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ANALYTICAL ASPECTS OF THE BROWNIAN MOTOR EFFECT IN RANDOMLY FLASHING RATCHETS

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ABSTRACT: The muscle contraction, operation of ATP synthase, maintaining the shape of a cell are believed to be secured by motor proteins, which can be modelled using the Brownian ratchet mechanism. We consider the randomly flashing ratchet model of a Brownian motor, where the particles can be in two states, only one of which is sensitive the applied spatially periodic potential (the mathematical setting is a pair of weakly coupled reaction-diffusion and Fokker-Planck equations). We prove that this mechanism indeed generates unidirectional transport by showing that the amount of mass in the wells of the potential decreases/increases from left to right. The direction of transport is unambiguously determined by the location of each minimum of the potential with respect to the so-called diffusive mean of its adjacent maxima. The transport can be generated not only by an asymmetric potential, but also by a symmetric potential and asymmetric transition rates, and as a consequence of the general result we derive explicit conditions when the latter happens.

KEYWORDS: flashing ratchet, motor protein, Fokker-Planck equation, stationary solution, diffusive mean, transport.
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1. Introduction

Brownian motors are nano-scale or molecular machines which can produce directed motion when the average force and average temperature gradient are zero [3, 21]. At first glance, the existence of such devices seems to be a paradox, and discretization of the idea really did lead to Parrondo's paradox in game theory [2, 6]. Typically, the mechanism involved (*ratchet*) is based on an interplay between the Brownian motion (*diffusion*), an asymmetric (ratchet-like) *potential*, and *nonequilibrium* of the system due to chemical or thermal *fluctuations*.

The ratchet principle is ubiquitous and appears everywhere from political system to famine cycles, from production strategy to cultural studies. Motor

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proteins, which provide muscle contraction (myosin, kinesin, dynein), ATP synthase, as well as membrane-bound motor proteins maintaining the shape of a cell, can be modelled using the Brownian ratchet mechanism [1, 9, 19, 20]. A ribosome can also be considered as a Brownian ratchet device [22].

The motor proteins can attach to and detach from a substrate of vectorial symmetry [1, 20] under the action of a chemical energy source. This leads to the following boundary value problem [1, 14, 15]:

$$\begin{cases} p_t - \sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1),\ t \geq 0, \\ P_t - \varsigma P_{xx} = -\nu P + \eta p, & x \in (0,1),\ t \geq 0, \\ \sigma p_x + \kappa \psi_x p = 0, & x = 0,1,\ t \geq 0, \\ P_x = 0, & x = 0,1,\ t \geq 0, \\ p \geq 0,\ P \geq 0, & \\ \int\limits_0^1 p(t,x) + P(t,x)\, dx = 1,\ t \geq 0. & \end{cases} \tag{1}$$

Here $p(t,x)$ and $P(t,x)$ are the unknown densities of the particles in "attached" and "detached" states, resp., at a time t and a spatial point x; σ and ς are the diffusion coefficients of "attached" and "detached" particles, resp.; $\psi(x)$ is the potential; κ is a coefficient inversely proportional to temperature; $\nu(x) > 0$ and $\eta(x) > 0$ are the rates of transition from one state to another (i.e. ν indicates the probability of seizing a motor protein by a "detached" particle (located at a spatial point x), and η expresses the probability of losing its motor protein for an "attached" particle). A typical "ratchet-like" potential ψ with k teeth, $k > 1$, is $1/k$-periodic in x and has a unique local (and, hence, global) minimum within each period.

Let us compare this model with a somehow simpler one called the *flashing ratchet* [3]. Here there is only one state, ρ is the unknown density of particles, σ is the diffusion coefficient, and ψ is the potential, which is switched on and off cyclically:

$$\begin{cases} \rho_t = \sigma \rho_{xx} + h(t)(\psi_x \rho)_x, \qquad x \in (0,1), \\ \sigma \rho_x + h(t)\psi_x \rho = 0, \qquad x = 0,1, \\ \rho \geq 0, \\ \int\limits_0^1 \rho(x,t)dx = 1, \\ h(t) = 1,\ nT < t \leq nT + T_{tr},\ n = 0,1,\dots, \\ h(t) = 0,\ nT + T_{tr} < t \leq nT + T,\ n = 0,1,\dots. \end{cases} \tag{2}$$

Here each particle is potential-sensitive and the potential-insensitive for a priori known moments of time, whereas in the first model this is determined by random attachments and detachments of the motor protein. Therefore model (1) is sometimes referred to as the *randomly flashing ratchet*.

Another model related to (1) is the *collaborative ratchet* [5, 9, 19, 20] where the particles in two states are sensitive to two different potentials ψ and Ψ which help each other to achieve the motor effect:

$$\begin{cases} p_t - \sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1),\ t \geq 0, \\ P_t - \varsigma P_{xx} - \kappa(\Psi_x P)_x = -\nu P + \eta p, & x \in (0,1),\ t \geq 0, \\ \sigma p_x + \kappa \psi_x p = 0, & x = 0, 1,\ t \geq 0, \\ \varsigma P_x + \kappa \Psi_x P = 0, & x = 0, 1,\ t \geq 0, \\ p \geq 0,\ P \geq 0, & \\ \int\limits_0^1 p(t,x) + P(t,x)\, dx = 1,\ t \geq 0. & \end{cases} \tag{3}$$

This model is relevant not only in connection with biology, but also in transport of cold rubidium atoms [12].

