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Symmetric linear potential and imperfect Brownian ratchet in molecular motor function*

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Biomolecular motors are tiny engines that transport materials at the microscopic level within biological cells. In recent years, Elston and Peskin *et al* have investigated the effect of the elastic properties of the tether that connects the motor to its cargo at the speed of the motor. In this paper we extend their work and present a tether in the form of symmetric linear potential. Our results show that when the driving mechanism is an imperfect Brownian ratchet, the average speed decreases as the stiffness of the tether increases in the limit of large motor diffusion coefficient, which is similar to the results of Elston and Peskin. However, a threshold for the stiffness of the tether connecting the motor to its cargo is found in our model. Only when the tether is stiffer than the threshold can the motor and its cargo function co-operatively, otherwise, the motor and its cargo depart from each other. This result is more realistic than that of the spring model of Elston and Peskin.

Keywords: biomolecular motors, Brownian ratchet, protein flexibility, symmetric linear potential
PACC: 0540, 0250, 8715

1. Introduction

Molecular motors are a particular kind of proteins which can move linearly along its designated track against an external force by utilizing the biochemical energy source, adenosine triphosphate (ATP). The tracks, called protein tracks, are filamentous structures: for example, myosin slides along an actin filament, kinesin and dynein along a microtubule. Many of the molecular motors, for example the bacterial flagellar motor and F0F1-ATP synthase, have the ability to rotate. In this manner, the motor proteins act as miniature engines converting chemical energy to mechanical work. Experimental studies on the motor proteins at the level of single molecule have stimulated the interest of many physicists to explore the physical mechanism of motor proteins. While the question about how molecular motors operate has not been answered definitively, many reasonable models for motor protein function have been suggested, of which the Brownian ratchet model is a well-known example.[1−7] In such a mechanism, the performance of the motor depends on its own diffusion coefficient and also on the diffusion coefficient of the "cargo" that the motor transports.

It is instructive that within cells, cargo often consists of larger organelles such as synaptic vesicles or melanosomes but not single molecules.[8] Thus, in general, the cargo the motor transports is considerably larger than the motor itself in size. For example, while the size of kinesin's motor domain is only 7×4.5×4.5nm, it transports freshly synthesized synaptic vesicles with a diameter of 20–50nm from the soma of a neuron to the synapses at the end of the axons up to a metre away. The torque generating stators of the bacterial flagellar motor are nanometres in size, whereas flagella are generally several microns in length. In in-vitro motility assay in bead geometry, the diameter of a bead is $\sim 1\mu$m. According to the Einstein relation $D = kT/\gamma = k_{\rm B}T/6\pi\eta r$, where γ is the drag coefficient, diffusion constants decrease sharply as particle size increases. Therefore, for the Brownian ratchet models the relatively small diffusion coefficient of cargo would seem to inhibit seriously any step in the motor's operating cycle that requires thermal diffusion. However, an ingenious way to overcome this problem was suggested by Berg and Kahn,[2] and

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Meister *et al*,[3] who argued that an advantage could be gained if the linkage between the motor (stator) and cargo (flagellum) were elastic. The basic idea was that an elastic linkage would allow the small motor to diffuse rapidly, thus stretching the linkage. As the connection between motor and cargo relaxed to its equilibrium length, it would provide the force necessary to transport the cargo.

In recent years, Elston and Peskin *et al*[9,10] have investigated, in the frame of thermal ratchets, the effect of the elastic properties of the tether that connects the motor to its cargo at the speed of the motor. In their studies the linkage was a linear spring with zero rest length. The motor's speed increased as the spring was softened when the driving mechanism was an imperfect Brownian ratchet, and when the driving mechanism was a correlated ratchet the behaviour was the reverse. It should be noted that, to date, the exact form of the linkage has not been clarified. When the spring model gives a possible type of linkage, it always seems a little lacking somewhere. Because the force produced by the spring is proportional to the distance between the motor and the cargo, this force will become unlimitedly large when the distance is sufficiently increased. This is obviously not in accord with the reality, in which the interaction between the motor and its cargo will disappear at a sufficiently long distance. Such an unrealistic property of the spring model leads to an unrealistic behaviour of the motor–cargo system in the case of soft linkage. Namely, the mean speed of the system approaches a maximum when the linkage is fully softened. However, from the physical point of view too soft a linkage should not be capable of dragging one cargo. Thus, in this paper we adopt the symmetric linear potential as the linkage between the motor and its cargo and investigate on this assumption the influence of protein flexibility on the speed of an imperfect Brownian ratchet. We expect to overcome the above shortcoming of the spring model. For the facts mentioned above, and for simplicity as well, we mainly consider the case of large diffusion coefficient of the motor.

This paper is arranged as follows. In Section 2 a preliminary discussion of the Brownian ratchet is presented. This section provides the necessary background for the analyses in later sections. A description of the problem under consideration is formulated in Section 3. In Section 4 the behaviour of the motor–cargo system is investigated for the case of large motor diffusion coefficient. This is followed in Section 5 by an analysis of the problem for the case of soft linkage. We end with some concluding remarks in Section 6.

