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Efficiency of Brownian motors in terms of entropy production rate

MIN QIAN[1], XUEJUAN ZHANG[1,2(a)], R. J. WILSON[2] and JIANFENG FENG[2,3]

[1] *Shaoxing College of Arts and Sciences - Zhejiang Province 312000, PRC*
[2] *Department of Computer Science, Warwick University - Coventry CV4 7AL, UK, EU*
[3] *Centre for Computational System Biology, Fudan University - Shanghai 210000, PRC*

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Abstract – This paper presents a novel approach to the investigation of the efficiency of Brownian motors in the framework of nonequilibrium theory. We derive an explicit expression of the entropy production rate (EPR) for a chemically driven Brownian motor and use this to develop an expression for motor efficiency in terms of the EPR. Our result is consistent with earlier derivations but is more general and physically transparent and thus applicable to a wider range of biological motors.

Introduction. – Many active processes in biology, such as muscular contraction [1] and various cellular transport processes [2], are performed by a certain kind of enzyme called a molecular motor that moves in one direction along a periodic, polar filament by transducing chemical energy (usually from the catalysis of ATP into ADP · Pi) into mechanical work. These molecular motors are dominated by thermal motion and viscous forces and can be understood by modelling them as Brownian particles whose direction is derived from nonequilibrium fluctuations in an asymmetric potential [3–7].

During ATP hydrolyzing reaction, the motor, denoted as M, will undergo the following states of nucleotide binding:

$$\overset{1}{\mathrm{M}} \rightleftharpoons \overset{2}{\mathrm{M}} \cdot \mathrm{ATP} \rightleftharpoons \overset{3}{\mathrm{M}} \cdot \mathrm{ADP} \cdot \mathrm{Pi} \rightleftharpoons \overset{4}{\mathrm{M}} \cdot \mathrm{ADP} \rightleftharpoons \overset{1}{\mathrm{M}}.$$

Let these states (M, M · ATP, M · ADP · Pi, M · ADP) be denoted simply as $i(1,2,3,4)$. In parallel with these state changes, the motor will move along its track: let its position be x. The corresponding physical model, a Brownian motor (BM), can be described by the following diffusion-reaction equation [5,6]:

$$\frac{\partial}{\partial t}p_i(t,x) = -\frac{\partial}{\partial x}J_i(t,x) + \sum_j \left(p_j(t,x)q_{ji}(x) - p_i(t,x)q_{ij}(x)\right), \qquad (1)$$

where $p_i(t,x)$ is the probability density of the motor with state i in position x at time t, q_{ij} is the transition rate from state i to j, and $J_i(t,x)$ is the probability flux in the spatial direction for the i-th state. Here we express J as

$$J_i(t,x) = [F - V_i'(x)]p_i(t,x) - \frac{D^2}{2} \cdot \frac{\partial}{\partial x}p_i(t,x), \qquad (2)$$

where F is a load, $V_i(x)$ are potentials satisfying $V_i(x+L) = V_i(x)$ with period L, and $D^2 = 2k_BT$ gives the diffusion coefficient with k_B being the Boltzmann constant and T the temperature.

An important issue in studying BM is about its efficiency. Thermodynamic efficiency defines how well a motor converts chemical free energy into useful work [5,6,8]

$$\eta_{therm} \triangleq \frac{\langle \dot{x} \rangle F}{P_{in}}, \qquad (3)$$

where $\langle \dot{x} \rangle$ is the mean velocity of the motor, F is the external load, and P_{in} is the total input power. An alternative measure, Stokes efficiency, has been devised for purely viscous loads such as a motor encounters in normal transport. Stokes efficiency is defined as [9,10]

$$\eta_{Stokes} \triangleq \frac{\langle \dot{x} \rangle F + \langle \dot{x} \rangle^2}{P_{in}}, \qquad (4)$$

where the term $\langle \dot{x} \rangle^2$ reflects the power working against the viscous drag. In both cases, input power must be formulated to ensure that the defined efficiencies are bounded by 1. In the case of thermodynamic efficiency, the input power is usually expressed as $P_{in} = r \cdot \Delta\mu$, where $\Delta\mu$ is chemical free energy consumed in one reaction

(a) E-mail: xuejuanzhang@gmail.com.