The mathematical studies of Brownian ratchet models start with the question whether they indeed generate unidirectional transport (which is observed in experiments and simulations), and what assumptions are needed for that. For example, model (1) is too general to produce transport with any choice of parameters: setting

$$\eta/\nu = \exp\left(\kappa\psi/\sigma\right),$$

we observe that the total amount of mass in the "wells" of the potential, i.e. in the segments $[\frac{i}{k}, \frac{i+1}{k}]$, $i = 0, \ldots, k-1$, eventually with the course of time tends to $1/k$. This shows that the ratchets should be "tuned" to work well.

Comparing eventual distribution of mass between the "wells" of the potential ψ, it is possible to mathematically endorse the motor effect [10]. A left-to-right chain of inequalities in this distribution would mean unidirectional transport.

The occurrence of transport in model (3) for small $\sigma = \varsigma$ and certain interplay between the potentials was shown in [4]. Some of the results of that paper — in particular, existence of unique solutions to (3) and to the stationary problem

$$\begin{cases} -\sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1), \\ -\varsigma P_{xx} - \kappa(\Psi_x P)_x = -\nu P + \eta p, & x \in (0,1), \\ \sigma p_x + \kappa \psi_x p = 0, & x = 0,1, \\ \varsigma P_x + \kappa \Psi_x P = 0, & x = 0,1, \\ p \geq 0, \ P \geq 0, & \\ \int\limits_0^1 p(x) + P(x)\, dx = 1, & \end{cases} \tag{4}$$

and eventual convergence of solutions to (3) to the solutions of (4) — are valid for $\Psi \equiv$ *const* as well. The transport result was generalized to the multi-state systems with several interacting non-flat potentials in [7, 17].

The analytical proof of the motor effect for the flashing ratchet (2) was given in [23], based on a framework developed in [10]. The unidirectional transport occurs when the potential is asymmetric, and its direction is determined by the location of the minima of the potential with respect to the centres of the corresponding wells. A homogenization approach to the flashing ratchet (2) was proposed in [18]. This approach was applied to the randomly flashing ratchet (1) in [16] (see also [13]). There were presented examples of transport in the case of a sawtooth potential (which is asymmetric) and constant transition rates (which are obviously symmetric), and with a symmetric potential and asymmetric transition rates. We are not aware of any works with rigorous mathematical evidences of transport for the non-homogenized problem (1).

In this paper, we show that the motor effect in model (1) is due to a subtle interplay between the asymmetries of the potential ψ and the transition rate ν. More precisely, an asymmetry of the transition function ν yields a deviation of the so-called *diffusive means* of the edge points of the wells of the potential — these edge points are the maxima of ψ — from the centres of the wells. The direction of transport is determined by the location of the minima of the potential with respect to that biased centres (the diffusive means of the adjacent maxima). The ratchet is tuned when the influence of the potential on the particles which carry the motor protein dominates their diffusion (which is a natural assumption since these complex particles are larger and thus diffuse slower).

The paper is organized as follows. In the next section, we set the problem more rigorously, define the notion of the diffusive mean, observe its main properties and evaluate it, and finally formulate the main result (Theorem 2.1). In the third section, we introduce a semidiscretized device, the *squeezing ratchet*, and prove that it generates unidirectional transport. The proof of the main result is provided in the forth section, where we show that the squeezing ratchet and the original randomly flashing ratchet have similar behaviour. The last section contains a discussion of the results.

2. Preliminaries

We consider the stationary boundary value problem for the randomly flashing ratchet equation with Neumann boundary conditions

$$\begin{cases} -\sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1), \\ -\varsigma P_{xx} = -\nu P + \eta p, & x \in (0,1), \\ \sigma p_x + \kappa \psi_x p = 0, & x = 0, 1, \\ P_x = 0, & x = 0, 1, \\ p \geq 0, \;\; P \geq 0, & \\ \int\limits_0^1 p(x) + P(x)\, dx = 1, & \end{cases} \tag{5}$$

which describes the eventual distribution of particles subjected to the action of the ratchet.

The potential $\psi(x)$ and the transition rates $\nu(x) > 0$ and $\eta(x) > 0$ are assumed to be smooth scalar functions on $[0,1]$ of period $1/k$, with $k > 1$ being a fixed integer. The potential ψ should have maxima at points x_i and minima at points a_i, and be monotonic (without zero slopes) between these points, where

$$x_i = \frac{i-1}{k}, \;\; i = 1, \ldots, k+1, \tag{6}$$

$$a_i = a + x_i, \;\; i = 1, \ldots, k. \tag{7}$$

The positive parameter a should be less than $1/k$.

The symbol δ_x denotes the Dirac delta centered at $x \in \mathbb{R}$. The symbol C will stand for a generic positive constant that can take different values in different lines. We use the bra-ket notation $\langle \mu, f \rangle = \int\limits_A^B f \, d\mu$, where $\mu \in C^*[A,B]$, and f is a continuous function on $[A,B]$.

Definition 2.1. Unless otherwise specified, we say that $u \in L_1(A, B)$ is a solution to the problem

$$\begin{cases} (k_1 u)_{xx}(x) + (k_2 u)_x(x) + k_3(x)u(x) = \Theta(u)(x), & x \in (A, B), \\ (k_1 u)_x(A) = (k_1 u)_x(B) = 0, \end{cases}$$

where functions $k_1, k_2, k_3 \in C[A, B]$, $k_2(A) = k_2(B) = 0$, and a linear operator $\Theta : L_1(A, B) \to C^*[A, B]$ are prescribed, if

$$\int_A^B k_1(x)u(x)\varphi_{xx}(x) - k_2(x)u(x)\varphi_x(x) + k_3(x)u(x)\varphi(x)\,dx = \langle \Theta(u), \varphi \rangle \quad (8)$$

for any $\varphi \in C^2[A, B]$, $\varphi_x(A) = \varphi_x(B) = 0$.