2. The tilted periodic potential and imperfect Brownian ratchet[1]

Consider a motor moving in a "tilted" periodic potential $\phi(x)$. A tilted periodic potential refers to a potential that satisfies the condition[9]

$$\phi(x+L) = \phi(x) + \Delta\phi, \tag{1}$$

where $\Delta\phi$ is a constant. In an overdamped environment the dynamics of molecular motors on a periodic potential $\phi(x)$ is described by the following Fokker–Planck equation:[11]

$$\frac{\partial \rho(x,t)}{\partial t} + \frac{\partial J(x,t)}{\partial x} = 0, \tag{2}$$

$$J(x,t) = -D\left(\frac{\partial \rho}{\partial x} + \frac{\rho}{k_{\mathrm{B}}T}\frac{\mathrm{d}\phi}{\mathrm{d}x}\right), \tag{3}$$

where $\rho(x,t)$ is the probability density for finding the motor at the position x at the time t and $J(x,t)$ is the probability flux. Equation (2) reflects a conservation of probability, from which it is inferred that a stationary solution $P(x,t) = P(x)$ implies a constant current J. Stationarity means that the time derivative of $P(x,t)$ equals zero. By using the following periodicity and normalization conditions:

$$\rho(x+L) = \rho(x), \tag{4}$$

$$\int_0^L \rho(x)\mathrm{d}x = 1, \tag{5}$$

we can obtain the mean velocity of the particle in the stationary state, that is[11]

$$v = JL = \frac{DL}{\alpha\int_0^L E^{-1}(x)\mathrm{d}x\int_0^L E(x)\mathrm{d}x - \int_0^L E^{-1}(x)\int_0^x E(x')\mathrm{d}x'\mathrm{d}x}. \tag{6}$$

[1] The main content of Sections 2–3 has been discussed by Elston and Peskin.[9] To completely depict the problems, here we recapitulate part of their work.

where

$$\alpha = \frac{\exp\left(-\dfrac{\Delta\phi}{k_{\rm B}T}\right)}{\exp\left(-\dfrac{\Delta\phi}{k_{\rm B}T}\right)-1} \tag{7}$$

and

$$E(x) = \exp(\frac{\phi(x)}{k_{\rm B}T}). \tag{8}$$

Next consider the potential shown in Fig. 1. This potential represents a "staircase" potential moving against an applied load force F_l. It was called the "imperfect" Brownian ratchet by Elston and Peskin. The mathematical description of the imperfect Brownian ratchet potential is as follows:[9]

$$\phi(x) = F_l x, \quad 0 \le x < L, \tag{9}$$

$$\phi(x+L) = \phi(x) - (F_0 - F_l)L. \tag{10}$$

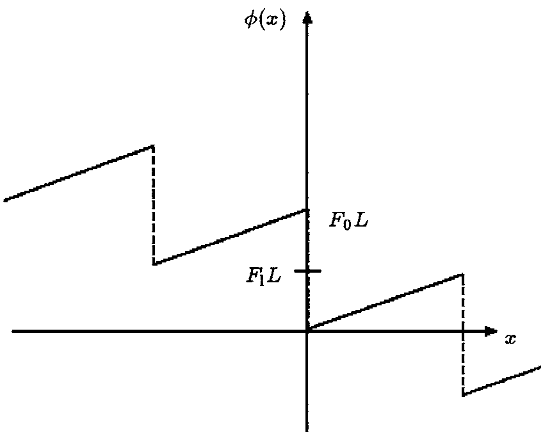

Fig.1. The imperfect ratchet potential plus an applied load force F_l. The ratchet is characterized by the barrier height F_0L. (Adopted from Fig. 3 in Ref.[9]).

By substituting (9) into (6) the mean velocity of an imperfect ratchet[12] is obtained, i.e.

$$v = \frac{D}{L}\frac{\omega_l^2}{\dfrac{(\exp(\omega_0)-1)(\exp(\omega_l)-1)}{\exp(\omega_0)-\exp(\omega_l)} - \omega_l}, \tag{11}$$

where

$$\omega_0 = \frac{F_0 L}{k_{\rm B}T}, \tag{12}$$

$$\omega_l = \frac{F_l L}{k_{\rm B}T}. \tag{13}$$

The unloaded velocity of an imperfect Brownian ratchet is given by[9]

$$v_{(F_l=0)} = \frac{2D}{L}\frac{\exp(\omega_0)-1}{\exp(\omega_0)+1}. \tag{14}$$

3. Formulation of the problem[9]

Image a rapidly diffusing motor moving along a one-dimensional track towing a "heavy" (slowly diffusing) cargo. Practically, the cargo is free to move in all three dimensions. However, it is obvious that the mean velocity of the cargo perpendicular to the track is zero. So, for the sake of simplicity, in this paper we only consider the motion of the cargo parallel to the track. Let the position of the motor be denoted by x_1 and the position of the cargo be denoted by x_2, then the potential energy of the system will be of the form[9]

$$U(x_1, x_2) = \phi(x_1) + S(|x_1 - x_2|), \tag{15}$$

where $\phi(x_1)$ describes the interaction between the motor and track, whereas $S(|x_1 - x_2|)$ describes the tether that connects the cargo to the motor. It is assumed that $\phi(x_1)$ is a tilted periodic potential, as shown in Eq.(1)

For the case of symmetric linear potential between the motor and its cargo, $S(r)$ takes the form

$$S(r) = \kappa|r|, \tag{16}$$

where the gradient of the potential κ is a measure of the intensity of the potential and r is the distance between the motor and cargo.