cycle and r is the chemical reaction rate measuring the average number of ATP molecules consumed per unit time [8]. For Stokes efficiency, authors differ as to the quantity P_{in}. Wang and Oster [11] propose that $\eta_{Stokes} \triangleq \frac{\langle \dot{x} \rangle^2}{r \cdot \Delta\mu + F\langle \dot{x} \rangle}$, contrasting this with thermodynamic efficiency. We note, however, that $r \cdot \Delta\mu + F\langle \dot{x} \rangle$ is not the difference of free energy since F is not a conservative force, while $\eta_{Stokes} \leqslant 1$ is only demonstrated for a detailed balance condition of the transition rate q_{ij}. Derenyi *et al.* [9] present a general definition of Stokes efficiency, but they only show $\eta_{Stokes} \leqslant 1$ for the case where input power comes purely from the transition of states; while Suzuki and Munakata [10] only consider the case of potential energy.

In this article we do not intend to give a new definition of the efficiency of motor, but will present a new and unified approach to the calculation of input power P_{in} using the entropy production rate (EPR), an important concept in nonequilibrium steady-state theory. EPR is the rate of total energy dissipation of a physical system [12–15]. We develop an expression for the total input power (the rate of free energy dissipation) as

$$P_{in} = e_r - \langle \dot{x} \rangle F. \tag{5}$$

An explicit mathematical formula of EPR e_r is derived for the general diffusion-reaction equation (1).

Compared with previous work, our expression is both more general and more physically explicit: i) Restricted by particular forms of the energy converter, expressions of input power derived in [8–10] can be considered as special cases of the formula (5). ii) In contrast to the treatments in [8–11], we do not need to assume a value for chemical potential difference though our derived expression is essentially the same as $r \cdot \Delta\mu$. iii) In contrast to that of Wang and Oster [11], our treatment allows either thermodynamic efficiency or Stokes efficiency with respect to the same input power and it is easy to prove that $\eta_{Stokes} \leqslant 1$ without imposing any special conditions on the transition rates or potentials. iv) Given the new formula of EPR in non-stationary systems [16], we expect to extend our approach to be applicable to time-inhomogeneous motors, such as BMs subjected to asymmetric potentials and time-periodic forces, and also to computational neuroscience [17].

Entropy production rate and free energy dissipation. – In statistical physics, entropy, entropy production rate (EPR) and heat dissipation rate (HDR) are important thermodynamic quantities. According to the well-established formula, the entropy of a system (1) at time t can be expressed as

$$S(t) = -k_B \sum_i \int p_i(t,x) \ln p_i(t,x) \mathrm{d}x. \tag{6}$$

Generally, for an isothermal Brownian dynamical system, the relationship between EPR, HDR and entropy can be stated in the following entropy balance equation [13,14]

$$T \cdot \frac{\mathrm{d}S(t)}{\mathrm{d}t} = e_r - h_d, \tag{7}$$

where e_r is the EPR, and h_d is the HDR of the system. In the steady state, the EPR of the system is balanced by the HDR.

The physical meaning of EPR and HDR are well established [13] but their mathematical formulae depend on the physical systems under analysis. To prepare for our discussion of the EPR of system (1), we first use existing expressions of EPR and HDR in two simple systems to show the relationship between EPR and free-energy dissipation.

i) *Kinetic systems* described by the following master equation:

$$\frac{\mathrm{d}p_i(t)}{\mathrm{d}t} = \sum_{j \neq i} \left[-p_i(t) q_{ij} + p_j(t) q_{ji} \right], \tag{8}$$

with $p_i(t)$ the probability and q_{ij} the transition rate. According to the balance condition of entropy, the EPR and the HDR in the steady state can be expressed as [14,18]

$$\begin{aligned} e_r &= \frac{1}{2} k_B T \sum_{i \neq j} (\pi_i q_{ij} - \pi_j q_{ji}) \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}}, \\ h_d &= \frac{1}{2} k_B T \sum_{i \neq j} (\pi_i q_{ij} - \pi_j q_{ji}) \ln \frac{q_{ij}}{q_{ji}}, \end{aligned} \tag{9}$$

respectively.

