathbf{g} \times \mathbf{n} = 0$. We then obtain from Eqs. (1) and (5)–(9) that

$$\gamma \Omega_z = v E_z - b\mu\Delta(\mathbf{p}_\beta \cdot \mathbf{n}_\perp) n_z. \qquad (10)$$

This equation shows that a constant angular velocity arises even in the case where $\mathbf{E} = 0$, but the tilt angle Θ must have a finite value for the effect to occur. Tilting of the γ-unit induced by the energy transfer to this sub-unit from the heat bath results in the appearance of the electric current $\mathbf{j}$ even at $\mathbf{E} = 0$ (see Eq. (1a)). We note that the motor does not produce mechanical work, i. e., $\mathbf{g} \cdot \mathbf{N} = 0$, when the rotation of the axle occurs with constant velocity (10).

In the general case, the sum

$$\mathbf{j} \cdot \mathbf{E} + \mathbf{g} \cdot \mathbf{N} = \sigma E^2 + \gamma N^2 + \Delta(\mathbf{e} \cdot \mathbf{E} + \mathbf{v} \cdot \mathbf{N}) \qquad (11)$$

can change its sign only if the sign of $\Delta(\mathbf{e}\cdot\mathbf{E}+\mathbf{v}\cdot\mathbf{N})$ changes. In the regimes with $u\Delta > 0$ and $\mathbf{j}\cdot\mathbf{E}+\mathbf{g}\cdot\mathbf{N} < 0$, the motor produces mechanical work if $\Delta(\mathbf{e}\cdot\mathbf{E}+\mathbf{v}\cdot\mathbf{N})$ is negative and $\mathbf{g}\cdot\mathbf{N}$ is negative. Thus, we conclude that the sign of the angular velocity can change only if the direction of the vector $\mathbf{E}$ and the sign of Δ are reversed to preserve the negative signs of $\mathbf{j}\cdot\mathbf{E}+\mathbf{g}\cdot\mathbf{N}$ and $\mathbf{g}\cdot\mathbf{N}$. This means that to preserve the positive sign of $u\Delta$, the sign of u must change; for example, the hydrolysis of ATP in excess must change to using ADP in excess. At the same time, the direction of $\mathbf{E}$ is reversed. If the motor also generates the electric current, i. e., $\mathbf{j}\cdot\mathbf{E} < 0$, the change of the $\mathbf{E}$ direction results in changing the direction of the electric current $\mathbf{j}$ in the case where energy is taken from the heat bath.

In the acting motor [1], the regime $u\Delta > 0$ seems to determine the binding of ADP in excess and phosphate to the enzyme and the release of ATP (i. e., $u < 0$ and $\Delta < 0$). This results in only one way for the enzyme to react, i. e., the directions of the angular velocity Ω and of the current $\mathbf{j}$ are strictly determined. The hydrolysis of ATP in excess and the release of ADP (i. e., $u > 0$ and $\Delta > 0$) must lead to reversing the directions of Ω and $\mathbf{j}$. We note that at $\mathbf{E} = 0$, the dissipation rate $\dot{S}$ is equal to $\lambda\Delta^2$, with $\mathbf{N} = \mathbf{g} = 0$ and $\mathbf{j} = \mathbf{e}\Delta$, i. e., the motor does not produce work. Thus, to produce mechanical work, a certain electric field inside the biomembrane and the inclination of the γ-unit at a certain angle must occur.

4. ELECTRIC CURRENT WORK AND EFFICIENCY OF THE ROTARY MOTOR

For the motor with a constant rotation velocity ($\mathbf{g}\cdot\mathbf{N} = 0$, with the mechanical work not produced), we see from Eqs. (5)–(11) that $\mathbf{j}\cdot\mathbf{E} < 0$ if

$$\left(\sigma + \frac{v^2\Theta^2}{\gamma}\right) E_z^2 - \Delta\left(c + \frac{bv\mu\Theta^2}{\gamma}\right) \times \times (\mathbf{n}_\perp \cdot \mathbf{p}_\beta)(n_z E_z) \le 0. \quad (12)$$