The probability density for finding the motor at the position x_1 and the cargo at the position x_2 at the time t is denoted by $\rho(x_1, x_2, t)$. It is governed by the diffusion equation[9]

$$\frac{\partial\rho}{\partial t} + \frac{\partial J_1}{\partial x_1} + \frac{\partial J_2}{\partial x_2} = 0, \tag{17}$$

$$J_1(x_1,x_2,t) = -D_1\left(\frac{\partial\rho}{\partial x_1} + \frac{\rho}{k_{\rm B}T}\frac{\partial U}{\partial x_1}\right), \tag{18}$$

$$J_2(x_1,x_2,t) = -D_2\left(\frac{\partial\rho}{\partial x_2} + \frac{\rho}{k_{\rm B}T}\frac{\partial U}{\partial x_2}\right), \tag{19}$$

where J_1 and J_2 are probability fluxes for the motor and cargo, respectively, and D_1 is the diffusion coefficient of the motor and D_2 is the diffusion coefficient of the cargo.

Because, as expatiated in the Introduction, the diffusion coefficient of the motor is much larger than that of the cargo, it is reasonable to assume the limit $D_1 \to \infty$. Define the marginal probability density $\rho^{(0)}(x_2, t)$ and the "marginal" probability flux

$J^{(0)}(x_2,t)$ respectively as follows:

$$\rho^{(0)}(x_2,t) = \int_{-\infty}^{\infty} \rho(x_1,x_2,t)\mathrm{d}x_1 \qquad (20)$$

$$J^{(0)}(x_2,t) = \int_{-\infty}^{\infty} J_2(x_1,x_2,t)\mathrm{d}x_1. \qquad (21)$$

Here $\rho^{(0)}(x_2,t)$ is probability density of finding the cargo at the position x_2 at the time t, disregarding the status of the motor, and $J^{(0)}(x_2,t)$ is flux corresponding to $\rho^{(0)}(x_2,t)$. It can be proved that they satisfy the diffusion equation[9]

$$\frac{\partial \rho^{(0)}}{\partial t} + \frac{\partial J^{(0)}}{\partial x_2} = 0, \qquad (22)$$

$$J^{(0)}(x_2,t) = -D_2\left(\frac{\partial \rho^{(0)}}{\partial x_2} + \frac{\rho^{(0)}}{k_{\mathrm{B}}T}\frac{\mathrm{d}\phi^{(0)}(x_2)}{\mathrm{d}x_2}\right), \qquad (23)$$

In the above equation, $\phi^{(0)}(x_2)$ represents an "effective potential" felt by the cargo and has the form[9]

$$\phi^{(0)}(x_2) = -k_{\mathrm{B}}T\ln\int_{-\infty}^{\infty}\exp\left(-\frac{U(x_1,x_2)}{k_{\mathrm{B}}T}\right)\mathrm{d}x_1. \qquad (24)$$

It is easy to verify that $\phi^{(0)}(x_2)$ satisfies the tilted periodicity condition

$$\phi^{(0)}(x_2+L) = \phi^{(0)}(x_2) + \Delta\phi. \qquad (25)$$

Equations (22), (23) and (25) are exactly those for a particle with diffusion coefficient D_2 moving in a tilted periodic potential $\phi^{(0)}(x_2)$. We can obtain the mean velocity of system only if we calculate out $\phi^{(0)}(x_2)$, which is the task of next section.

4. Solutions for $\kappa > F_0$

The form of $\phi^{(0)}(x_2)$ is now studied in detail. Using Eqs.(15) and (16) for U in Eq.(24) yields

$$\begin{aligned}\phi^{(0)}(x_2) &= -k_{\mathrm{B}}T\ln\int_{-\infty}^{\infty}\exp\left(-\frac{1}{k_{\mathrm{B}}T}[\phi(x_1)+\kappa|x_1-x_2|]\right)\mathrm{d}x_1\\ &= -k_{\mathrm{B}}T\ln\int_{-\infty}^{\infty}\exp\left(-\frac{1}{k_{\mathrm{B}}T}[\phi(r+x_2)+\kappa|r|]\right)\mathrm{d}r,\end{aligned} \qquad (26)$$

where use is made of the transformation $r = x_1 - x_2$ in the second step. The tilted periodicity of $\phi(x_1)$ allows it to be written in the form

