Fluctuation Theorem for Channel-Facilitated Membrane Transport of Interacting and Noninteracting Solutes†

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In this paper, we discuss the fluctuation theorem for channel-facilitated transport of solutes through a membrane separating two reservoirs. The transport is characterized by the probability, $P_n(t)$, that n solute particles have been transported from one reservoir to the other in time t. The fluctuation theorem establishes a relation between $P_n(t)$ and $P_{-n}(t)$: The ratio $P_n(t)/P_{-n}(t)$ is independent of time and equal to $\exp(n\beta A)$, where βA is the affinity measured in the thermal energy units. We show that the same fluctuation theorem is true for both single- and multichannel transport of noninteracting particles and particles which strongly repel each other.

1. Introduction

This paper is devoted to statistics of translocations of solute particles in channel-facilitated transport through a membrane that separates left (L) and right (R) reservoirs containing the particles in concentrations $c_{\rm L}$ and $c_{\rm R}$ as shown in Figure 1. The driving force for the transport may be the difference in the solute concentrations, $c_{\rm L} \neq c_{\rm R}$, or a potential drop between the reservoirs, and of course, both factors may act simultaneously. The key quantity of our analysis is the probability, $P_n(t)$, that n particles have been transported from the left reservoir to the right one in time t, which is the probability that the difference between the numbers of L → R and R → L transitions between the reservoirs in time t is equal to n. We will see that the probabilities $P_n(t)$ and $P_{-n}(t)$ are related to each other and obey the fluctuation theorem. This theorem states that the ratio $P_n(t)/P_{-n}(t)$ is independent of time and establishes a relation between the ratio and the affinity that may be considered as a measure of the distance from equilibrium for a nonequilibrium system.[1]

Recently, we derived this theorem for transport of strongly repelling solute particles through a single membrane channel using an exact solution for the Laplace transform of $P_n(t)$.[2] In what follows, we show that the same relation between the ratio $P_n(t)/P_{-n}(t)$ and the affinity is fulfilled for transport of noninteracting solute particles through a single channel, as well as for multichannel transport.

The outline of this paper is as follows: An exact solution for $P_n(t)$ and the fluctuation theorem for single-channel transport of noninteracting particles are derived in the next section. Then we outline the derivation of the exact solution for the Laplace transform of $P_n(t)$ and the fluctuation theorem for single-channel transport of strongly repelling particles in Section 3. Finally, we discuss the fluctuation theorem for multichannel transport in Section 4. In Appendix A, we give a list of symbols used as notations throughout the paper.

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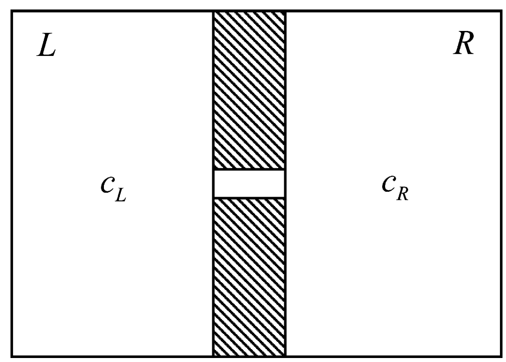

Figure 1. Schematic representation of a channel in a membrane that separates the left (L) and right (R) reservoirs containing the solute particles in concentrations $c_{\rm L}$ and $c_{\rm R}$, respectively.

2. Single-Channel Transport of Noninteracting Solutes

A distinctive feature of transport of noninteracting solutes is that transitions/fluxes in the L → R and R → L directions do not affect each other. To characterize these transitions we introduce probabilities $Q_{\rm L\to R}(n|t)$ and $Q_{\rm R\to L}(n|t)$ that the number of transitions in the corresponding direction in time t is equal to n, $n \geq 0$, assuming that the system is in a steady state at time $t = 0$ when the observation starts.