Note that (8) already includes the Neumann boundary condition.

Definition 2.2. Let A and B be real numbers, and $\phi(x) > 0$ be a continuous scalar function on $[A, B]$. The number $s \in (A, B)$ is called the *ϕ-diffusive mean* of A and B provided the system

$$\begin{cases} \phi U - U_{xx} = \delta_s, & x \in (A, B), \\ U(A) = U(B), \\ U_x(A) = U_x(B) = 0 \end{cases} \quad (9)$$

has a solution U.

Proposition 2.1. *The ϕ-diffusive mean always exists and is unique.*

We give the proof at the end of this section.

Example 2.1. Let

$$\tilde{\phi}(x) = \phi(A + B - x).$$

Then the ϕ-diffusive mean of A and B is equal to their sum minus their $\tilde{\phi}$-diffusive mean. In particular, if ϕ is a constant function or merely

$$\phi(x) = \tilde{\phi}(x),\ A \le x \le \frac{A + B}{2}, \quad (10)$$

then the diffusive mean coincides with the arithmetic mean $\frac{A+B}{2}$.

Another example is given by

Proposition 2.2. *Let*

$$\phi(x) \leq \tilde{\phi}(x),\ A \leq x \leq \frac{A+B}{2}, \tag{11}$$

and the inequality is strict at least at one point. Then the ϕ-diffusive mean of A and B is strictly larger than the arithmetic mean $\frac{A+B}{2}$.

The proof is located at the end of the section. A symmetry argument shows that if

$$\phi(x) \geq \tilde{\phi}(x),\ A \leq x \leq \frac{A+B}{2}, \tag{12}$$

and the inequality is strict at least at one point, then the diffusive mean is strictly less than $\frac{A+B}{2}$.

For any integrable scalar function Φ on $(0,1)$, we denote

$$\widehat{\Phi}_i = \int\limits_{x_i}^{x_{i+1}} \Phi(x)\,dx,\ i = 1,\dots,k. \tag{13}$$

The main result of the paper is

Theorem 2.1. *Let S be the $\frac{\nu}{\varsigma}$-diffusive mean of 0 and $1/k$. If $a < S$, then, for sufficiently small σ and sufficiently large κ,*

$$\widehat{p}_1 > \widehat{p}_2 > \cdots > \widehat{p}_k, \tag{14}$$

$$\widehat{P}_1 > \widehat{P}_2 > \cdots > \widehat{P}_k. \tag{15}$$

Theorem 2.1 means, in particular, that, if the diffusion of potential-sensitive particles is slow, and the influence of the potential is strong (or the temperature is low), and if $a < S$, then, given any initial distribution of density, the mass of particles of each kind in the wells will eventually decrease from left to right, i.e. the motor effect is present.

Remark 2.1. We will even prove that

$$P(x) > P(x + 1/k),\ 0 \leq x \leq 1 - 1/k, \tag{16}$$

which is stronger than (15).

Example 2.2. Let the potential ψ be symmetric, i.e. $\psi(x) = \psi(1-x)$, which can only happen when $a = \frac{1}{2k}$. The one-state flashing ratchet cannot generate transport in this case. However, the randomly flashing ratchet can. Assume that

$$\nu(x) \le \nu(-x + 1/k),\ 0 \le x \le \frac{1}{2k}, \tag{17}$$

with strict inequality at least at one point. Then $a = \frac{1}{2k} < S$ by Proposition 2.2, and the transport occurs.

Remark 2.2. If $a > S$, then Theorem 2.1 implies $\widehat{p}_1 < \widehat{p}_2 < \cdots < \widehat{p}_k$, $\widehat{P}_1 < \widehat{P}_2 < \cdots < \widehat{P}_k$ — to see this it suffices to make the change of variables $x \to 1 - x$, to apply the reasoning of Example 2.1 with $\phi = \frac{\nu}{\varsigma}$, $A = 0$ and $B = 1/k$, and to take into account that $\tilde{\phi}(x) = \phi(\frac{1}{k} - x) = \phi(1 - x)$ due to periodicity.

Example 2.3. Let ν be symmetric, i.e. $\nu(x) = \nu(1-x)$. Then periodicity of ν and Example 2.1 imply that $S = \frac{1}{2k}$. The motor effect is provided by the condition $a \neq \frac{1}{2k}$, i.e. the potential should be asymmetric, and the direction of transport is determined by the location of a with respect to $\frac{1}{2k}$, as for the one-state flashing ratchet [23].

We can renormalize (5) to get

$$\begin{cases} -\sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1), \\ -\varsigma P_{xx} = -\nu P + \eta p, & x \in (0,1), \\ \sigma p_x + \kappa \psi_x p = 0, & x = 0, 1, \\ P_x = 0, & x = 0, 1, \\ p \ge 0,\ P \ge 0, & \\ \int\limits_0^1 \eta(x)p(x) + \nu(x)P(x)\, dx = 2. & \end{cases} \tag{18}$$

Integration of (18) implies

$$\int\limits_0^1 \eta(x)p(x) - \nu(x)P(x)\, dx = 0. \tag{19}$$

Since 0 and 1 are maxima of ψ, we have $\psi_x(0) = \psi_x(1) = 0$. Thus, (18) is equivalent to

$$\begin{cases} -\sigma p_{xx} - \kappa(\psi_x p)_x = \nu P - \eta p, & x \in (0,1), \\ -\varsigma P_{xx} = -\nu P + \eta p, & x \in (0,1), \\ p_x = 0, & x = 0, 1, \\ P_x = 0, & x = 0, 1, \\ p \geq 0, \ P \geq 0, & \\ \int\limits_0^1 \eta(x) p(x)\, dx = 1, & \\ \int\limits_0^1 \nu(x) P(x)\, dx = 1. & \end{cases} \tag{20}$$

Since problem (5) is linear, it is enough to prove Theorem 2.1 for the renormalized problem (20).