$$\phi(x_1) = \varphi(x_1) - Fx_1, \qquad (27)$$

where $F = -\Delta\phi/L$ and $\varphi(x_1)$ is periodic in the general sense (i.e., $\varphi(x_1+L) = \varphi(x_1)$). By substituting Eq.(27) into Eq.(26) we obtain

$$\begin{aligned}\phi^{(0)}(x_2) &= -k_{\mathrm{B}}T\ln\int_{-\infty}^{\infty}\exp\left(-\frac{1}{k_{\mathrm{B}}T}[\varphi(r+x_2)-F(r+x_2)+\kappa|r|]\right)\mathrm{d}r\\ &= -Fx_2 - k_{\mathrm{B}}T\ln\left[\int_0^{\infty}\exp\left(-\frac{1}{k_{\mathrm{B}}T}[\varphi(-r+x_2)+(F+\kappa)r]\right)\mathrm{d}r\right.\\ &\quad\left.+\int_0^{\infty}\exp\left(-\frac{1}{k_{\mathrm{B}}T}[\varphi(r+x_2)+(\kappa-F)r]\right)\mathrm{d}r\right].\end{aligned} \qquad (28)$$

The second integration in logarithm is infinite as $\kappa \le F$, so we have to limit κ to being larger than F. In this case $\phi^{(0)}(x_2)$ can be calculated out through some algebra, resulting in

$$\phi^{(0)}(x_2) = -Fx_2 - k_{\mathrm{B}}T\ln\left[\frac{I_1(x_2)}{1-\exp\left(-\frac{1}{k_{\mathrm{B}}T}(\kappa+F)L\right)} + \frac{I_2(x_2)}{1-\exp\left(-\frac{1}{k_{\mathrm{B}}T}(\kappa-F)L\right)}\right], \qquad (29)$$

where

$$I_1(x_2) = \int_0^L \exp\left(-\frac{1}{k_{\mathrm{B}}T}[\varphi(-t+x_2)+(\kappa+F)t]\right)\mathrm{d}t \qquad (30)$$

and

$$I_2(x_2) = \int_0^L \exp\left(-\frac{1}{k_{\mathrm{B}}T}[\varphi(t+x_2)+(\kappa-F)t]\right)\mathrm{d}t. \qquad (31)$$

The details of this calculation are outlined in the appendix. Note that $I_1(x_2)$ and $I_2(x_2)$ are both periodic with respect to x_2. Equations (29)–(31) may be used to compute the effective potential for any κ which satisfies $\kappa > F$. There appears an additional advantage of allowing the limiting behaviour of $\phi^{(0)}$ as $\kappa \gg F$ or as $\kappa \to F$ to be read off by inspection. When κ is much larger than F in Eq.(31), the value of $\varphi(t+x_2)$ is much smaller than that of $(\kappa - F)t$ for any given t. Therefore, how $\varphi(t+x_2)$ depends on t is of little significance to the value of the integration; it is the same for the case of Eq.(30). Thus, we can replace $\varphi(t+x_2)$ by $\varphi(x_2)$ in Eq.(31) and $\varphi(-t+x_2)$ by $\varphi(x_2)$ in Eq.(30) and obtain

$$I_1(x_2) \approx \exp\left(-\frac{1}{k_\mathrm{B}T}\varphi(x_2)\right) \times \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa+F)t\right)\mathrm{d}t, \quad (32)$$

$$I_2(x_2) \approx \exp\left(-\frac{1}{k_\mathrm{B}T}\varphi(x_2)\right) \times \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa-F)t\right)\mathrm{d}t. \quad (33)$$

By substituting them into Eq.(29) and replacing $\exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa+F)L\right)$ and $\exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa-F)L\right)$ by zero we obtain the following expression for $\phi^{(0)}$ as $\kappa >> F$:

$$\begin{aligned}\phi^{(0)}_{(\kappa>>F)}(x_2) &\approx -Fx_2 - k_\mathrm{B}T\ln(I_1+I_2)\\ &\approx -Fx_2 + \varphi(x_2) + \text{const}\\ &= \phi(x_2) + \text{const}, \end{aligned} \quad (34)$$

where

$$\text{const} = -k_\mathrm{B}T\ln\left[\int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa+F)t\right)\mathrm{d}t + \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa-F)t\right)\mathrm{d}t\right], \quad (35)$$

which is independent of x_2. On the other hand, obviously, $\phi^{(0)}$ approaches negative infinite as $\kappa \to F$, but it is interesting to examine the shape of $\phi^{(0)}$ for κ approximating to F. Denote the limit of I_2 by I_2' as $\kappa \to F$, i.e.

$$I_2' = \lim_{\kappa\to F} I_2 = \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}\varphi(t+x_2)\right)\mathrm{d}t. \quad (36)$$

