# Thermodynamics of Isothermal Brownian Motors

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**Abstract.** A thermodynamics of Brownian motors working in contact with a single thermal bath is developed. The First and Second Law of Thermodynamics are derived from the Fokker-Planck equation of an arbitrary overdamped Brownian particle in a periodic potential changing in time. We also study Brownian motors in the adiabatic limit, introducing reversible ratchets which can transport particles with zero entropy production. As an application, we calculate the efficiency of motors based on the *sluice ratchet*.

## 1 Introduction

How does a Brownian system exchange energy with the environment? The interest in this question has increased in the last years, mainly because it has been recognized that thermal fluctuations play an important and probably constructive role in biological energy transducers, the so-called protein or molecular motors.

In Physics the issue has been addressed by Feynman [5, 8] in a different context: the possibility of a ratchet that extracts energy out of thermal fluctuations.

The energetics of a Brownian particle looks rather trivial at first sight. A Brownian particle is, by definition, in contact with a thermal bath. The particle exchanges energy with the bath via fluctuations and dissipation. Fluctuations tend, in average, to increase the energy of the particle, whereas dissipation is an energy flow which always goes from the particle to the thermal bath. In equilibrium these two flows of energy cancel each other and the mean energy of the particle remains constant.

In order to have a less trivial behaviour one must drive the system out of equilibrium. In this paper we consider the following setup for a Brownian motor: a Brownian particle at temperature $T$ in a periodic potential, which is changed by some *external agent*, and is also subject to some external and constant force.

Protein motors, such as kinesins, myosins or ion pumps in the cell membrane, fit into the above description. They move small particles against a force and can be considered as a Brownian degree of freedom $x(t)$ in a potential determined by the shape of a protein. Depending on the type of motor, the

degree of freedom is the position of the protein itself or the position of an ion. ATP hydrolysis changes the shape of the protein and consequently changes the potential [3, 7]. Therefore, the external agent in this case is a chemical reaction driven by non-equilibrium concentrations of ATP and ADP.

Along this paper, we discuss the energetics of the Brownian motors described above. Most of our results are model-independent, and therefore can be applied to biological protein motors.

The paper is organized as follows. We present in Sect. 2 the mathematical model of the motor. In Sects. 3 and 4 we derive, respectively, the First and Second Law of Thermodynamics from the Fokker-Planck equation, and we apply both, in Sect. 5, to find an upper bound for the efficiency of the motor. Section 6 studies the adiabatic limit, and the concept of *reversible ratchet* is introduced. In Sect. 7 we calculate and discuss the efficiency of reversible ratchets and, finally, we present our conclusions in Sect. 8.

## 2 Brownian particles in a field

Consider an overdamped Brownian particle positioned in the interval $[0, L]$ at temperature $T$ and within a potential $V(x, t)$ periodic in space with period $L$, i.e., $V(L, t) = V(0, t)$. We consider also an external and constant force $F$ acting on the particle. The Langevin equation for the position $x(t)$ reads:

$$\dot{x}(t) = \kappa \left[-V'(x, t) + F + \xi(t)\right] \tag{1}$$

where the prime denotes derivative with respect to $x$ and $\kappa = D/(kT)$, $D$ being the diffusion coefficient and $k$ the Boltzmann constant[1]. The stochastic force $\xi(t)$ is a white Gaussian noise with zero mean and correlation given by:

$$\langle \xi(t)\xi(t')\rangle = 2kT\kappa^{-1}\delta(t - t') = 2D\kappa^{-2}\delta(t - t'). \tag{2}$$

The Fokker-Planck equation for the probability distribution $P(x, t)$ can be written as:

$$\partial_t P(x, t) = -\partial_x J(x, t) \tag{3}$$

where $J(x, t)$ is the current:

$$J(x, t) \equiv \kappa \left[-V'(x, t) + F\right] P(x, t) - D\partial_x P(x, t). \tag{4}$$

The distribution $P(x, t)$ must also satisfy the following boundary conditions:

$$P(0, t) = P(L, t); \qquad J(0, t) = J(L, t). \tag{5}$$

The relationship between the current and the velocity will be important later on. Integrating the current (4) over the interval $[0, L]$, one finds:

$$\int_0^L dx\, J(x, t) = \kappa \left\langle -V'(x, t) + F\right\rangle \tag{6}$$