Proof: (Proposition 2.1) Let $G(x, y)$ be Green's function of the Sturm-Liouville operator

$$\mathcal{L} = -\frac{d^2}{dx^2} + \phi$$

on (A, B) with homogeneous Neumann boundary condition. Then $U(x) = G(x, s)$ is a solution to (9) if an only if $G(A, s) = G(B, s)$.

By the distributional maximum principle [11, Theorem B], $G(x, y) > 0$. Observe that

$$G_x(x, A) = \int\limits_B^x \phi(z) G(A, z)\, dz, \tag{21}$$

$$G_x(x, B) = \int\limits_A^x \phi(z) G(B, z)\, dz. \tag{22}$$

Hence, the function $G(x, A)$ is decreasing in x, and $G(x, B)$ is increasing. Thus, the function

$$g(x) = G(A, x) - G(B, x)$$

is also (strictly) decreasing. At the ends of the segment, we have $g(A) = G(A, A) - G(B, A) > 0$ and $g(B) = G(A, B) - G(B, B) < 0$. Since g is a continuous function, there is unique $s \in (A, B)$ such that $G(A, s) = G(B, s)$. ■

Proof: (Proposition 2.2) Let

$$g_1(x) = G(\frac{A+B}{2}, x) - G(\frac{A+B}{2}, A+B-x).$$

We claim that

$$g_1(A) > 0. \tag{23}$$

Since G is Green's function,

$$(g_1)_x(A) = 0, \tag{24}$$

and

$$\begin{aligned}
&(g_1)_{xx}(x) \\
&= \phi(x)G(\frac{A+B}{2}, x) - \phi(A+B-x)G(\frac{A+B}{2}, A+B-x) \\
&= \phi(x)g_1(x) + [\phi(x) - \tilde{\phi}(x)]G(\frac{A+B}{2}, A+B-x) \\
&\le \phi(x)g_1(x),\ A \le x < \frac{A+B}{2},
\end{aligned} \tag{25}$$

and the inequality is strict at least at one point. In particular, g_1 cannot be identically zero.

Assume that $g_1(A) \le 0$. By the maximum principle, g_1 cannot have non-positive minima within $(A, \frac{A+B}{2})$. But

$$g_1(\frac{A+B}{2}) = 0, \tag{26}$$

so A must be a minimum point. Let $g_2(x) = g_1(x) - g_1(A)$. Then g_2 is non-negative, and

$$(g_2)_{xx}(x) \le \phi(x)g_2(x),\ A \le x < \frac{A+B}{2}. \tag{27}$$

Thus,

$$(g_2)_x(x) \le \int_A^x \phi(t)g_2(t)\,dt,\ A \le x \le \frac{A+B}{2}. \tag{28}$$

By the mean value theorem,

$$\begin{aligned} g_2(x) &= g_2(x) - g_2(A) = (x-A)(g_2)_x(c) \\ &\le (x-A)\int_A^c \phi(t)g_2(t)\,dt \le \frac{1}{2}(B-A)\int_A^x \phi(t)g_2(t)\,dt \end{aligned} \tag{29}$$

for some c, $A < c < x \le \frac{A+B}{2}$. The Gronwall lemma implies $g_2 \equiv 0$, so, by (26), $g_1 \equiv 0$, and we get a contradiction.

Hence,

$$g(\frac{A+B}{2}) = g_1(A) > 0.$$

Then (cf. the proof of Proposition 2.1) there is $s \in (\frac{A+B}{2}, B)$ such that $g(s) = 0$, and this number s is the ϕ-diffusive mean. ■

3. Squeezing ratchet

Let $G(x,y)$ be Green's function of the Sturm-Liouville operator

$$\mathcal{L} = -\varsigma\frac{d^2}{dx^2} + \nu$$

on $(0,1)$ with homogeneous Neumann boundary condition. Let $q_i(x) = G(x, a_i)$, i.e.

$$\begin{cases} \nu q_i - \varsigma q_{ixx} = \delta_{a_i}, & x \in (0,1), \\ q_{ix}(0) = q_{ix}(1) = 0, \end{cases} \tag{30}$$

and let

$$q = \sum_{i=1}^{k} q_i. \tag{31}$$

As we already observed in the proof of Proposition 2.1,

$$q_i(x) > 0, \ x \in [0,1]. \tag{32}$$

Our core tool for catching the motor effect is the following theorem.

Theorem 3.1. *There exists a unique function $Q \in C[0,1]$ solving the following problem:*

$$\begin{cases} \nu Q - \varsigma Q_{xx} = \sum\limits_{i=1}^{k} \widehat{(\nu Q)}_i \delta_{a_i}, \ \ x \in (0,1), \\ Q_x(0) = Q_x(1) = 0, \\ \int\limits_0^1 \nu(x) Q(x)\, dx = 1. \end{cases} \tag{33}$$

Moreover, if

$$q(x) \geq q(x+1/k) + \gamma, \ 0 \leq x \leq 1 - 1/k, \tag{34}$$

with some $\gamma > 0$, then

$$Q(x) \geq Q(x+1/k) + M\gamma, \ 0 \leq x \leq 1 - 1/k, \tag{35}$$

where $M = \min_{i=1,\dots,k} \widehat{(\nu q_i)}_k$.