Due to the periodicity of $\varphi(x)$, I_2' is a constant, independent of x_2. In addition, when κ approaches F the second term in the logarithm of Eq.(29) dominates the logarithm, which means that we can omit the first term. Thus, for κ that is only a bit larger than F, $\phi^{(0)}$ has the following approximate form:

$$\begin{aligned}\phi^{(0)}_{(\kappa\to F)}(x_2) &\approx -Fx_2 - k_\mathrm{B}T\ln\frac{I_2'}{1-\exp\left(-\frac{1}{k_\mathrm{B}T}(\kappa-F)L\right)}\\ &= -Fx_2 + \text{const}. \end{aligned} \quad (37)$$

Therefore, in the limit of high-gradient linear potential the cargo feels the same tilted periodic potential as the motor, except for an additive constant, but in the limit of F-gradient linear potential the cargo feels only a constant force, independent of the detailed shape of the potential in which the motor moves. If thermal activation is required for the motor to surmount energy barriers as it moves along the track, a symmetric linear potential with a low gradient between the motor and the cargo can significantly increase the velocity at which the cargo is transported.

Consider the particular case in which $\phi(x)$ has the form of an imperfect Brownian ratchet (with no load applied), that is

$$\phi(x) = 0, \quad 0 \le x < L, \quad (38)$$

$$\phi(x+L) = \phi(x) - F_0L. \quad (39)$$

In this case $\varphi(x)$ becomes

$$\varphi(x) = F_0x, \quad 0 \le x < L. \quad (40)$$

By using Eq.(40) in Eqs.(30) and (31), respectively, and making some derivations we obtain the following expressions for I_1 and I_2:

$$I_1(x_2) = \frac{k_\mathrm{B}T}{\kappa}\exp\left(-\frac{F_0x_2}{k_\mathrm{B}T}\right)\left[1+\left(\exp\left(-\frac{F_0L}{k_\mathrm{B}T}\right)-1\right)\exp\left(-\frac{\kappa x_2}{k_\mathrm{B}T}\right)-\exp\left(-\frac{(\kappa+F_0)L}{k_\mathrm{B}T}\right)\right],$$
$$0 \le x_2 < L, \quad (41)$$

$$I_1(x_2+L) = I_1(x_2), \quad (42)$$

and

$$I_2(x_2) = \frac{k_BT}{\kappa}\exp\left(-\frac{F_0x_2}{k_BT}\right)\left[1+\left(\exp\left(\frac{F_0L}{k_BT}\right)-1\right)\exp\left(-\frac{\kappa(L-x_2)}{k_BT}\right)-\exp\left(-\frac{(\kappa-F_0)L}{k_BT}\right)\right],$$
$$0 \le x_2 < L, \tag{43}$$
$$I_2(x_2+L) = I_2(x_2). \tag{44}$$

Hence, $\phi^{(0)}$ can be evaluated by substituting Eqs.(41)–(44) into Eq.(29). Figure 2 shows plots of $\phi^{(0)}$ versus x_2 for different values of κ, where they are compared with the imperfect ratchet potential. The two limiting cases, i.e. Eqs.(34) and (37), are clearly exposed.

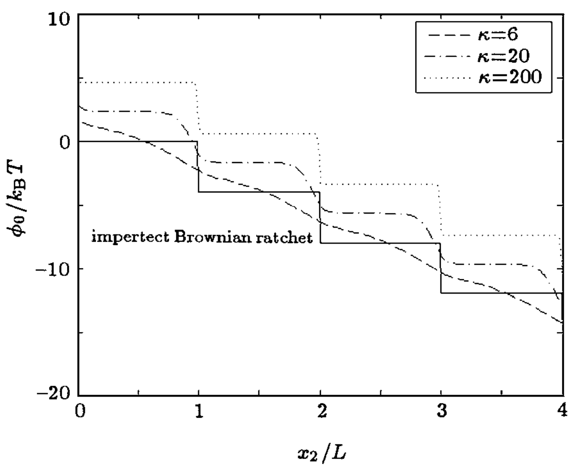

Fig.2. The effective potential (in units of k_BT) felt by the cargo for an imperfect Brownian ratchet. The different curves represent different values of κ (in units of k_BT/L). The imperfect ratchet potential with zero load force is also plotted against a control (solid line).

In the limit of high-gradient linear potential it is shown that $\phi(x)$ plus a constant is the effective potential in which the cargo moves. Therefore, the mean speed in this limit is given by Eq.(14) with $D = D_2$, that is, for an imperfect Brownian ratchet,

$$\lim_{\kappa\to\infty}\lim_{D_1\to\infty} v = \frac{2D_2}{L}\times\frac{\exp\left(\frac{F_0L}{k_BT}\right)-1}{\exp\left(\frac{F_0L}{k_BT}\right)+1}. \tag{45}$$