In the steady state, after the system transits from state i to state j, the corresponding free energy change $\Delta\mu_{ij}$ is proportional to $\ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}}$, here we define it as: $\Delta\mu_{ij} \triangleq \frac{1}{2} k_B T \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}}$. Since the probability current caused by the transition $i \to j$ in unit time is $J_{ij} = \pi_i q_{ij} - \pi_j q_{ji}$, the free energy dissipation in unit time caused by the state transition of $i \to j$ is $\Pi_{ij} = \frac{1}{2} k_B T \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}} J_{ij} = \frac{1}{2} k_B T \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}} (\pi_i q_{ij} - \pi_j q_{ji})$. Thus, the rate of total free-energy dissipation of the system is

$$\Pi_{free} = \frac{1}{2} k_B T \sum_{i \neq j} \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}} J_{ij} = \frac{1}{2} k_B T \sum_{i \neq j} \ln \frac{\pi_i q_{ij}}{\pi_j q_{ji}} (\pi_i q_{ij} - \pi_j q_{ji}). \tag{10}$$

Hence the EPR in kinetic systems is actually the rate of free energy dissipation, *i.e.*

$$e_r = \Pi_{free}. \tag{11}$$

ii) *Diffusion processes on a circle* with an equation written as

$$\mathrm{d}x(t) = (F - V'(x))\mathrm{d}t + D\mathrm{d}B(t), \quad x \in S^1, \tag{12}$$

where $D^2 = 2k_BT$, and $V(x)$ is a periodic function satisfying $V(x+L) = V(x), \forall x \in S^1,\ L > 0$.

The entropy of the system at time t is

$$S(t) = -k_B \int p(t,x) \ln p(t,x). \tag{13}$$

Let $\pi(x)$ and $J(x)$ be the stationary probability density and stationary probability flux, respectively. The HDR of the system in the steady state is [13,15]

$$h_d \triangleq \int_0^L [F - V'(x)] \cdot J(x) \mathrm{d}x. \tag{14}$$

According to the entropy balance equation (7), the EPR of the system in the steady state can be expressed as [13,15]

$$e_r \triangleq \int_0^L [F - V'(x) - \frac{D^2}{2} \cdot \frac{\mathrm{d}}{\mathrm{d}x} \ln \pi(x)] \cdot J(x) \mathrm{d}x = \int_0^L \frac{J^2(x)}{\pi(x)} \mathrm{d}x \tag{15}$$

For such diffusion systems, the rate of free energy dissipation is $\Pi_{free} = \int_0^L [-V'(x) - k_BT \cdot \frac{\mathrm{d}}{\mathrm{d}x} \ln \pi(x)] \cdot J(x)\mathrm{d}x$. In the case $F \cdot \langle \dot{x} \rangle = 0$, $e_r = \Pi_{free}$, which means that the free energy is totally dissipated. In the case $F \cdot \langle \dot{x} \rangle < 0$ (F is an external load), the consumption of total free energy in unit time is in two parts: the energy used to do useful work to drag the load: $W = -\int_0^L F \cdot J(x)\mathrm{d}x$, and the energy that is dissipated in the form of entropy production: e_r. If $F \cdot \langle \dot{x} \rangle > 0$, the environment does work on the system, according to energy conservation law, the rate of total dissipated energy is $e_r = \int_0^L F \cdot J(x)\mathrm{d}x + \Pi_{free}$. Hence in all three cases, we have

$$\Pi_{free} = e_r + W. \tag{16}$$

Entropy production rate and Brownian motor efficiency. – Based on the above preliminary results, we now investigate the EPR in BM described by eq. (1). The corresponding entropy of the system at time t is given by eq. (6). Give a derivative of $S(t)$ with respect to the time t, we have

$$T \cdot \frac{\mathrm{d}S(t)}{\mathrm{d}t} = \sum_i k_BT \int_0^L \ln p_i(t,x) \cdot \frac{\partial}{\partial x} J_i(t,x)\mathrm{d}x - \sum_i \sum_j k_BT \int_0^L p_j(t,x) q_{ji}(x) \ln p_i(t,x) \mathrm{d}x. \tag{17}$$

In the steady state, we have

$$k_BT \sum_i \int_0^L \ln \pi_i(x) \cdot J_i'(x) \mathrm{d}x - k_BT \sum_i \sum_j \int_0^L \pi_j(x) q_{ji}(x) \ln \pi_i(x) \mathrm{d}x = 0, \tag{18}$$

where $\pi_i(x)$ is the steady distribution of the system at state i in position x.