Proof: Consider the set of functions

$$B = \left\{ y(x) \in L_1(0,1) \,\middle|\, \int\limits_0^1 \nu(x) y(x)\, dx = 1, \ \widehat{(\nu y)}_k \geq M, \right.$$

$$\left. y(x) \geq y(x+1/k) + M\gamma, \ \text{for a.a. } 0 \leq x \leq 1 - 1/k. \right\}$$

Inverse induction shows that for any $i = 1, \dots, k$ and $y \in B$ one has

$$\widehat{(\nu y)}_i \geq M. \tag{36}$$

Let us define a mapping $\mathcal{A}$ on B. For each $y \in B$, we let $\mathcal{A}(y) = Y$, where Y is the solution of the problem

$$\begin{cases} \nu Y - \varsigma Y_{xx} = \sum\limits_{i=1}^{k} \widehat{(\nu y)}_i \delta_{a_i}, \ \ x \in (0,1), \\ Y_x(0) = Y_x(1) = 0. \end{cases} \tag{37}$$

To put it differently,

$$Y = \sum_{i=1}^{k} \widehat{(\nu y)}_i q_i. \tag{38}$$

Then, the set B is invariant for the map $\mathcal{A}$. In fact, let $y \in B$. Then (37) implies

$$\int_0^1 \nu(x)Y(x)\,dx = \sum_{i=1}^k \widehat{(\nu y)}_i = \int_0^1 \nu(x)y(x)\,dx = 1.$$

Further,

$$\widehat{(\nu Y)}_k = \sum_{i=1}^k \widehat{(\nu y)}_i \widehat{(\nu q_i)}_k \geq M \sum_{i=1}^k \widehat{(\nu y)}_i = M.$$

Finally, fix $x_* \in [0, 1-1/k]$. Then there is a number n such that $x_* \in [x_n, x_{n+1})$. Set

$$N_* = \begin{cases} \widehat{(\nu y)}_n, & x_* \leq a_n, \\ \widehat{(\nu y)}_{n+1}, & x_* > a_n. \end{cases} \tag{39}$$

We claim that

$$(\widehat{(\nu y)}_i - N_*)[q_i(x_*) - q_i(x_* + 1/k)] \geq 0,\ i = 1, \dots, k. \tag{40}$$

Indeed, integration of (30) gives

$$\varsigma q_{ix}(x) = \int_0^x \nu(z)q_i(z)\,dz,\ x < a_i, \tag{41}$$

$$\varsigma q_{ix}(x) = \int_1^x \nu(z)q_i(z)\,dz,\ x > a_i. \tag{42}$$

Thus, the function q_i is increasing on the segment $[0, a_i]$ and decreasing on $[a_i, 1]$. Assume first $x_* \leq a_n$. Then, if $i < n$, we have $q_i(x_*) > q_i(x_* + 1/k)$. Since $y \in B$, we also have $\widehat{(\nu y)}_i > \widehat{(\nu y)}_n = N_*$, and (40) holds true. If $i > n$, we have $q_i(x_*) < q_i(x_* + 1/k)$ and $\widehat{(\nu y)}_i < N_*$, and (40) again holds. If $i = n$, (40) is trivial. Now, let $x_* > a_n$. In this case, if $i < n+1$, $q_i(x_*) > q_i(x_* + 1/k)$ and $\widehat{(\nu y)}_i > \widehat{(\nu y)}_{n+1} = N_*$; if $i > n+1$, $q_i(x_*) < q_i(x_* + 1/k)$ and $\widehat{(\nu y)}_i < N_*$; and if $i = n+1$, (40) is again trivial.

Formulas (38), (40), (34) and (36) yield

$$Y(x_*) - Y(x_* + 1/k) = \sum_{i=1}^k \widehat{(\nu y)}_i [q_i(x_*) - q_i(x_* + 1/k)]$$

$$\geq \sum_{i=1}^{k} N_*[q_i(x_*) - q_i(x_* + 1/k)] = N_*[q(x_*) - q(x_* + 1/k)] \geq M\gamma,$$

so the invariance of B is confirmed.

Observe that $\mathcal{A}$ is a compact linear operator in $L_1(0,1)$. Indeed, let $\mathbb{B}$ be the unit ball of the space $L_1(0,1)$. Due to (38), its image $\mathcal{A}(\mathbb{B})$ is a bounded subset of the linear span of $\{q_1, \dots, q_k\}$, thus being a relatively compact subset of a finite-dimensional subspace of $L_1(0,1)$.

Let us show that (33) may have at most one solution, so $\mathcal{A}$ can have at most one fixed point in B. If not, let $\tilde{Q}$ be the difference of two distinct solutions. Then

$$\int_0^1 \nu(z)\tilde{Q}(z)\,dz = 0. \tag{43}$$

Moreover,

$$\tilde{Q} = \sum_{i=1}^{k} \widehat{(\nu\tilde{Q})}_i q_i, \tag{44}$$

whence

$$\widehat{(\nu\tilde{Q})}_j = \sum_{i=1}^{k} \widehat{(\nu\tilde{Q})}_i \widehat{(\nu q_i)}_j, \;\; j = 1, \dots, k. \tag{45}$$

From (30) we deduce

$$\int_0^1 \nu(z) q_i(z)\,dz = 1. \tag{46}$$

Therefore, the matrix $[\mathcal{P}_{ij}] = \left[\widehat{(\nu q_i)}_j\right]$ is *ergodic*, i.e. it has positive entries, and the sum of the elements in every row is equal to one. By the Perron-Frobenius theorem, it has an eigenvector $[\xi_i]$ corresponding to the simple eigenvalue 1, so that $\xi_j = \sum\limits_{i=1}^{k} \xi_i \mathcal{P}_{ij}$, and all the components ξ_i are positive. On the other hand, by (45), $[\Xi_i] = \left[\widehat{(\nu\tilde{Q})}_i\right]$ is another eigenvector of $[\mathcal{P}_{ij}]$ corresponding to the same eigenvalue. The sum of its components is zero due to (43), so it cannot be collinear with $[\xi_i]$ unless it is a zero vector. Since 1 is a simple eigenvalue, all $\widehat{(\nu\tilde{Q})}_i$ are zeros, so $\tilde{Q} \equiv 0$ by virtue of (44).