On the other hand, in the limit of F-gradient linear potential the cargo merely feels a constant force F_0, so its speed is

$$\lim_{\kappa\to F_0}\lim_{D_1\to\infty} v = \frac{D_2F_0}{k_BT}. \tag{46}$$

Returning to the case of arbitrary value of κ (within the region $\kappa > F_0$), the effective potential in which the cargo moves is given by Eq.(29) and satisfies the requirements for the property of a tilted periodic potential. But the mean speed for such a system is already known and given by Eq.(6), that is,

$$\lim_{D_1\to\infty} v = \frac{D_2L}{\alpha\int_0^L E^{-1}(x_2)\mathrm{d}x_2\int_0^L E(x_2)\mathrm{d}x_2 - \int_0^L E^{-1}(x_2)\int_0^{x_2} E(x_2')\mathrm{d}x_2'\mathrm{d}x_2}, \tag{47}$$

where

$$\alpha = \frac{\exp\left(\frac{F_0L}{k_BT}\right)}{\exp\left(\frac{F_0L}{k_BT}\right)-1} \tag{48}$$

and

$$E^{-1}(x_2) = \exp\left(-\frac{\phi^{(0)}(x_2)}{k_BT}\right) = \frac{I_1(x_2)\exp\left(\frac{Fx_2}{k_BT}\right)}{1-\exp\left(-\frac{1}{k_BT}(\kappa+F)L\right)} + \frac{I_2(x_2)\exp\left(\frac{Fx_2}{k_BT}\right)}{1-\exp\left(-\frac{1}{k_BT}(\kappa-F)L\right)}. \tag{49}$$

In the above equation $I_1(x_2)$ and $I_2(x_2)$ have been given by Eqs.(41)–(44). In fact, Eq.(46) can be also achieved by taking the limit of $\kappa \to F_0$ in Eq.(47). In doing so, use is made of Eq.(36). Finally, for large D_1 Eqs.(41)–(44) and (47)–(49) give a formula for the mean speed of the motor–cargo system when the motor is driven by an imperfect Brownian ratchet and tethered to the cargo through a symmetric linear potential with gradient κ larger than the ratchet's strength F_0. A computational result for the mean speed is plotted in Fig. 3, where the speed v is in units of $\frac{D_2}{L}$ and the potential strength κ is in units of $\frac{k_\mathrm{B}T}{L}$. The height of the ratchet barrier is $4k_\mathrm{B}T$. The upper horizontal line represents the F_0-gradient limit for infinite D_1, and the lower horizontal line corresponds the strong potential limit for infinite D_1.

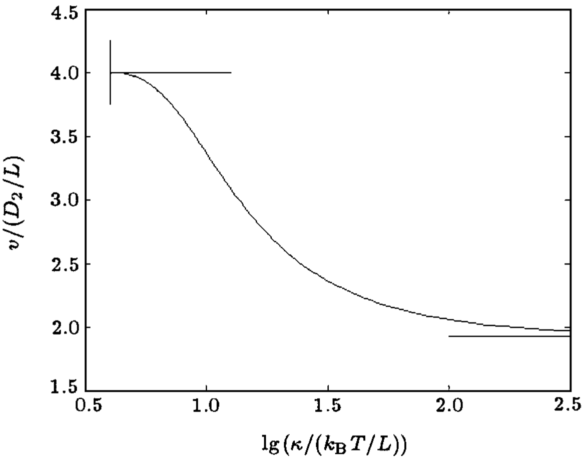

Fig.3. The average speed in units of $\frac{D_2}{L}$ versus the logarithm of the potential strength κ in units of $\frac{k_\mathrm{B}T}{L}$ for an imperfect Brownian ratchet with the barrier height $4k_\mathrm{B}T$ in the limiting case $D_1 \to \infty$. The upper horizontal line denotes the value of the speed in the limit $\kappa \to F_0$, and the lower horizontal line is for $\kappa \to \infty$. The vertical line represents the threshold $\kappa_0 = F_0$.

5. Solutions for $\kappa \le F_0$

Alternatively, consider the case of small values of κ (compared to F_0) for finite values of D_1 and D_2. Under the circumstances the cargo mainly trails far behind the motor, and it seems reasonable to expect that the net effect of the cargo on the motor is to produce a constant load force κ in the negative $\hat{x}$ direction. On the other hand, the fact that the effective potential $\phi^{(0)}(x_2)$ is of linear form for the limiting case $D_1 \to \infty$ and $\kappa \to F_0$, which is the result of the previous section (see Eq.(37)), also indicates the rationality of our assumption. Thus, the cargo feels a constant force κ and moves at a speed

$$v^{\mathrm{cargo}} = \frac{D_2 \kappa}{k_\mathrm{B}T} = \frac{D_2}{L}\omega_\mathrm{l}, \tag{50}$$

where $\frac{D_2}{k_\mathrm{B}T}$ is the mobility of the cargo and similar to $\omega_\mathrm{l} = \frac{\kappa L}{k_\mathrm{B}T}$ as discussed before. On the other hand, the load–speed curve of an imperfect Brownian ratchet gives the speed of the motor which is followed by the constant load force κ. Using Eq.(11) with $D = D_1$ yields

$$v^{\mathrm{motor}} = \frac{D_1}{L} \times \frac{\omega_\mathrm{l}^2}{\dfrac{(\exp(\omega_0)-1)(\exp(\omega_\mathrm{l})-1)}{\exp(\omega_0)-\exp(\omega_\mathrm{l})} - \omega_\mathrm{l}}. \tag{51}$$