[1] The Einstein's fluctuation-dissipation relation states that $\kappa$ is equal to the inverse of the friction coefficient, i.e., the damping force is $F_{\rm damp} = -\dot{x}/\kappa$.

since the integration of the term proportional to $T$ vanishes due to the periodicity of $P(x,t)$. Averaging the Langevin equation (1) we conclude that the mean value of the velocity is the integral of the current:

$$\langle \dot{x}(t) \rangle = \int_0^L dx\, J(x,t). \tag{7}$$

This expression must be taken with some caution since $\langle \dot{x}(t) \rangle$ can be different from the time derivative of $\langle x(t) \rangle$:

$$\begin{aligned} \frac{d}{dt}\langle x(t) \rangle &= \int_0^L dx\, x\, \partial_t P(x,t) = -\int_0^L dx\, x\, \partial_x J(x,t) \\ &= \langle \dot{x}(t) \rangle - LJ(L,t) \end{aligned} \tag{8}$$

and they coincide if and only if the current vanishes at the boundary. The derivative of the average position does not take into account that the particle can cross the boundary $x = L$ and is then re-injected in the interval $[0, L]$ through $x = 0$. For instance, consider the case where $V(x,t) = 0$. The mean velocity is $\langle \dot{x} \rangle = \kappa F$, but the particle soon reaches a stationary regime where the probability distribution $P(x,t)$ is uniform. Then, the mean value is constant and located at the middle point of the interval, i.e., $\langle x(t) \rangle = L/2$.

## 3 The First Law

Let us discuss the energetics of the system. As internal energy we only consider the periodic potential:

$$\mathcal{U}(t) \equiv \int_0^L dx\, V(x,t) P(x,t) = \langle V(x,t) \rangle. \tag{9}$$

The external force does not contribute to the internal energy, but it performs work adding or extracting energy. The work done by the force on the particle per unit of time is the force times the mean velocity, i.e.:

$$\dot{W}(t) \equiv F \langle \dot{x}(t) \rangle = \int_0^L dx\, F J(x,t) \tag{10}$$

and it is the energy entering into the system via the external force $F$.

The particle also gains or releases some energy due to the changes of the potential $V(x,t)$, i.e., there is an energy exchange between the particle and the external agent which modifies the potential. Although the energy that the external agent introduces into the system could also be considered "work" in the thermodynamical sense, we separate it from the work $\dot{W}$ done by the external force. In the biological examples discussed in the introduction, the work done by the external agent is in fact the "fuel" of the Brownian motor.

Then, we call *input energy* the work done by the external agent, reserving the term "work" only for the energy introduced by the external force into the system. The input energy is then given by:

$$\dot{E}_{\rm in}(t) \equiv \int_0^L dx\, P(x,t)\partial_t V(x,t). \tag{11}$$

Finally, there is a transfer of energy from the thermal bath to the system, which is given by:

$$\dot{Q}(t) \equiv \int_0^L dx\, \left[V(x,t)\partial_t P(x,t) - FJ(x,t)\right]. \tag{12}$$

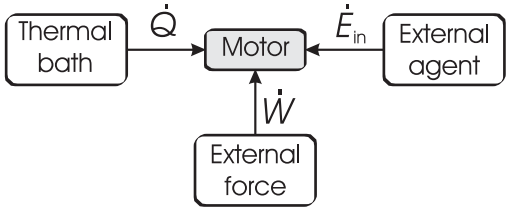


**Fig. 1.** Diagram of the energetics of the Brownian motor. The arrows indicate the direction of the flow when the corresponding energy transfer, $\dot{W}$, $\dot{Q}$ or $\dot{E}_{\rm in}$, is positive, i.e., when energy enters into the motor

Figure 1 represents the three energy flows that we have considered. From the above definitions, it is straightforward to prove the *First Law*:

$$\frac{d\mathcal{U}(t)}{dt} = \dot{Q}(t) + \dot{W}(t) + \dot{E}_{\rm in}(t) \qquad \text{for all } t. \tag{13}$$

Notice that we reserve the dot only for quantities that cannot be written as the time derivative of a function. This is the case of heat, work, and input energy and it is equivalent to the fact that heat and work are non exact differentials in Thermodynamics.