The set B is closed, convex and bounded in $L_1(0,1)$. By Schauder's fixed point principle, $\mathcal{A}$ has a fixed point Q in B, which is automatically a solution to (33). It remains to notice that Q is continuous as a linear combination of q_i, so (35) holds for all $0 \le x \le 1 - 1/k$. ■

Remark 3.1. Theorem 3.1 may be considered as a continuous version of a purely algebraic fact, [23, Lemma 3.2].

Lemma 3.1. *If $a < S$, then there is $\gamma > 0$ such that (34) holds true.*

Proof: Let us notice that

$$q = u + v, \tag{47}$$

where u and v are the (unique) solutions to the following problems

$$\begin{cases} \nu u - \varsigma u_{xx} = \sum\limits_{i=1}^{k} \delta_{S_i}, \ \ x \in (0,1), \\ u_x(0) = u_x(1) = 0, \end{cases} \tag{48}$$

$$\begin{cases} \nu v - \varsigma v_{xx} = \sum\limits_{i=1}^{k} (\delta_{a_i} - \delta_{S_i}), \ \ x \in (0,1), \\ v_x(0) = v_x(1) = 0, \end{cases} \tag{49}$$

and

$$S_i = S + x_i, \ i = 1, \dots, k. \tag{50}$$

Since S is the ν/ς-diffusive mean of 0 and $1/k$, there exists a solution U_1 to the problem

$$\begin{cases} \nu U_1 - \varsigma U_{1xx} = \delta_{S_1}, & x \in (0, 1/k), \\ U_{1x}(0) = U_{1x}(1/k) = 0, \\ U_1(0) = U_1(1/k). \end{cases} \tag{51}$$

The solution u to (48) can be constructed in the following way:

$$u(x) = U_1(x - x_i), \ x_i \le x \le x_i + 1/k, \ i = 1, \dots, k. \tag{52}$$

Thus, u is $1/k$-periodic, i.e.

$$u(x) - u(x + 1/k) = 0, \ 0 \le x \le x_k. \tag{53}$$

Set

$$d(x) = v(x) - v(x + 1/k), \ 0 \le x \le x_k. \tag{54}$$

Then it suffices to show that

$$\gamma = \min_{0 \le x \le x_k} d(x) > 0. \tag{55}$$

Note that

$$\nu d - \varsigma d_{xx} = 0,\ \ x \in (0, x_k). \tag{56}$$

By the maximum principle, if the minimum of d is non-positive, it is attained at 0 or x_k. To ascertain that this cannot happen, we are going to prove that

$$d_x(0) < 0,\ \ d_x(x_k) > 0. \tag{57}$$

Set

$$V(x) = \int\limits_0^x \nu(z)v(z)\,dz, \tag{58}$$

and let θ be the solution of the Cauchy problem

$$\begin{cases} \theta_x = \sum\limits_{i=1}^{k}(\delta_{a_i} - \delta_{S_i}), \quad x \in (0,1), \\ \theta(0) = 0. \end{cases} \tag{59}$$

Note that θ is non-negative and $1/k$-periodic.

Integration of (49) gives

$$V - \varsigma v_x = \theta. \tag{60}$$

Therefore

$$d_x = \frac{V(x) - V(x + 1/k)}{\varsigma}. \tag{61}$$

From (60) we deduce

$$V(0) = V(1) = 0, \tag{62}$$

and

$$V - \varsigma \left(\frac{V_x}{\nu}\right)_x = \theta \geq 0. \tag{63}$$

Using the distributional maximum principle [11, Theorem B], we conclude that

$$V(x) > 0,\ \ 0 < x < 1, \tag{64}$$

so

$$d_x(0) = -\frac{V(1/k)}{\varsigma} < 0,\ \ d_x(x_k) = \frac{V(1 - 1/k)}{\varsigma} > 0. \tag{65}$$

■

The results of this section can be interpreted as follows. Consider a semidiscretized device which we refer to as the "squeezing ratchet", and which acts as follows. The particles can be in two states, ground and excited, and $\nu(x)$ and $\eta(x)$ are probabilities of transition from the first to the second state and back, resp. The particles in the ground state diffuse with diffusion coefficient ς. If a particle positioned at the segment (x_i, x_{i+1}) suddenly changes its state from the ground to the excited one, then it instantly jumps to the point a_i (located to the left from the $\frac{\nu}{\varsigma}$-diffusive mean of the points x_i and x_{i+1}). Then, given any initial allocation of particles, the renormalized eventual distribution Q of ground particles satisfies (35), i.e. their mass is transported to the left. Moreover, the excited particles are eventually concentrated at the points a_i, and one can observe that the asymptotic amounts $\chi_i \sim \widehat{(\nu Q)}_i$ of excited particles at the points a_i decrease from left to right. A reflection argument shows that if a_i are located to the right from the $\frac{\nu}{\varsigma}$-diffusive means of the corresponding endpoints x_i and x_{i+1}, then both ground and excited mass is transported to the right.