We will describe entrance of the particles into the channel from the two reservoirs by the bimolecular rate constants $k_{\rm on}^{(I)}$, I = L, R. When the potential drop is localized on the membrane, $k_{\rm on}^{(I)}$ are given by the Hill formula for the trapping rate by an absorbing circular disk on the otherwise reflecting planar wall[3] or its generalization to non-circular absorbers.[4] The probability $Q_I(n|t)$ that n solute particles have entered the channel from reservoir I in time t is given by the Poisson distribution,[1]

$$Q_I(n|t) = \frac{1}{n!}\,(k_{\rm in}^{(I)}t)^n \exp(-k_{\rm in}^{(I)}t) \qquad (2.1)$$

where $k_{\rm in}^{(I)}$ is the monomolecular rate constant, $k_{\rm in}^{(I)} = k_{\rm on}^{(I)}c_I$, which is the inverse of the mean time between successive entrances of new particles into the channel from the reservoir I.

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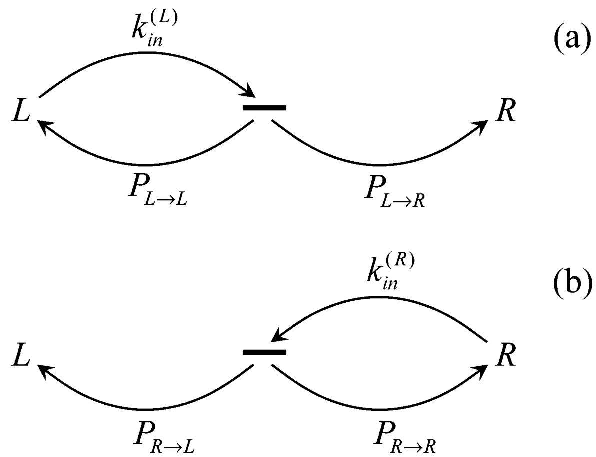

Figure 2. Schematic representation of the fate of a solute particle entering the channel from the left (L) and right (R) reservoirs (panels a and b, respectively). The two reservoirs and the channel are shown as a three-state system. The state in the middle shows the channel that separates the two reservoirs.

The fate of the particle in the channel depends on the side from which the particle enters. A particle entering the channel from the left reservoir traverses the channel and escapes to the right reservoir with probability $P_{L\to R}$ and returns to the left reservoir with probability $P_{L\to L} = 1 - P_{L\to R}$ (see Figure 2). Corresponding translocation and return probabilities for particles entering the channel from the right reservoir are $P_{R\to L}$ and $P_{R\to R} = 1 - P_{R\to L}$.

When m particles enter the channel from the left reservoir, the probability that n of them pass through the channel and exit into the right reservoir while the rest $m - n$ particles return to the initial reservoir is given by ${P_{L\to R}}^n {P_{L\to L}}^{m-n} m!/[n!(m-n)!]$, $n \le m$. Keeping this in mind, we can write $Q_{L\to R}(n|t)$ as an infinite sum,

$$Q_{L\to R}(n|t) = \sum_{m=n}^{\infty} \frac{m!}{n!(m-n)!} {P_{L\to R}}^n {P_{L\to L}}^{m-n} Q_L(m|t) = \frac{1}{n!} {P_{L\to R}}^n \exp(-k_{in}^{(L)} t) \sum_{m=n}^{\infty} \frac{1}{(m-n)!} {P_{L\to L}}^{m-n} (k_{in}^{(L)} t)^m \quad (2.2)$$

where we have used the expression for $Q_L(n|t)$ in eq 2.1. Using the relation

$$\sum_{m=n}^{\infty} \frac{1}{(m-n)!} {P_{L\to L}}^{m-n} (k_{in}^{(L)} t)^m = (k_{in}^{(L)} t)^n \exp(k_{in}^{(L)} P_{L\to L} t) \quad (2.3)$$

we find that the probability, $Q_{L\to R}(n|t)$, is given by the Poisson distribution of the form

$$Q_{L\to R}(n|t) = \frac{1}{n!} (k_{eff}^{(L)} t)^n \exp(-k_{eff}^{(L)} t) \quad (2.4)$$

where $k_{eff}^{(L)}$ is the inverse of the mean time between successive L → R translocations given by

$$k_{eff}^{(L)} = k_{in}^{(L)} P_{L\to R} = k_{on}^{(L)} c_L P_{L\to R} \quad (2.5)$$