The above definitions of heat (12) and input energy (11) are easily justified for $F = 0$. They can be found for instance in [4]. As discussed in Ref. [9], they naturally come out when one considers abrupt changes of the potential $V(x,t)$. The idea is that the external agent provides the energy to change the potential, whereas the thermal bath provides the energy for the subsequent relaxation of the probability distribution.

For $F \neq 0$, the definition (10) for $\dot{W}(t)$ follows from the mechanical definition of work done by a force. The definition (12) of heat $\dot{Q}(t)$ can be derived with the following argument: take the particle moving in the whole real axis $(-\infty < y < \infty)$ in the potential $V(y,t) - yF$, with $V(y,t)$ the periodic extension of $V(x,t)$; apply the definitions of heat and work given in [4] or [9]; then go back to the interval $[0, L]$ by taking $x \equiv y \bmod L$.

## 4 The Second Law

In this section we derive the Second Law of Thermodynamics for the Brownian motor. First, we take the usual definition of the entropy of the motor:

$$S(t) \equiv -k \int_0^L dx\, P(x,t) \ln P(x,t) = -k \langle \ln P(x,t) \rangle. \tag{14}$$

It is convenient to write the current (4) in terms of the *chemical potential* $\mu(x,t)$:

$$J(x,t) = -\kappa P(x,t) \left[ \partial_x \mu(x,t) - F \right] \tag{15}$$

with

$$\mu(x,t) \equiv V(x,t) + kT \ln P(x,t). \tag{16}$$

The average of the chemical potential is:

$$\langle \mu(x,t) \rangle = \mathcal{U}(t) - TS(t) \tag{17}$$

as expected (remember that the chemical potential is the Gibbs free energy per particle, and the Gibbs free energy is equal to the Hemholtz free energy if the particle is in a confining potential). Taking the time derivative of (17) we get:

$$\frac{d}{dt} \langle \mu(x,t) \rangle = \frac{d}{dt} \mathcal{U}(t) - T \frac{d}{dt} S(t). \tag{18}$$

On the other hand, the time derivative of the average chemical potential can be written as

$$\frac{d}{dt} \langle \mu(x,t) \rangle = \int_0^L dx\, P(x,t) \partial_t \mu(x,t) + \int_0^L dx\, \mu(x,t) \partial_t P(x,t). \tag{19}$$

This equation can be further simplified. First notice that $\langle \partial_t \ln P(x,t) \rangle$ is zero, since the norm of $P(x,t)$ is constant. Using the Fokker-Planck equation (3), one has:

$$\frac{d}{dt} \langle \mu(x,t) \rangle = \dot{E}_{\rm in}(t) - \int_0^L dx\, \mu(x,t) \partial_x J(x,t). \tag{20}$$

Integrating by parts and taking into account that $\mu(L)J(L) = \mu(0)J(0)$:

$$\frac{d}{dt} \langle \mu(x,t) \rangle = \dot{E}_{\rm in}(t) + \int_0^L dx\, J(x,t) \partial_x \mu(x,t). \tag{21}$$

The second term can be transformed as:

$$\begin{aligned} \int_0^L dx\, J(x,t) \partial_x \mu(x,t) &= \dot{W} + \int_0^L dx\, \left[ \partial_x \mu(x,t) - F \right] J(x,t) \\ &= \dot{W} - \kappa \int_0^L dx\, \left[ \partial_x \mu(x,t) - F \right]^2 P(x,t) \end{aligned} \tag{22}$$

where we have used the relationship between the current and the chemical potential given in (15). Combining (18), (20), and (22), one finds:

$$\frac{d}{dt}\mathcal{U}(t) - T\frac{d}{dt}S(t) = \dot{E}_{\rm in} + \dot{W} - T\dot{S}_{\rm prod} \tag{23}$$

with

$$\dot{S}_{\rm prod}(t) \equiv \frac{\kappa}{T}\left\langle [\partial_x \mu(x,t) - F]^2 \right\rangle, \tag{24}$$

which is non negative. Using the First Law (13), (23) can be written as:

$$\frac{d}{dt}S(t) - \frac{\dot{Q}(t)}{T} = \dot{S}_{\rm prod}(t) \geq 0. \tag{25}$$

This is the *Second Law* of Thermodynamics. The l.h.s of the equation contains two terms: the first one, $dS/dt$, is the increase of the entropy of the system; the second one, $-\dot{Q}/T$, is the increase of the entropy of the thermal bath. Then, the sum $\dot{S}_{\rm prod}$ is the increase of the entropy of the universe or entropy production per unit of time, which we have proved to be positive. $\dot{S}_{\rm prod}$ vanishes only in equilibrium, i.e., only if both the external force $F$ and the gradient of the chemical potential vanish.