4. Asymptotics of the time-discretized Fokker-Planck equation and behaviour of the randomly flashing ratchet

Denote by d the Wasserstein metric of order two on the space of probability measures on $[0,1]$, see e.g. [8]. The convergence in Wasserstein metric is equivalent to the weak-* convergence of probability measures:

$$d(\mu_n, \mu) \to 0 \Leftrightarrow \langle \mu_n - \mu, f\rangle \to 0, \ f \in C[0,1]. \tag{66}$$

Set $b(x) = \psi_x(x)/\eta(x)$. Note that $b(x)$ is zero at the extrema a_i and x_i of the potential ψ, is negative for $x_i < x < a_i$, and is positive for $a_i < x < x_{i+1}$, $i = 1, \ldots, k$.

Lemma 4.1. *If $\omega \in C^*[0,1]$ satisfies*

$$\langle \omega, \varphi + \kappa b \varphi_x \rangle = 0 \tag{67}$$

for any $\varphi \in C^2[0,1]$, $\varphi_x(0) = \varphi_x(1) = 0$, then $\omega = 0$.

Proof: It suffices to prove that the set

$$O = \left\{ \varphi + \kappa b \varphi_x \middle| \varphi \in C^2[0,1], \varphi_x(0) = \varphi_x(1) = 0 \right\}$$

is dense in $C[0,1]$.

Let $h \in C^2[0,1]$ be an arbitrary function which is locally constant near the zeros of b. These functions constitute a dense subset O_1 of $C[0,1]$. Let

$$\varphi(x) = h(x) + \int\limits_x^{a_i} \exp\left(\int\limits_x^y \frac{1}{\kappa b(t)}\,dt\right) h_y(y)\,dy,$$

$$x_i \le x \le x_{i+1},\ i = 1, \dots, k. \tag{68}$$

Clearly, φ is equal to a constant c_i^- (resp. c_i^+) in a left (resp. right) neighbourhood of the point x_i. But

$$h = \varphi + \kappa b \varphi_x, \tag{69}$$

so $c_i^- = c_i^+ = h(x_i)$. Thus, φ is C^2-smooth and $\varphi_x(0) = \varphi_x(1) = 0$. By virtue of (69), O_1 is contained in O. ∎

Consider the system

$$\begin{cases} r - \kappa(br)_x = R, & x \in (0,1) \\ r \ge 0, \end{cases} \tag{70}$$

where

$$R \in L_1(0,1),\ R \ge 0,\ \int\limits_0^1 R(x)\,dx = 1,$$

is prescribed. Clearly, $\int\limits_0^1 r(x)\,dx = 1$, so r can be considered as a probability measure.

Lemma 4.2. *We have*

$$\lim_{\kappa \to +\infty} \sup_{R \in L_1(0,1),\ R \ge 0,\ \int\limits_0^1 R(x)\,dx = 1} d(r, \sum_{i=1}^k \widehat{R}_i \delta_{a_i}) = 0. \tag{71}$$

Proof: The solution r to (70) can be written explicitly:

$$r(x) = -\frac{1}{\kappa b(x)} \int\limits_{x_i}^{x} \exp\left(\int\limits_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds,\ x_i < x < a_i, \tag{72}$$

$$r(x) = \frac{1}{\kappa b(x)} \int\limits_x^{x_{i+1}} \exp\left(\int\limits_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds,\ a_i < x < x_{i+1}. \tag{73}$$

Note that it is unique in $L_1(0,1)$. Indeed, if r_1 is another solution, then $\omega = r - r_1$ satisfies the conditions of Lemma 4.1.

We need to show that $r \to \sum_{i=1}^{k} \widehat{R}_i \delta_{a_i}$ weakly-$*$, uniformly with respect to R. It suffices to prove that, for each i, $r \to \widehat{R}_i \delta_{a_i}$ weakly-$*$ on the interval (x_i, x_{i+1}), uniformly in R. We restrict ourselves to the case $i = 1$, and the others are analogous.

We calculate, integrating by parts,

$$
\begin{aligned}
\widehat{r}_1 &= \int_0^{1/k} r(x)\,dx \\
&= -\int_0^a \frac{1}{\kappa b(x)} \int_0^x \exp\left(\int_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx \\
&\quad + \int_a^{1/k} \frac{1}{\kappa b(x)} \int_x^{1/k} \exp\left(\int_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx \\
&= -\int_0^a \frac{\exp\left(\int^x \frac{1}{\kappa b(t)}\,dt\right)}{\kappa b(x)} \int_0^x \exp\left(\int_s \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx \\
&\quad + \int_{1/k}^a \frac{\exp\left(\int^x \frac{1}{\kappa b(t)}\,dt\right)}{\kappa b(x)} \int_{1/k}^x \exp\left(\int_s \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx \\
&= \left[\int_0^x \exp\left(\int_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\right]_a^0 + \int_0^a R(x)\,dx \\
&\quad + \left[\int_{1/k}^x \exp\left(\int_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\right]_{1/k}^a + \int_a^{1/k} R(x)\,dx
\end{aligned}
$$

$$= \qquad \widehat{R}_1 \quad - \int\limits_0^{1/k} \exp\left(\int\limits_s^a \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds \qquad = \qquad \widehat{R}_1. \quad (74)$$