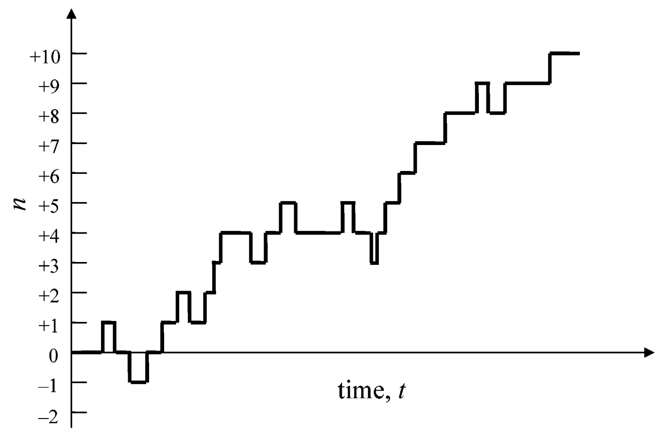

Figure 3. The number of solute particles transported from the left reservoir to the right one as a function of time in the situation when there is a net flux of the particles in the L → R direction.

Respectively, the probability $Q_{R\to L}(n|t)$ is

$$Q_{R\to L}(n|t) = \frac{1}{n!} (k_{eff}^{(R)} t)^n \exp(-k_{eff}^{(R)} t) \quad (2.6)$$

where

$$k_{eff}^{(R)} = k_{in}^{(R)} P_{R\to L} = k_{on}^{(R)} c_R P_{R\to L} \quad (2.7)$$

We use the expressions in eqs 2.4 and 2.6 to find the probability that the difference between the number of particles passing from the left reservoir to the right one in time t and the number of particles passing for this time in the opposite direction is equal to n, $P_n^{(ni)}(t)$,

$$P_n^{(ni)}(t) = \sum_{l,m=0}^{\infty} Q_{L\to R}(l|t) Q_{R\to L}(m|t)\, \delta_{(l-m)n} \quad (2.8)$$

where δ_{ij} is the Kronecker delta and the superscript "ni" indicates that this probability describes transport of noninteracting particles. Thus

$$P_n^{(ni)}(t) = \sum_{k=0}^{\infty} Q_{L\to R}(k+n|t)\, Q_{R\to L}(k|t) \qquad n \ge 0 \quad (2.9)$$

and

$$P_{-n}^{(ni)}(t) = \sum_{k=0}^{\infty} Q_{L\to R}(k|t)\, Q_{R\to L}(k+n|t) \qquad n \ge 0 \quad (2.10)$$

Using eqs 2.4 and 2.6 and the relation[5]

$$\sum_{k=0}^{\infty} \frac{x^k}{k!(n+k)!} = \frac{1}{x^{n/2}} I_n(2\sqrt{x}) \quad (2.11)$$

where $I_n(z)$ is the modified Bessel function of the first kind, which is a symmetric function of n, $I_n(z) = I_{-n}(z)$, we obtain

$$P_n^{(ni)}(t) = \left(\frac{k_{eff}^{(L)}}{k_{eff}^{(R)}}\right)^{n/2} I_n(2\sqrt{k_{eff}^{(L)} k_{eff}^{(R)}}\, t) \exp[-(k_{eff}^{(L)} + k_{eff}^{(R)})t] \quad (2.12)$$

Note that this result can be obtained using an alternative approach based on the idea that the probability $P_n^{(ni)}(t)$ can be considered as a propagator for a nearest-neighbor random walk between identical sites in one dimension

$$\rightleftarrows -3 \rightleftarrows -2 \rightleftarrows -1 \rightleftarrows 0 \rightleftarrows 1 \rightleftarrows 2 \rightleftarrows 3 \rightleftarrows \qquad (2.13)$$

Different sites correspond to different numbers of the particles transported in time t, $P_n^{(ni)}(t) = P_{ni}(n, t|0, 0)$. A trajectory of such a random walk is shown in Figure 3. According to eqs 2.4 and 2.6 the random walk is Markovian with the probability density for the lifetime on a site, $\chi_{ni}(t)$, given by

$$\chi_{ni}(t) = (k_{eff}^{(L)} + k_{eff}^{(R)}) \exp[-(k_{eff}^{(L)} + k_{eff}^{(R)})t] \qquad (2.14)$$