## 5 Efficiency

Consider now a cyclic motor, i.e., a potential $V(x,t)$ periodic in time with period $\tau$: $V(x,t+\tau) = V(x,t)$. The system, after a number of cycles, reaches a stationary regime where $P(x,t)$ and every state function, like the entropy $S(t)$ or the internal energy $\mathcal{U}(t)$, are periodic in time. The system works as a cyclic motor when:

$$W \equiv \int_0^\tau dt\, \dot{W}(t) \tag{26}$$

is negative, i.e., when the particle moves against the force. This is possible in some potentials which are usually termed as *ratchets*. Ratchets exhibit a non zero current in the absence of the external force $F$. If $F$ is small enough, the particle can still move against the external force and $W$ is negative. There is a *stopping force* $F_{\rm stop}$ which suppresses the flow of the particle. Above $F_{\rm stop}$, the particle moves in the same direction of the applied force and $W$ is positive.

Since the entropy $S(t)$ is periodic, an integration the Second Law (25) along the whole cycle yields:

$$Q \equiv \int_0^\tau dt\, \dot{Q}(t) = -T\int_0^\tau dt\, \dot{S}_{\rm prod}(t) \leq 0 \tag{27}$$

i.e., there is an unavoidable dissipation of heat to the thermal bath (see Fig. 1). The energy $W$ is then provided by the external agent and therefore

$$E_{\rm in} \equiv \int_0^\tau dt\, \dot{E}_{\rm in}(t) \tag{28}$$

is positive. From the First Law (13) and the periodicity of the internal energy one concludes that $-W = E_{\rm in} + Q$, i.e., part of the input energy is used to perform work against the force and part is dissipated to the heat bath. The efficiency of the motor is given by:

$$\eta = \frac{-W}{E_{\rm in}} = 1 + \frac{Q}{E_{\rm in}} \tag{29}$$

which is smaller than one, due to (27). The Second Law, as expected, imposes an upper bound to the efficiency of a Brownian motor. What we have presented is, in fact, a proof of the compatibility between the Langevin and Fokker-Planck approaches to the Brownian motion and the two laws of Thermodynamics.

The same proof of compatibility, for $F = 0$ and for underdamped particles, can be found in [12]. It is worth also to mention that the inequality (25) can be violated if the external agent possesses information about the position of the particle and modifies the potential according to this information. This can happen in macroscopic systems undergoing symmetry breaking phase transitions as we have shown in [11], in close relation with the Maxwell demon.

## 6 The adiabatic limit: reversible transport

In the previous sections we have derived relationships and inequalities for the three types of energy transfer: $Q$, $W$, and $E_{\rm in}$. In this and the following section, we explicitly calculate these quantities in the adiabatic limit, i.e., when the potential is changed infinitely slowly. This limit is interesting, not only because it allows us to find exact and analytical expressions for the energetics of the motor, but also because the motor works close to equilibrium, i.e., with maximum efficiency.

Let us start with $F = 0$. In this case, the work $\dot{W}(t)$ is obviously zero, but we can still calculate the current $J(x,t)$ which will be useful to obtain $\dot{W}(t)$ later on.

At first sight, the adiabatic limit looks trivial. At any time $t$, the system is in equilibrium with the potential $V(x,t)$, i.e., the probability distribution is:

$$P_-(x,t) \equiv \frac{e^{-\beta V(x,t)}}{Z_-(t)} \tag{30}$$

where $\beta = 1/(kT)$ and $Z_-(t)$ is a normalization constant (the subindex will be clear below). For this probability distribution the current vanishes. However, the integral of the current along the cycle is different from zero for some class of motors called *reversible ratchets* [9, 10].