Corresponding to every state i, the first term of eq. (18) can be written as

$$k_BT \int_0^L \ln \pi_i(x) \cdot J_i'(x) \mathrm{d}x = -\int_0^L [F - V_i'(x)] \cdot J_i(x) \mathrm{d}x + \int_0^L [F - V_i'(x) - k_BT \cdot \frac{\mathrm{d}}{\mathrm{d}x} \ln \pi_i(x)] \cdot J_i(x) \mathrm{d}x, \tag{19}$$

Recalling the forms of HDR and EPR in the diffusion process (12), the first term in eq. (19) reflects the HDR; while the second term, denoted as Π_i, expresses the EPR due to the diffusion on a circle, *i.e.*

$$\Pi_i = \int_0^L [F - V_i'(x) - k_BT \cdot \frac{\mathrm{d}}{\mathrm{d}x} \ln \pi_i(x)] \cdot J_i(x) \mathrm{d}x. \tag{20}$$

Every term in eq. (20) corresponds to a physical quantity. The first term $\int_0^L F \cdot J_i(x)\mathrm{d}x$ is due to the work done of the system in the presence of an external force; the second term $\int_0^L [-V'(x)] \cdot J_i(x)\mathrm{d}x$ is the dissipation of the potential energy during transport along a filament; and the third term $\int_0^L \frac{\mathrm{d}}{\mathrm{d}x} [\ln \pi_i(x)] \cdot J_i(x)\mathrm{d}x$ is the increment of entropy due to the change of the probability with the shift of the position.

The integral function in the second term of eq. (18) in a steady state can be expressed as follows:

$$-k_BT \sum_i \sum_j \pi_j(x) q_{ji}(x) \ln \pi_i(x) = -\frac{1}{2} k_BT \sum_{i \neq j} [\pi_i(x) q_{ij}(x) - \pi_j(x) q_{ji}(x)] \cdot \ln \frac{q_{ij}(x)}{q_{ji}(x)} + \frac{1}{2} k_BT \sum_{i \neq j} [\pi_i(x) q_{ij}(x) - \pi_j(x) q_{ji}(x)] \cdot \ln \frac{\pi_i(x) q_{ij}(x)}{\pi_j(x) q_{ji}(x)}.$$

Recalling the forms of HDR and EPR in kinetic systems (8), the first term in the above equation describes the heat dissipation of a motor at position x after undergoing a chemical state transition; while the second term corresponds to the EPR of the motor due to state transitions in position x. Denote

$$\Pi_{ij} = \frac{1}{2} k_BT \int_0^L [\pi_i(x) q_{ij}(x) - \pi_j(x) q_{ji}(x)] \cdot \ln \frac{\pi_i(x) q_{ij}(x)}{\pi_j(x) q_{ji}(x)} \mathrm{d}x. \tag{21}$$

Hence in the steady state, the EPR of the chemically driven BM (1) is contributed by $\sum_i \Pi_i$ and $\sum_{i \neq j} \Pi_{ij}$. Applying (20) and (21), the total EPR of the system is

$$e_r = \sum_i \Pi_i + \sum_{i \neq j} \Pi_{ij} = \sum_i \int_0^L [F - V_i'(x) - k_BT \cdot \frac{\mathrm{d}}{\mathrm{d}x} \ln \pi_i(x)] \cdot J_i(x) \mathrm{d}x + \frac{1}{2} k_BT \int_0^L \sum_{i \neq j} [\pi_i(x) q_{ij}(x) - \pi_j(x) q_{ji}(x)] \cdot \ln \frac{\pi_i(x) q_{ij}(x)}{\pi_j(x) q_{ji}(x)} \mathrm{d}x, \tag{22}$$

and the total HDR is

$$h_d = -\sum_i \int_0^L [F - V_i'(x)] \cdot J_i(x)\mathrm{d}x$$
$$-\frac{1}{2}k_B T \int_0^L \sum_{i\neq j} [\pi_i(x)q_{ij}(x) - \pi_j(x)q_{ji}(x)] \cdot \ln\frac{q_{ij}(x)}{q_{ji}(x)}\mathrm{d}x. \tag{23}$$