The probabilities $W_+^{(ni)}$ and $W_-^{(ni)}$ that the random walk makes a step in the positive or negative directions are

$$W_+^{(ni)} = \frac{k_{eff}^{(L)}}{k_{eff}^{(L)} + k_{eff}^{(R)}} = \frac{k_{on}^{(L)} c_L P_{L\to R}}{k_{on}^{(L)} c_L P_{L\to R} + k_{on}^{(R)} c_R P_{R\to L}} \qquad (2.15)$$

$$W_-^{(ni)} = \frac{k_{eff}^{(R)}}{k_{eff}^{(L)} + k_{eff}^{(R)}} = \frac{k_{on}^{(R)} c_R P_{R\to L}}{k_{on}^{(L)} c_L P_{L\to R} + k_{on}^{(R)} c_R P_{R\to L}} \qquad (2.16)$$

For such a random walk, one can find an exact solution for the propagator,[6,7] which is identical to the result in eq 2.12.

We will assume that the potential drop between the two reservoirs is localized on the membrane. Denoting the potential energies of a solute particle in the left and right reservoirs by U_L and U_R, respectively, and using the condition of detailed balance,

$$k_{on}^{(L)} P_{L\to R} \exp(-\beta U_L) = k_{on}^{(R)} P_{R\to L} \exp(-\beta U_R) \quad (2.17)$$

where $\beta = (k_B T)^{-1}$ with k_B and T denoting the Boltzmann constant and the absolute temperature, we can write the probabilities in eqs 2.15 and 2.16 in terms of the affinity, $A(c_L/c_R, \Delta U)$, defined by[1]

$$\beta A(c_L/c_R, \Delta U) = \ln\left(\frac{c_L}{c_R}\right) + \beta \Delta U \qquad (2.18)$$

where $\Delta U = U_L - U_R$. The affinity is the difference in the electrochemical potential of a solute particle in the two reservoirs. The result is

$$W_\pm^{(ni)} = \frac{1}{1 + \exp[\mp \beta A(c_L/c_R, \Delta U)]} \qquad (2.19)$$

In equilibrium, $A(c_L/c_R, \Delta U) = 0$ and $W_+^{(ni)} = W_-^{(ni)} = 1/2$.

The propagator in eq 2.12 satisfies the relation

$$\frac{P_n^{(ni)}(t)}{P_{-n}^{(ni)}(t)} = \left(\frac{k_{eff}^{(L)}}{k_{eff}^{(R)}}\right)^n = \left(\frac{k_{on}^{(L)} c_L P_{L\to R}}{k_{on}^{(R)} c_R P_{R\to L}}\right)^n \qquad (2.20)$$

where we have used the above-mentioned symmetry of the Bessel functions, $I_n(z) = I_{-n}(z)$. Using the relations in eqs 2.15, 2.16, and 2.19 we can write eq 2.20 in the form

$$\frac{P_n^{(ni)}(t)}{P_{-n}^{(ni)}(t)} = \left(\frac{W_+^{(ni)}}{W_-^{(ni)}}\right)^n = \exp[n\beta A(c_L/c_R, \Delta U)] \qquad (2.21)$$

which shows that the probability $P_n(t)$ obeys the fluctuation theorem.[8−23] Specifically, this form of the fluctuation theorem has been discussed by Andrieux and Gaspard in ref 18, in which they analyze ion transport in the framework of Schnakenberg's model of the ion channel.[24] We will see that the relations in eqs 2.19 and 2.21 are universal in the sense that the same relations are fulfilled for particles that strongly repel each other, as well as for multichannel membrane transport.