In order to prove it, let us now solve the Fokker-Planck equation up to linear terms in $\partial_t V(x,t)$. We introduce the correction $\varphi(x,t)$ as:

$$P(x,t) = P_-(x,t)\,[1 + \varphi(x,t)]\,. \tag{31}$$

For this distribution the current reads:

$$J(x,t) = -DP_-(x,t)\partial_x\varphi(x,t) \tag{32}$$

and the Fokker-Planck equation up to first order in $\partial_t V(x,t)$, is:

$$\partial_t P_-(x,t) = D\partial_x P_-(x,t)\partial_x\varphi(x,t), \tag{33}$$

which determines $\varphi(x,t)$ along with the periodic boundary condition $\varphi(0,t) = \varphi(L,t)$. A first integration of (33) yields:

$$DP_-(x,t)\partial_x\varphi(x,t) = -J(L,t) + \int_0^x dx'\,\partial_t P_-(x',t) \tag{34}$$

where we have identified the integration constant with $-J(L,t)$ using (32). Integrating this equation and imposing the periodic boundary condition, one finally finds the current at $x = L$:

$$J(L,t) = \int_0^L dx \int_0^x dx'\,P_+(x,t)\partial_t P_-(x',t) \tag{35}$$

where $P_+(x,t)$ is a new probability distribution:

$$P_+(x,t) \equiv \frac{e^{\beta V(x,t)}}{Z_+(t)} \tag{36}$$

$Z_+(t)$ being a normalization constant.

In the adiabatic limit, the time derivative of $P_-(x,t)$ vanishes, and so does the current $J(L,t)$. However, the integral of $J(L,t)$ along the cycle $[0,\tau]$ can be, in some cases, different from zero. We define the *integrated flow* as:

$$\phi_0 \equiv \int_0^\tau dt\,J(x,t), \tag{37}$$

which does not depend on the point $x$. Therefore, $\phi_0$ can be calculated integrating with $J(L,t)$ as given by (35). We call *reversible ratchets* those systems where the integrated flow is different from zero. They exhibit *reversible transport*, i.e., the particle moves toward a direction and nevertheless is in equilibrium at any time. There is a trivial example of this phenomenon discussed in Ref. [6], namely, a Brownian particle in a confining potential which is shifted infinitely slowly. It is worth to mention also that a slow modulation between two potentials $V_A(x)$ and $V_B(x)$, i.e., if $V(x,t) = r(t)V_A(x) + [1-r(t)]V_B(x)$, with $r(t)$ a periodic function oscillating between 0 and 1, can never be a reversible ratchet. This is proved by means of the change of variable $t \to r(t)$ in the integral (37). Notice that this is the case of the *flashing ratchet* [2]. In order to have a non trivial reversible ratchet, the potential $V(x,t)$ must depend on two or more parameters and it must describe a loop in the space of parameters [9]. We present an explicit example below (see Fig. 2).

The input energy $E_{\rm in}$ in the adiabatic limit also vanishes for $F = 0$. The reason is that

$$\dot{E}_{\rm in} = \int_0^L dx\, P_-(x,t)\partial_t V(x,t) = -kT\partial_t \ln Z_-(t) \tag{38}$$

is an exact differential and therefore the integral along $[0,\tau]$ is zero (remember that $Z_-(t)$ is periodic). The dissipated heat also vanishes along the cycle due to the First Law. Consequently, a reversible ratchet exhibits transport without any energy consumption and without heat dissipation.

In the next section, we will need the first correction of the input energy. It can be calculated using the correction $\varphi(x,t)$ defined by (31). The calculation is cumbersome but straightforward. The result is:

$$E_{\rm in} = b/\tau \tag{39}$$

with

$$b \equiv -\frac{\tau}{\kappa}\int_0^\tau dt\, Z_-(t)Z_+(t)\Big\{J(L,t)^2 + \int_0^L dx \int_0^x dx' \int_0^{x'} dx''\ [\partial_t P_-(x,t)]\ \ P_+(x',t)\,[\partial_t P_-(x'',t)]\Big\} \tag{40}$$

which is finite in the adiabatic limit (provided that $\partial_t V(x,t)$ is of order $1/\tau$ for all $t$). We see that the input energy is of order $1/\tau$ . Since $W = 0$, then $Q = -E_{\rm in}$ and therefore the Second Law implies that $b > 0$. This can also be proved by manipulating (40).