During transport, the work done in a unit time by the motor against a load is

$$W = -\int_0^L F \cdot \sum_i J_i(x)\mathrm{d}x. \tag{24}$$

The rest of the energy is dissipated in the form of entropy production. Hence the total input (free energy) power comprises two terms:

$$P_{in} \triangleq \prod\nolimits_{free} = e_r + W. \tag{25}$$

Noticing that in the steady state, $J'(x) = \sum_j(\pi_i(x)q_{ij}(x) - \pi_j(x)q_{ji}(x))$, then adding formulae (22) and (24) together, we have

$$e_r + W = \sum_i \int_0^L \sum_j [\pi_j(x)q_{ji}(x) - \pi_i(x)q_{ij}(x)] \cdot V_i(x)\mathrm{d}x$$
$$+\frac{1}{2}k_B T \sum_{i\neq j} \int_0^L [\pi_i(x)q_{ij}(x) - \pi_j(x)q_{ji}(x)] \cdot \ln\frac{q_{ij}(x)}{q_{ji}(x)}\mathrm{d}x. \tag{26}$$

From eq. (26) one can see that the total input energy is from two sources: one is from the chemical energy released during the state transitions of the enzyme (*i.e.* the ATPase), the other is from the coupling of the potential and the state transition of the motor (though the potential does no work in the spatially average sense).

The thermodynamic efficiency of a Brownian motor can thus be expressed as

$$\eta_{therm} \triangleq \frac{W}{\prod_{free}} = \frac{W}{e_r + W}. \tag{27}$$

As the entropy production rate e_r is nonnegative, then for a Brownian motor dragging a load ($W > 0$), we have $0 \leqslant \eta < 1$.

Furthermore, we can unify the definition of Stokes efficiency under the same input power:

$$\eta_{Stokes} \triangleq \frac{W + \langle\dot{x}\rangle^2}{\Pi_{free}} = \frac{W + \langle\dot{x}\rangle^2}{e_r + W}. \tag{28}$$

Without imposing any specific condition on the transition rates and potentials, it is easy to prove that this efficiency measure is bounded by 1. Actually, applying Cauchy-Schwarz inequality and noticing the expression of EPR in eq. (22), we have

$$\begin{aligned}\langle\dot{x}\rangle^2 &= \left(\int_0^L \sum_i J_i(x)\mathrm{d}x\right)^2 = \left(\int_0^L \sum_i \sqrt{\pi_i(x)} \cdot \frac{J_i(x)}{\sqrt{\pi_i(x)}}\mathrm{d}x\right)^2 \\ &\leqslant \int_0^L \sum_i \pi_i(x)\mathrm{d}x \cdot \int_0^L \sum_i J_i^2(x)/\pi_i(x)\mathrm{d}x \\ &= \int_0^L \sum_i J_i^2(x)/\pi_i(x)\mathrm{d}x \\ &\leqslant e_r\end{aligned}$$

then

$$\eta_{Stokes} \leqslant 1.$$

Remark: Equation (25) is a general formula, it is valid for all physical systems. Previous work usually regarded the energy source of motor protein from chemical potential difference $\Delta\mu$ of fuel and products. To check whether formula (25) is consistent with this treatment. Let us further consider the biological setup of ATP hydrolysis by the catalytic motor protein

$$\mathrm{ATP} + \mathrm{M} \underset{q_{21}}{\overset{q_{12}}{\rightleftharpoons}} \mathrm{M} + \mathrm{ADP} + \mathrm{Pi},$$

with transition rate satisfying the chemical kinetics [8]

$$\frac{q_{12}}{q_{21}} = e^{(V_1 - V_2 + \Delta\mu)}.$$

In this setup, the average rate of ATP consumption $r = \int_0^L [\pi_1(x)q_{12}(x) - \pi_2(x)q_{21}(x)]\mathrm{d}x$. Calculating the energy dissipation rates according to the method proposed in sect. D in [8] and the EPR according to formula (22), it is not difficult to prove that the total input power in formula (25) is just the amount of chemical energy consumed per unit time, *i.e.*, $e_r + W = r\Delta\mu$. This is consistent with the energy formula (35) in [8].