3. Single-Channel Transport of Strongly Repelling Solutes

This section is focused on transport of solute particles, which strongly repel each other, through a single membrane channel. We will discuss some of the results from ref 2, where the repulsion is modeled by the requirement that the channel cannot be occupied by more than one particle. This implies that a particle can enter only an empty channel and, once inside, it blocks the channel. Such a model of a singly occupied channel has been used in refs 25−29 to analyze the steady-state flux with the goal to find an optimal solute-channel interaction that maximizes the flux through the channel. As for noninteracting particles, the probability, $P_n^{(sr)}(t)$, is the propagator $P_{sr}(n, t|0, 0)$ for a random walk, $P_n^{(sr)}(t) = P_{sr}(n, t|0, 0)$, where the subscript/superscript "sr" indicates that the quantity characterizes strongly repelling particles.

A random walk, in general, is characterized by the probabilities of making a step in the positive and negative directions, $W_+^{(sr)}$ and $W_-^{(sr)} = 1 - W_+^{(sr)}$, respectively, as well as the probability densities for the waiting time before the corresponding step is made, $\chi_+^{(sr)}(t)$ and $\chi_-^{(sr)}(t)$. Relations between these probabilities and probability densities and quantities that characterize dynamics of the particles in the channel and the reservoirs have been established in ref 2. Specifically, it has been shown that

$$W_\pm^{(sr)} = W_\pm^{(ni)} \qquad (3.1)$$

and that the two probability densities for the waiting time are identical.

$$\chi_+^{(sr)}(t) = \chi_-^{(sr)}(t) = \chi_{sr}(t) \qquad (3.2)$$

This implies that the waiting time distribution is independent of the passage direction.

In ref 2, we derived an expression for the Laplace transform of $\chi_{sr}(t)$ denoted by $\hat{\chi}_{sr}(s) = \int_0^\infty e^{-st}\chi_{sr}(t)\, dt$. This expression contains six probabilities only three of which are independent. In addition to the translocation and return probabilities mentioned above, it also contains probabilities that a new particle enters the channel from the left or right reservoir, $P_{in}^{(L)}$ and $P_{in}^{(R)} = 1 - P_{in}^{(L)}$, respectively. These probabilities are given by

$$P_{in}^{(I)} = \frac{k_{in}^{(I)}}{k_{in}^{(L)} + k_{in}^{(R)}} = \frac{k_{on}^{(I)} c_I}{k_{on}^{(L)} c_L + k_{on}^{(R)} c_R} \qquad I = L, R \quad (3.3)$$

The expression for $\hat{\chi}_{sr}(s)$ also contains the Laplace transforms of four probability density functions, $\varphi_{emp}(t)$, $\varphi_{L\to L}(t)$, $\varphi_{R\to R}(t)$, and $\varphi_{tr}(t)$. Function $\varphi_{emp}(t)$ is the probability density for the channel lifetime in the empty state,

$$\varphi_{emp}(t) = (k_{in}^{(L)} + k_{in}^{(R)})\exp[-(k_{in}^{(L)} + k_{in}^{(R)})t] = (k_{on}^{(L)} c_L + k_{on}^{(R)} c_R) \exp[-(k_{on}^{(L)} c_L + k_{on}^{(R)} c_R)t] \quad (3.4)$$

Functions $\varphi_{L\to L}(t)$ and $\varphi_{R\to R}(t)$ are the probability densities of the lifetimes in the channel for nontranslocating particles entering the channel from the left and right reservoirs and coming back to the same reservoir from which they entered. As shown in refs 30−32, the probability density of the lifetime in the channel for translocating particles is independent of the translocation direction. This probability density is denoted as $\varphi_{tr}(t)$.

The expression for $\hat{\chi}_{sr}(s)$ derived in ref 2 has the form

$$\hat{\chi}_{sr}(s) = \frac{(P_{in}^{(L)}P_{L\to R} + P_{in}^{(R)}P_{R\to L})\hat{\varphi}_{emp}(s)\hat{\varphi}_{tr}(s)}{1 - [P_{in}^{(L)}P_{L\to L}\hat{\varphi}_{L\to L}(s) + P_{in}^{(R)}P_{R\to R}\hat{\varphi}_{R\to R}(s)]\hat{\varphi}_{emp}(s)} \quad (3.5)$$