## 7 Efficiency of reversible ratchets

To build a Brownian motor from a reversible ratchet we must apply a small external force $F$. The Fokker-Planck equation (3) can be solved up to first order of $F$ and $1/\tau$ [10] and the integrated flow reads:

$$\phi = \phi_0 + \nu\tau FL \tag{41}$$

where

$$\nu \equiv \frac{\kappa}{\tau}\int_0^\tau dt\, \frac{1}{Z_-(t)Z_+(t)}, \tag{42}$$

which can be interpreted as an *average mobility* of the Brownian particle in the potential $V(x,t)$. The work is $W = FL\phi$ and it is negative only if $F$ is between zero and the stopping force $F_{\rm stop} = -\phi_0/(\nu\tau L)$. We see that the stopping force is of order $1/\tau$ ($\phi_0$ and $\nu$ are finite in the adiabatic limit). This is expected, since the force is acting along the whole cycle $[0,\tau]$ and induces a current $J(x,t)$ of order $F$ *at any time*. This current, when integrated over the cycle, yields a contribution of order $F\tau$. Still, we can have a motor in the

adiabatic limit if $F$ goes to zero as $1/\tau$. Notice however that this is possible *only for reversible ratchets*.

Up to first order of $F$ and $1/\tau$, the input energy along the cycle is [10]:

$$E_{\rm in} = FL\phi_0 + b/\tau. \tag{43}$$

Therefore, the efficiency is:

$$\eta = \frac{-FL(\phi_0 + \nu\tau FL)}{FL\phi_0 + b/\tau} = -\frac{\phi_0\alpha + \nu\alpha^2}{\phi_0\alpha + b} \tag{44}$$

with $\alpha \equiv FL\tau$. This result *is exact in the adiabatic limit* and all the parameters in the last equation are finite.

Let us apply the previous theory to a concrete example. As a reversible ratchet we consider the following potential with $L = 1$ (see Fig. 2a):

$$V(x,t) = \begin{cases} V_1(t) & \text{if} \quad x < a \\ 0 & \text{if} \quad a < x < 1-a \\ V_2(t) & \text{if} \quad 1-a < x < 1. \end{cases} \tag{45}$$

The temporal evolution of $V_1(t)$ and $V_2(t)$ is shown in Fig. 2b. In each step, one of them varies between $-V_{\rm max}$ and $V_{\rm max}$ at a constant velocity $8V/\tau$. The shape of the potential at four points of the cycle is represented in Fig. 2c. The ratchet works as a *sluice* and is a possible model for biological ion pumps.

For the *sluice ratchet* one can calculate $\phi_0$, $\nu$, and $b$ using (37), (42), and (40) respectively. The integrated flow $\phi_0$ is positive as expected by simple inspection of Fig. 2c. We then consider negative external forces. Fig. 3a depicts analytical results of the efficiency as a function of $\alpha = |F|\tau$ in the adiabatic limit and for $a = 0.25$, $V_{\rm max} = 5$, and $D = \kappa = kT = 1$.

In the same figure we have plotted the efficiency of a random version of the sluice ratchet, which is not adiabatic but can still be treated analytically. The

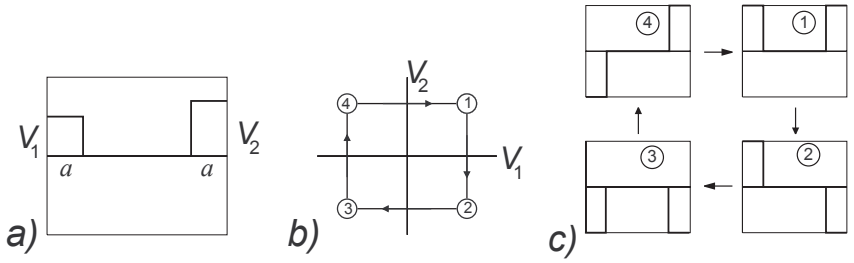


**Fig. 2.** An example of reversible ratchet: the *sluice ratchet*. The potential is depicted in a) and b) represents how the parameters $V_1$ and $V_2$ vary along the cycle. Finally, c) shows the shape of the potential corresponding to the four states labelled in b)