Thus, the motor generates electric current until $\mathbf{j}\cdot\mathbf{E} < 0$ occurs at a finite value of E_z when condition (12) is satisfied. In this case, the j_z value is

$$j_z = \left(\sigma + \frac{v^2\Theta^2}{\gamma}\right) E_z - \Delta\left(c + \frac{bv\mu\Theta^2}{\gamma}\right)(\mathbf{n}_\perp \cdot \mathbf{p}_\beta) n_z = \quad (13)$$

$$= \sigma E_z - c\Delta p_\beta \Theta n_z + v\Theta^2\Omega_z. \quad (14)$$

We conclude from relations (12)–(14) that certain threshold conditions (for the Θ value at a given value of E_z or for the E_z value at a given value of Θ) must occur for the motor to generate the current. In weak fields and at small tilt angles, the threshold condition must have the form

$$\sigma n_z E_z \approx c\Delta p_\beta \Theta. \quad (15)$$

At the threshold condition, we have $j_z = 0$. The motor stops to generate current when E_z overcomes the threshold value determined by Eq. (15) or, in other words, when the tilt angle Θ is less than the threshold value determined by Eq. (15). We also see from relations (12)–(14) that the change of the sign of Δ results in sign changes of E_z, j_z, and Ω_z when the motor generates electric current in another regime with $u\Delta > 0$. Thus, the change of regimes reverses the directions of the electric current and the angular velocity. In the regime with $u < 0$ and $\Delta < 0$, the same threshold conditions take place for the electric field of the opposite direction. Because the experimental data show that the rotation and the current flow start and stop simultaneously, i. e., $j_z = 0$ and $\Omega_z = 0$ at the same time, we conclude from Eqs. (10) and (14) that the parameters σ, v, b, and c are related by

$$b\mu\sigma \approx cv. \quad (16)$$

It is useful to note that relation (16) can also be obtained when $E_z = 0$ if we consider Ω_z and j_z in Eqs. (10) and (14) as induced by the effective field

$$E_{z,eff} \approx -\frac{b\Delta\mu p_\beta\Theta}{v} n_z \approx -\frac{c\Delta p_\beta\Theta}{\sigma} n_z. \quad (17)$$

This is quite reasonable physically because the current density $j_z = \sigma E_{z,eff}$ and the angular velocity $\Omega_z = vE_{z,eff}/\gamma$ must have the same origin: these closely related quantities have the same meaning as in the Lehmann effect in chiral liquid crystals [8]. These relations show again that the flow of ions and the γ-unit rotation are related to each other and exist due to the tilting of the γ-unit. According to the data known today [3–5], both the tilt and the rotation of the γ-unit open the way for the ion motion and the effect of moving ions (the transfer of their energy) on the sequence of β- and α-units; the latter ones are prepared (by a change of the unit shape) for the subsequent processes of the ADP and phosphate binding to the enzyme and of releasing ATP. It is important for the motor that the rotation of the γ-unit involves a cycle: while the γ-unit interacts with one of the β-units (see the products $(\mathbf{n}_\perp\cdot\mathbf{p}_\beta)$ and $(\mathbf{p}_\beta\times\xi)$), two other β-units are deformed by the ion flow to be ready for the next interaction with the γ-unit (with the steric end electric dipoles probably appearing during the process).

To induce the γ-unit tilting in the membrane, the heat bath must transfer a portion of energy to the enzyme, for example by chemical reactions. The simplest assumption is that this portion of energy, which is proportional to the tilt angle squared, is related to the chemical potential difference Δ via $\Delta = a\Theta^2$, where a is a constant that has the scale of the intermolecular interaction energy. Thus, Θ is determined by Δ and vanishes at $\Delta = 0$.

It is interesting to estimate the efficiency of the considered regime. As for any macroscopic motor, we can define the electric efficiency of the molecular motor η by the ratio of the electric current work performed to the chemical energy consumed,

$$\eta = -\frac{j_z E_z}{u\Delta} \approx \frac{c\Delta p_\beta \Theta n_z E_z - \sigma E_z^2}{\lambda\Delta^2 + c\Delta p_\beta \Theta n_z E_z}. \tag{18}$$

For other regimes, in which the chemical energy is generated from the electric input, the chemical efficiency is the inverse of expression (18). It is seen from Eq. (18) that the efficiency maximum η_{max} occurs at the values of $\Delta(E_z)$ given by

$$\Delta(E_z) \approx \frac{\lambda\sigma + \sqrt{\lambda^2\sigma^2 + \lambda\sigma(cp_\beta\Theta)^2}}{c\lambda p_\beta \Theta}\,(n_z E_z). \tag{19}$$

Thus, η_{max} has a constant value along the straight line $\Delta = \mathrm{const}E_z$. It is independent of the force E_z, is close to zero at small tilt angles Θ, and is close to 1 at large values of Θ (when $\Theta \gg \lambda\sigma/c^2p_\beta^2$). This general statement is independent of the assumption about a relation between Δ and Θ. Such a molecular motor is an isothermal chemical motor working irreversibly far from equilibrium, i. e., it differs principally from the reversible Carnot engines [7].