This function and the probabilities W_+ and W_- completely characterize the random walk. Note that although the probabilities of the step direction for noninteracting and strongly repelling solutes are identical (eq 3.1), the probability densities $\chi_{ni}(t)$ and $\chi_{sr}(t)$ are quite different. Whereas the former is single exponential, the latter is definitely not. This implies that that the equivalent random walk is Markovian for noninteracting solute particles and non-Markovian for strongly repelling particles. The second random walk is non-Markovian because the overall translocation process is viewed as at least a two-state process (entering the empty channel and translocating).[33,34]

After the problem of finding $P_n^{(sr)}(t)$ has been reduced to that of finding the random walk propagator, the latter can be analyzed by solving a set of integral equations. Using this set, one can obtain an exact solution for the Laplace transform of $P_n^{(sr)}(t)$. An expression giving $\hat{P}_n^{(sr)}(s)$ in terms of W_+, W_-, and $\hat{\chi}_{sr}(s)$ has been derived in ref 2:

$$\hat{P}_n^{(sr)}(s) = \left(\frac{W_+}{W_-}\right)^{n/2}\left[\frac{2\sqrt{W_+W_-}\hat{\chi}_{sr}(s)}{1 + \sqrt{1 - 4W_+W_-[\hat{\chi}_{sr}(s)]^2}}\right]^{|n|} \times \frac{1 - \hat{\chi}_{sr}(s)}{s\sqrt{1 - 4W_+W_-[\hat{\chi}_{sr}(s)]^2}} \quad (3.6)$$

This can also be obtained using the results presented in ref 7. Note that the Laplace transform in eq 3.6 might be used to derive $P_n^{(ni)}(t)$ in eq 2.12. This can be done by replacing $\hat{\chi}_{sr}(s)$ by the Laplace transform of its Markovian counterpart, $\hat{\chi}_{ni}(s) = (k_{eff}^{(L)} + k_{eff}^{(R)})/(s + k_{eff}^{(L)} + k_{eff}^{(R)})$, and inverting the resulting Laplace transform.[5,7]

One can see that $\hat{P}_n^{(sr)}(s)$ satisfies $W_-^n\hat{P}_n^{(sr)}(s) = W_+^n\hat{P}_{-n}^{(sr)}(s)$ and, hence, the probability $P_n^{(sr)}(t)$ obeys the same fluctuation theorem as $P_n^{(ni)}(t)$ (eq 2.21).

$$\frac{P_n^{(sr)}(t)}{P_{-n}^{(sr)}(t)} = \frac{P_n^{(ni)}(t)}{P_{-n}^{(ni)}(t)} = \left(\frac{W_+}{W_-}\right)^n = \exp[n\beta A(c_L/c_R, \Delta U)] \quad (3.7)$$

Thus, as has been mentioned above this fluctuation theorem is fulfilled for both noninteracting and strongly repelling solute particles.

4. Multichannel Transport

In this section, we consider transport between the two reservoirs through a membrane containing M independent channels that do not affect each other. Assuming that the probability $P_n(t)$ for each isolated channel obeys the fluctuation theorem,

$$\frac{P_n(t)}{P_{-n}(t)} = \left(\frac{W_+}{W_-}\right)^n = \exp[n\beta A(c_L/c_R, \Delta U)] \quad (4.1)$$

we will show that the probability $P_n^{(M)}(t)$ that n particles have been transported from the left reservoir to the right one through M channels in time t obeys the same fluctuation theorem,

$$\frac{P_n^{(M)}(t)}{P_{-n}^{(M)}(t)} = \frac{P_n(t)}{P_{-n}(t)} = \left(\frac{W_+}{W_-}\right)^n = \exp[n\beta A(c_L/c_R, \Delta U)] \quad (4.2)$$

There are several different ways to prove this relation. The way we chose is, presumably, the shortest one.

Since the channels are independent, the probability $P_n^{(M)}(t)$ can be written in terms of the single-channel probabilities $P_{n_i}(t)$, $i = 1, ..., M$ as

$$P_n^{(M)}(t) = \sum_{n_1,...,n_M=-\infty}^{\infty} P_{n_1}(t) \ldots P_{n_M}(t)\delta_{(n_1+...+n_M)n} \quad (4.3)$$

Using eq 4.1, one can see that each term in the sum satisfies

$$P_{n_1}(t) \ldots P_{n_M}(t) = \left(\frac{W_+}{W_-}\right)^{n_1+...+n_M} P_{-n_1}(t) \ldots P_{-n_M}(t) \quad (4.4)$$

Substituting this into eq 4.3 and taking the Kronecker delta into account, one arrives at the relation in eq 4.2.