On the ground of physics the motor and the cargo must move at the same speed. Combining (50) and (51) and making $v^{\mathrm{cargo}} = v^{\mathrm{motor}}$ produces the result

$$\varepsilon = \frac{D_2}{D_1} = \frac{\omega_\mathrm{l}}{\dfrac{(\exp(\omega_0)-1)(\exp(\omega_\mathrm{l})-1)}{\exp(\omega_0)-\exp(\omega_\mathrm{l})} - \omega_\mathrm{l}}. \tag{52}$$

Equation (52) implicitly determines ω_l, or equivalently, κ, which is denoted by κ_0. Substituting κ_0 into Eq.(50) or Eq.(51) determines the common speed of the motor and cargo, which is denoted by v_{κ_0}.

Now we understand that the motor–cargo system has the speed of v_{κ_0} as $\kappa = \kappa_0$. But what about the speeds when $\kappa > \kappa_0$ and $\kappa < \kappa_0$? Note that v^{cargo} is a linearly increasing function of κ, and v^{motor} a decreasing one. So v^{cargo} is larger than v^{motor} as $\kappa > \kappa_0$. We need not be afraid that the cargo moves so fast that the motor lags behind, because the cargo will be pulled back by the linear tether when it moves beyond the motor. However, when κ is smaller than κ_0, the speed of the cargo induced by the tether is lower than that of the motor, so the cargo always moves behind the motor and the distance between them becomes larger and larger, until eventually the cargo is dissociated from the motor and diffuses freely in liquid. Therefore, the constant force κ_0 may be interpreted as the minimum κ, thus the cargo can keep up with the motor. Namely, if we want the motor to be able to drag a cargo the tether connecting the motor to the cargo must be sufficiently strong. Here the common speed of the motor and cargo for the case of $\kappa > \kappa_0$ and finite values of D_1 and D_2 is not given, for this is not of current interest. Note that ω_l is within the range

$0 < \omega_l < \omega_0$, or equivalently, $0 < \kappa_0 < F_0$. The minimum potential gradient κ_0 depends not only on the strength of the ratchet F_0 but also on the ratio of diffusion coefficient of the cargo to that of the motor (i.e. ε). κ_0 increases with F_0 increasing and decreases with ε increasing. All these results accord with intuition, and confirm the rationality of κ_0. Figure 4 is a plot of κ_0 as a function of ε. The height of the ratchet barrier is taken as $4k_{\rm B}T$.

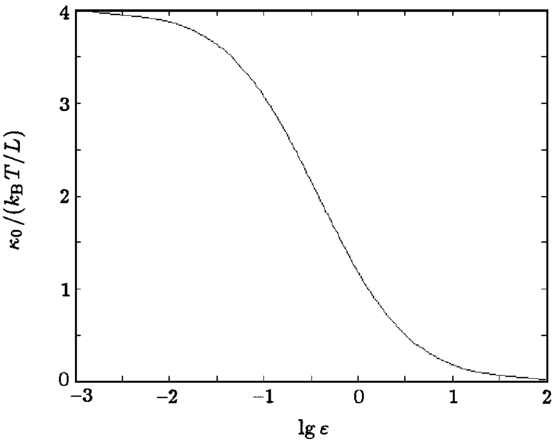

Fig.4. The minimum force κ_0 in units of $k_{\rm B}T/L$ as a function of ε. The height of the ratchet barrier is taken as $4k_{\rm B}T$.

The limiting case $D_1 \to \infty$, i.e. $\varepsilon \to 0$, is of our interest. Let $D_1 \to \infty$ with all other parameters fixed. From Eq.(52), this implies that $\omega_l \to \omega_0$, and then Eq.(50) yields

$$\lim_{D_1\to\infty} v_{\kappa\to F_0} = \frac{D_2}{L}\omega_0 = \frac{D_2 F_0}{k_{\rm B}T}. \tag{53}$$

This result is identical with that obtained in the above section (i.e. Eq.(46)), which confirms that our theory is exactly self-consistent. $\omega_l \to \omega_0$ means that, for large values of D_1, the minimum force κ_0 required for the cargo to move together with the motor approaches F_0-the strength of the ratchet dragging the motor.

6. Conclusions

Currently, researchers have suggested numerous models to understand the mechanism of how biomolecular motors convert chemical energy to mechanical work. However, most of them treat the structural proteins as rigid bodies. The work by Elston and Peskin represented initial investigations into the role of elasticity in molecular motor functions. In their studies they selected the form of the linkage between the motor and the cargo as a spring. Here we have extended their work and investigated the feasibility of an alternate form of tether between the motor and the cargo: namely, the symmetric linear potential. The result given here is qualitatively the same as the result given in Ref.[9]: that is, the mean speed of the motor–cargo system decreases monotonically as the linkage is stiffened. Our results show that the tether with the form of a symmetric linear potential is equally applicable but simpler. Analytical solutions are achieved for large D_1, whereas only solutions with the form of a Fourier series are obtained by Elston and Peskin.[9,10] This means that our results are more convenient for computing.