Numerical results. – To illustrate the applications of our theoretical developments above, let us consider some numerical issues. System 2 below has been investigated in details in [8], we include it here for the purpose to compare our approach and theirs. System 1 below is even more simple, it is included to provide a possible answer to some key questions such as how we can design a BM so that its efficiency is optimal.

i) *Variation of efficiency with external load.* System 1: a two-state motor with one periodic and one flat potential (fig. 1 A1). Here, we fix $q_{12} = 3$, $q_{21} = 1, U = 2$, $a = 0.1$, $L = 1$, $\gamma = 1$. Without any load ($F = 0$), the motor moves to the right. Figures 1 B1 and C1 plot, respectively, the thermodynamic efficiency η_{therm} and Stokes efficiency against external load ($F < 0$). Both η_{therm} and η_{Stokes} initially increase with greater load, reaching a maximum, and then decrease with further increase of the load.

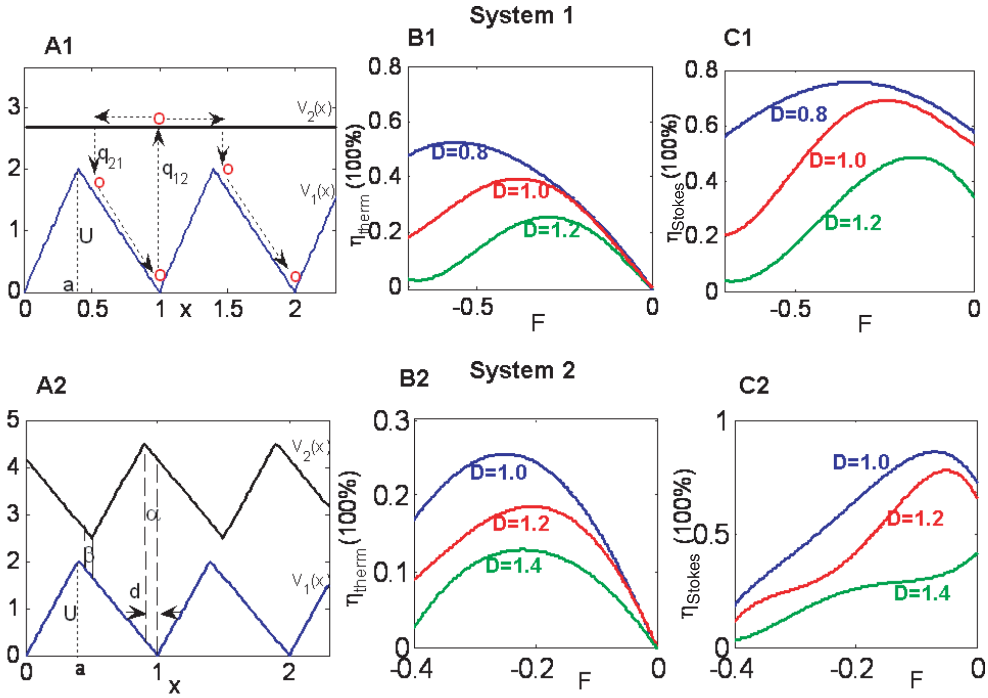

Fig. 1: (A1, A2) Schemes of the potentials. (B1, B2) Thermodynamic efficiency *vs.* the external load F for different noise intensities. (C1, C2) Stokes efficiency *vs.* the external load F for different noise intensities.

System 2: a two-state motor with two potentials of period $L=1$ and of equal amplitude U (see fig. 1A2). Similar to system A in ref. [8], we suppose that $V_2(x)=V_1(x-\delta)+U_0$, here $\delta=0.5$, $U_0=2.3$. The transition rate of the system obeys $q_{12}=\alpha(x)e^{(V_1-V_2+\Delta\mu)/D}+\beta(x)e^{(V_1-V_2)/D}$, $q_{21}=\alpha(x)+\beta(x)$, where $\alpha(x),\beta(x)$ are the same as in [8].

Employing the EPR formula to calculate the input power, one can see that the curves of η_{therm} *vs.* F for different noise intensities depicted in fig. 1B2 are similar to those in [8]. Turning to the Stokes efficiency, we see in fig. 1C2 that with the increase of external load, η_{Stokes} *vs.* F does not always exhibit a bell-shaped curve.

ii) *Variation of efficiency with the height of the potential.* To illustrate how the potential height affects the efficiency of the motor, we consider system 1. From fig. 2, one can see that with the increase of potential height, η_{Stokes} increases and tends to saturate. This numerical phenomenon may enable us to answer some key questions such as how we can design a BM so that its efficiency is optimal. Intuitively, increasing the height of the potential enhances the asymmetry of the system, which boosts the efficiency of the motor. However, the saturation of η_{Stokes} further tells us that increasing the potential height does not always improve its efficiency. The optimal height of the potential should be designed at a finite value of U. Figure 2 gives us some information on how to find this optimal height of the potential.