5. ESTIMATES OF THE MOTOR CHARACTERISTICS AND CONCLUDING REMARKS

We now make rough quantitative estimates of the above parameters using some characteristic values [10, 11] such as the intermolecular interaction energy $\varepsilon \sim 10^2$ kcal/mole $\sim 10^{-19}$ J, the volume per protein molecule $l^3 \sim 10^{-24}$ m^3 (linear dimension $l \sim 10^2$ Å), the dipole moment of proteins $p_\beta \sim 100D \sim 10^{-16}$ esu, the piezoelectric modulus $\mu \sim 10^{-3}$ C·m^{-2} (assumed to be of the order of unity in liquid crystals), i. e., $\mu p_\beta \sim 10^{-20}$ J, the rotation viscosity $\gamma \sim 10^{-1}$ Pa·s ~ 1 Poise (assumed to be of the order of unity in liquid crystals), and the conductivity $\sigma \sim 10^{-7}\Omega^{-1}\cdot$m$^{-1} \sim 10^3$ s^{-1}. From the dimensional considerations, we can conclude roughly that the coefficient a in the expected relation $\Delta = a\Theta^2$ is of the order ε, i. e., $\Delta \sim \varepsilon\Theta^2$; the coefficient b is of the order $(\varepsilon l^3)^{-1}$, i. e., $ab \sim l^{-3} \sim 10^{24}$ m^{-3}; the coefficient c is of the order $c \sim (\tau\varepsilon l^3)^{-1}$, where τ is a certain relaxation time that probably admits the estimate $\tau \sim \gamma l^3/\varepsilon$, i. e., $ac \sim (\varepsilon/\gamma l^6)$; the parameter v has the dimension [energy density]$^{1/2}$, i. e., $v \sim r(\varepsilon/l^3)^{1/2}$, where r is a factor characterizing a small part of chiral interactions with respect to the total energy of intermolecular interactions.

Thus, we obtain the estimate

$$E_{th} \sim \frac{c\Delta p_\beta\Theta}{\sigma} \sim 10^9\Theta^3\ \mathrm{V\cdot m^{-1}}, \tag{20}$$

which implies that for a typical value $\Theta \sim 10^{-1}$, we have $E_{th} \sim 10^6$ V·m^{-1}, which is close to the membrane parameter [10]. From Eq. (10), we obtain the estimate

$$E_{th} \sim \frac{b\Delta\mu p_\beta\Theta}{v} \sim \frac{10^4\Theta^3}{v}\mathrm{J^{1/2}\cdot m^{-3/2}} \sim \sim \frac{10^5\Theta^3}{v}\,\mathrm{V\cdot m^{-1}}, \tag{21}$$

where v is measured in J$^{1/2}\cdot$ m$^{-3/2}$. Thus, if the motor stops when the current flow and the angular rotation stop simultaneously, we obtain $v \sim 10^{-4}$ J$^{1/2}\cdot$ m$^{-3/2}$ from Eqs. (16), (20) and (21). Because $(\varepsilon/l^3)^{1/2} \sim 10^2$ J$^{1/2}\cdot$ m$^{-3/2}$, the factor r is of the order $r \sim 10^{-6}$. Because $vE_{th} \sim 10$ J$\cdot$m$^{-3} \sim 10^2$ erg/cm^3 and $\gamma \sim 1$ Poise, we obtain the order value of Ω_z as

$$\Omega_z \sim \frac{vE_{th}}{\gamma} \sim 10^2\mathrm{s^{-1}} \tag{22}$$

which also is comparable with the measured values [6]. It was also shown in [6] that when ATP is absent, there is no rotary motion apart from the Brownian fluctuations (a few turns in either direction). Therefore, the obtained estimates do not look fantastic, they can explain some experimental facts.

No doubt, the problem of molecular motors in biophysical objects is very important and very complicated. It opens many possibilities for the research by various experimental methods and by physical modelling. The present paper proposes a physical model and the description of a rotary (F_1-ATPase) motor type avoiding the purely biological complexity. Our approach is based on the knowledge of the structure and properties of liquid-crystalline substances including the structure of ultra-thin films, polarization properties of chiral materials, and the relations between dynamics of structural parameters and ionic currents in films. We have determined:

general symmetry principles for the operation of these motors using the polar and chiral properties of the molecular system under consideration, the order parameter for this molecular system being defined;

general relations between ionic currents across the membrane and the velocity characterizing the dynamics of order parameter;

the relations between generalized forces inducing the motor, including viscous friction forces between the motor and the surrounding solvent and the free energy change per consumed «fuel» molecule, and generalized currents, including the above-mentioned velocity and the consumption rate of fuel molecules;

the basic macroscopic parameters of the motor and the relations between them. This may explain the observed action of the motor.

We thank V. Lorman and M. Kleman for stimulating discussions and M. Gorkunov for assistance. Financial support from Russian Foundation for Basic Research (Grant 00-02-17801) is acknowledged. S. P. acknowledges the receipt of the research award from the Alexander von Humboldt-Stiftung.

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