Different from the spring model, in our model there is a threshold κ_0 for stiffness of the linkage (i.e. the strength of the symmetric linear potential) connecting the motor to its cargo. Only when the stiffness exceeds the threshold can the cargo keep up with the motor. Otherwise, the cargo will be dissociated from the motor and diffuse freely in liquid. Generally, this threshold is lower than the strength of the imperfect Brownian ratchet for finite motor diffusion coefficients. But with increasing motor diffusion coefficient (diffusion coefficient of cargo fixed) it achieves the strength of the imperfect Brownian ratchet as the diffusion coefficient of the motor approaches infinity. However, in the article of Elston and Peskin[9] the cargo always moves forward, keeping up with the motor, even when the linkage is sufficiently weak. Obviously, such a consequence of the spring model is not in accord with the reality, in which too soft a linkage should be not capable of dragging the cargo. Now, this discrepancy is erased by introducing the above threshold in our model. The explanation of such a difference between our model and the spring model is as follows. For a spring connecting the motor to the cargo, since the force produced by the spring is proportional to the distance between the motor and the cargo, the minimum force required for the cargo to keep up with the motor can always be reached by stretching their distance. However, in our model such a mechanism does not exist, in that the force produced by the symmetric linear potential is a constant, independent of the distance.

Appendix The procedure of deriving Eqs.(29)–(31) from Eq.(28)

In this appendix a brief description of how to derive Eqs.(29)–(31) from Eq.(28) is presented. First rewrite the integrations of Eq.(28) in a piecewise form by using the relationship

$$\int_0^\infty = \sum_{n=0}^\infty \int_{nL}^{(n+1)L} . \tag{54}$$

Then Eq.(28) becomes

$$\begin{aligned}\phi^{(0)}(x_2) = &- Fx_2 - k_\mathrm{B}T \ln \sum_{n=0}^\infty \left[\int_{nL}^{(n+1)L} \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(-r+x_2)+(F+\kappa)r]\right) \mathrm{d}r \right.\\ &\left. + \int_{nL}^{(n+1)L} \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(r+x_2)+(\kappa-F)r]\right) \mathrm{d}r \right] .\end{aligned} \tag{55}$$

Making the variable transformation $t = r - nL$ yields

$$\begin{aligned}\phi^{(0)}(x_2) = &- Fx_2 - k_\mathrm{B}T \ln \sum_{n=0}^\infty \left[\int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(-t+x_2-nL)+(F+\kappa)t+(F+\kappa)nL]\right) \mathrm{d}t \right.\\ &\left. + \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(t+x_2+nL)+(\kappa-F)t+(\kappa-F)nL]\right) \mathrm{d}t \right] .\end{aligned} \tag{56}$$

By using the periodic condition $\varphi(x+nL) = \varphi(x)$ and drawing the last term of each integrand out of the integrations we obtain

$$\begin{aligned}\phi^{(0)}(x_2) = &- Fx_2 - k_\mathrm{B}T \ln \sum_{n=0}^\infty \left[\exp\left(-\frac{(F+\kappa)nL}{k_\mathrm{B}T}\right) \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(-t+x_2)+(F+\kappa)t]\right) \mathrm{d}t \right.\\ &\left. + \exp\left(-\frac{(\kappa-F)nL}{k_\mathrm{B}T}\right) \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(t+x_2)+(\kappa-F)t]\right) \mathrm{d}t \right]\\ = &- Fx_2 - k_\mathrm{B}T \ln \sum_{n=0}^\infty \left[I_1(x_2) \exp\left(-\frac{(F+\kappa)nL}{k_\mathrm{B}T}\right) \right.\\ &\left. + I_2(x_2) \exp\left(-\frac{(\kappa-F)nL}{k_\mathrm{B}T}\right) \right] ,\end{aligned} \tag{57}$$

where

$$I_1(x_2) = \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(-t+x_2)+(\kappa+F)t]\right) \mathrm{d}t \tag{58}$$

and

$$I_2(x_2) = \int_0^L \exp\left(-\frac{1}{k_\mathrm{B}T}[\varphi(t+x_2)+(\kappa-F)t]\right) \mathrm{d}t. \tag{59}$$

Due to the periodicity of $\varphi(x)$, I_1 and I_2 are also periodic with respect to x_2, i.e.

$$I_1(x_2+L) = I_1(x_2) \tag{60}$$

and

$$I_2(x_2+L) = I_2(x_2). \tag{61}$$

Because I_1 and I_2 are independent of n, they can be drawn out of the summation symbols of Eq.(57). Then by using the following equation:

$$\frac{1}{1-x} = \sum_{n=0}^\infty x^n, \quad 0 \le x < 1, \tag{62}$$

Eq.(29) is finally achieved.

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