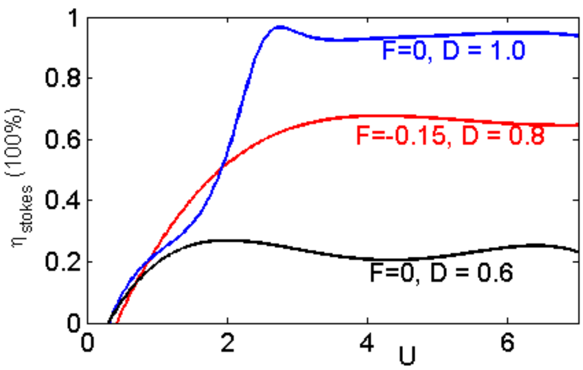

Fig. 2: Stokes efficiency *vs.* the height of the potential for different values of noise intensity and external load.

Conclusion. – Based on the theory of nonequilibrium steady state, we have elucidated the total input power as composed of the useful work done to the environment in unit time and the EPR (wasted energy), and given an explicit mathematical expression (see (26)) of the input power in diffusion-reaction systems (1). A more general and physically transparent formula of the efficiency of BMs is then derived in terms of EPR.

As has been extensively demonstrated in the literature that EPR is an important quantity in the theory of nonequilibrium steady state [15]. Our Discussion of efficiency of Brownian motor based on EPR gives another good example of how to apply nonequilibrium theory to explore the nonequilibrium phenomena. Working through examples showing how thermal and Stokes efficiency vary with external load and with the height of the potential, we conclude that our method is useful to investigate biological molecular motors and to design efficient artificial motors.

Moreover, thanks to the recent progress of extending the concept of EPR in time-dependent (non-stationary) system [16], we expect that our approach developed here would be extended to time-inhomogeneous BM.

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REFERENCES

[1] Huxley A. F., *Prog. Biophys. Chem.*, **7** (1957) 257.
[2] Howard J., *Annu. Rev. Physiol.*, **58** (1996) 703.
[3] Astumian R. D. and Bier M., *Phys. Rev. Lett.*, **72** (1994) 1766.
[4] Astumian R. D., *Science*, **276** (1997) 917.
[5] Zhou H. X. and Chen Y. D., *Phys. Rev. Lett.*, **77** (1996) 194.
[6] Jülicher F., Ajdari A. and Prost J., *Rev. Mod. Phys*, **69** (1997) 1269.
[7] Reimann P., *Phys. Rep.*, **361** (2002) 57.
[8] Parmeggiani A., Jülicher F., Ajdari A. and Prost J., *Phys. Rev. E*, **60** (1999) 2127.
[9] Derenyi I., Bier M. and Astumian R. Dean, *Phys. Rev. Lett.*, **83** (1999) 903.
[10] Suzuki D. and Munakata T., *Phys. Rev. E*, **68** (2003) 021906.
[11] Wang H. and Oster G., *Europhys. Lett.*, **57** (2002) 134.
[12] Hill T. L., *Free Energy Transduction in Biology* (Academic, New York) 1977.
[13] Qian H., *Phys. Rev. E*, **65** (2002) 016102; *J. Math. Chem.*, **27** (2000) 219; *Phys. Rev. E*, **65** (2002) 021111.
[14] Qian H., *Phys. Rev. E*, **64** (2001) 022101.
[15] Jiang D. Q., Qian M. and Qian M. P., *Mathematical Theory of Nonequilibrium Steady States, Lect. Notes Math.*, Vol. **1833** (Springer-Verlag, Berlin Heidelberg) 2004.
[16] Seifert U., *Phys. Rev. Lett.*, **95** (2005) 040602.
[17] Feng J. F., *Computational Neuroscience: A Comprehensive Approach* (Chapman and Hall/CRC, Boca Raton) 2004; Waxman D. and Feng J. F., *EPL*, **65** (2004) 434.
[18] Schnakenberg J., *Rev. Mod. Phys.*, **48** (1976) 571.