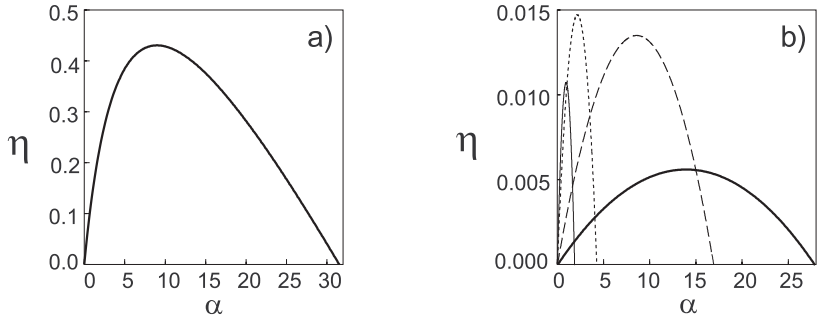


**Fig. 3.** Efficiency $\eta$ of the sluice ratchet as a function of $\alpha = |F|\tau$, for $a = 0.2$, $V_{\max} = 5$, and $kT = D = 1$. We present analytical results for a) the adiabatic limit and b) random jumps between the corners of the square in Fig. 2 with $\tau = 4/\omega = 1$ (thin solid), $\tau = 2$ (dashed), $\tau = 10$ (long dashed), and $\tau = 40$ (thick solid).

potential now randomly jumps among the four states, $V_i(x)$ $(i = 1, 2, 3, 4)$, at the corners of the cycle in Figs. 2b and 2c. The system is described by the probability distribution $P_i(x, t)$, which is the joint probability density for the position $x$ of the particle and for the state of the potential $i$. The rate equation for this distribution is:

$$\partial_t P_i(x,t) = -\kappa\partial_x \left[-V_i'(x) + F - kT\partial_x\right] P_i(x,t) + \sum_{j=1}^{4} \omega_{ji} P_j(x,t) \qquad (46)$$

where $\omega_{ji}$ is the transition rate from state $j$ to $i$. To compare with the reversible motor, we set $\omega_{12} = \omega_{23} = \omega_{34} = \omega_{41} = \omega$ and $\omega_{ji} = 0$ otherwise. Then the potential describes a similar trajectory as the one depicted in Fig. 2 with a random waiting time in each corner of the square. The mean value of the time to complete a cycle is $\tau = 4/\omega$. Analytical results of the efficiency are plotted in Fig. 3b. Comparing with the adiabatic motor, the efficiency decreases dramatically from 40% to 1.5%. The reason is that the system is far from equilibrium after each jump. We then conclude that adiabaticity is a necessary ingredient to reach high efficiencies.

These results differ completely if we consider irreversible ratchets. In Ref. [10] we have calculated the efficiency of the flashing ratchet [2] in two cases: a) when the ratchet potential is continuously modulated, b) when the ratchet potential is randomly switched on and off. The efficiency is similar in the two cases and below 5%.

## 8 Conclusions

We have presented general results for the energetics of a wide class of Brownian motors, those consisting of a potential deterministically modified by

an external agent. We have derived the First and Second Law of Thermodynamics from the Fokker-Planck equation and also calculated exactly the efficiency in the adiabatic limit. In this limit, only reversible ratchets can work as motors, exhibiting comparatively high efficiencies.

For the protein motors described in the introduction, two are the messages which can be extracted from the results presented here. A motor with high efficiency (above or around 30%) has to satisfy the following:

- The shape of the protein must change describing a loop in some abstract space of parameters, since the interaction potential between the protein and the degree of freedom of the motor has to be a reversible ratchet.
- The protein must change in a continuous way, avoiding abrupt jumps between stable or metastable states.

We believe that any model of efficient motor must accomplish these two prescriptions. Still, for a direct application of the results of the present work to biological systems, a chemical coordinate driving the change of the potential should be included. This coordinate would evolve stochastically with a bias depending on the concentration of some "fuel" reactants, such as ATP and ADP. Work in this direction is in progress.

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