In summary, the main results of this paper are the expressions in eqs 2.12 and 4.3 providing explicit solutions for $P_n(t)$ as well as expressions in eqs 2.21, 3.7, and 4.2, which represent the fluctuation theorem for single- and multichannel membrane transport of noninteracting solute particles and particles that strongly repel each other. These expressions have been derived using explicit solutions for $P_n(t)$ and its Laplace transform.

Appendix A: List of Symbols

$A(c_L/c_R, \Delta U)$	the affinity;
c_I	the solute concentration in the reservoir I;
I = L, R	the index of the reservoir;
$k_{eff}^{(L)}$	the inverse of the mean time between successive L → R translocations;
$k_{eff}^{(R)}$	the inverse of the mean time between successive R → L translocations;
$k_{in}^{(I)}$	the monomolecular rate constant that is equal to the inverse of the mean time between successive entrances of new particles into the channel from reservoir I;
$k_{on}^{(I)}$	the bimolecular rate constant for trapping particles entering the channel from reservoir I;
$P_{in}^{(I)}$	the probability that a new particle enters the channel from reservoir I;
$P_n(t)$	the probability that n solute particles have been transported from the left reservoir to the right one through a single channel in time t;
$P_n^{(M)}(t)$	the probability that n particles have been transported from the left reservoir to the right one through M channels in time t;
$P_{L\to R}$	the translocation probability for a particle entering the channel from the left reservoir;
$P_{L\to L}$	the return probability for a particle entering the channel from the left reservoir;
$P_{R\to L}$	the translocation probability for a particle entering the channel from the right reservoir;
$P_{R\to R}$	the return probability for a particle entering the channel from the right reservoir;

$P_{ni}(n, t|0, 0)$ the propagator for the nearest-neighbor random walk between identical sites in one dimension, which starts from the origin, $n = 0$, at $t = 0$; representing transport of noninteracting particles

$P_{sr}(n, t|0, 0)$ the propagator for the nearest-neighbor random walk between identical sites in one dimension, which starts from the origin, $n = 0$, at $t = 0$; representing transport of strongly repelling particles

$Q_I(n|t)$ the probability that n solute particles have entered the channel from reservoir I in time t;

$Q_{L\rightarrow R}(n|t)$ the probability that the number of transitions from the left reservoir to the right one in time t is equal to n;

$Q_{R\rightarrow L}(n|t)$ the probability that the number of transitions from the right reservoir to the left one in time t is equal to n;

U_I the potential energy of a solute particle in the reservoir I;

$W_{\pm}^{(ni)}$ the probability that the random walk, which represents transport of noninteracting particles, makes a step in the positive (+) or negative (−) direction;

$W_{\pm}^{(sr)}$ the probability that the random walk, which represents transport of strongly repelling particles, makes a step in the positive (+) or negative (−) direction;

ΔU the energy difference, $\Delta U = U_L - U_R$;

β the inverse thermal energy, $\beta = (k_B T)^{-1}$, with k_B and T denoting the Botlzmann constant and the absolute temperature;

$\varphi_{emp}(t)$ the probability density for the channel lifetime in the empty state;

$\varphi_{tr}(t)$ the probability density of the lifetime in the channel for a translocating particle;

$\varphi_{I\rightarrow I}(t)$ the probability density of the lifetime in the channel for a non-translocating particle entering the channel from reservoir I;

$\chi_{ni}(t)$ the probability density for the lifetime on a site of the Markovian random walk which represents transport of noninteracting particles;

$\chi_{sr}(t)$ the probability density for the lifetime on a site of the non-Markovian random walk which represents transport of strongly repelling particles;

$\chi_{\pm}^{(sr)}(t)$ the probability density for the lifetime on a site before the non-Markovian random walk, which represents transport of strongly repelling particles, makes a step in the corresponding (±) direction.

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