Let us show that for every $x_* \in (0,a)$

$$\lim_{\kappa\to+\infty} \int\limits_0^{x_*} r(x)\,dx = 0, \tag{75}$$

uniformly in R. Indeed, let $s_\kappa < x_*$ be such that

$$\int\limits_{x_*}^{s_\kappa} \frac{1}{b(t)}\,dt = \sqrt{\kappa}. \tag{76}$$

Observe that $s_\kappa \to 0$ as $\kappa \to +\infty$. We have

$$\int\limits_0^{x_*} r(x)\,dx$$

$$= - \int\limits_0^{x_*} \frac{1}{\kappa b(x)} \int\limits_0^{x} \exp\left(\int\limits_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx$$

$$= - \int\limits_0^{x_*} \frac{\exp\left(\int\limits^{x} \frac{1}{\kappa b(t)}\,dt\right)}{\kappa b(x)} \int\limits_0^{x} \exp\left(\int\limits_s \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\,dx$$

$$= \left[\int\limits_0^{x} \exp\left(\int\limits_s^x \frac{1}{\kappa b(t)}\,dt\right) R(s)\,ds\right]_{x_*}^{0} + \int\limits_0^{x_*} R(x)\,dx$$

$$= \int_0^{x_*} \left[1 - \exp\left(\int_s^{x_*} \frac{1}{\kappa b(t)}\, dt \right) \right] R(s)\, ds$$

$$\leq \int_0^{s_\kappa} \left[1 - \exp\left(\int_s^{x_*} \frac{1}{\kappa b(t)}\, dt \right) \right] R(s)\, ds + \int_{s_\kappa}^{x_*} \left[1 - \exp\left(\int_{s_\kappa}^{x_*} \frac{1}{\kappa b(t)}\, dt \right) \right] R(s)\, ds$$

$$\leq \int_0^{s_\kappa} R(s)\, ds + [1 - \exp(\kappa^{-1/2})] \int_{s_\kappa}^{x_*} R(s)\, ds \to 0 \quad (77)$$

as $\kappa \to +\infty$.

Due to (75), for any $f_0 \in C[0, 1/k]$,

$$\lim_{\kappa \to +\infty} \int_0^{x_*} r(x) f_0(x)\, dx = 0, \quad (78)$$

uniformly in R.

Similarly, for all $x^* \in (a, 1/k)$ and $f_0 \in C[0, 1/k]$,

$$\lim_{\kappa \to +\infty} \int_{x^*}^{1/k} r(x) f_0(x) v = 0, \quad (79)$$

uniformly in R.

Fix $\varepsilon > 0$ and $f \in C[0, 1/k]$. Let x_* and x^* be so close to a that $|f(x) - f(a)| \leq \varepsilon/2$ provided $x_* \leq x \leq x^*$. Then

$$\left| \int_{x_*}^{x^*} r(x)[f(x) - f(a)]\, dx \right| \leq \varepsilon/2. \quad (80)$$

Due to (78) and (79) with $f_0 = f - f(a)$,

$$\left| \int_0^{1/k} r(x)[f(x) - f(a)]\, dx - \int_{x_*}^{x^*} r(x)[f(x) - f(a)]\, dx \right| \leq \varepsilon/2 \quad (81)$$

for sufficiently large κ. Thus,

$$\langle r - \widehat{R}_1 \delta_{a_1}, f\rangle = \langle r - \widehat{r}_1 \delta_a, f\rangle = \int\limits_0^{1/k} r(x)[f(x) - f(a)]\, dx \le \varepsilon. \tag{82}$$

■

Now, consider the time-discretized Fokker-Planck problem:

$$\begin{cases} w_{\sigma,\kappa} - \sigma(w_{\sigma,\kappa}/\eta)_{xx} - \kappa(bw_{\sigma,\kappa})_x = R_{\sigma,\kappa}, \quad x \in (0,1), \\ (w_{\sigma,\kappa}/\eta)_x(0) = (w_{\sigma,\kappa}/\eta)_x(1) = 0, \\ w \ge 0, \end{cases} \tag{83}$$

where

$$R_{\sigma,\kappa} \in L_1(0,1), \; R_{\sigma,\kappa} \ge 0, \; \int\limits_0^1 R_{\sigma,\kappa}(x)\, dx = 1,$$

depends on σ and κ.

Lemma 4.3. *For each κ there exists $\epsilon_\kappa > 0$ so that*

$$\lim_{\kappa \to +\infty, \; \sigma \le \epsilon_\kappa} d(w_{\sigma,\kappa}, \sum_{i=1}^{k} \widehat{(R_{\sigma,\kappa})}_i \delta_{a_i}) = 0. \tag{84}$$

Proof: Let $r_{\sigma,\kappa}$ be the solution of the system

$$\begin{cases} r_{\sigma,\kappa} - \kappa(br_{\sigma,\kappa})_x = R_{\sigma,\kappa}, \quad x \in (0,1) \\ r_{\sigma,\kappa} \ge 0. \end{cases} \tag{85}$$

Then, by Lemma 4.2,

$$\lim_{\kappa \to +\infty} d(r_{\sigma,\kappa}, \sum_{i=1}^{k} \widehat{(R_{\sigma,\kappa})}_i \delta_{a_i}) = 0, \tag{86}$$

uniformly in σ. Thus, it suffices to prove that for every κ there is $\epsilon_\kappa > 0$ such that

$$\lim_{\kappa \to +\infty, \; \sigma \le \epsilon_\kappa} d(w_{\sigma,\kappa}, r_{\sigma,\kappa}) = 0.$$

This would follow from the claim that for every κ there is $\epsilon_\kappa > 0$ so that for $\sigma \le \epsilon_\kappa$ we have $d(w_{\sigma,\kappa}, r_{\sigma,\kappa}) < 1/\kappa$. If it is not true, then for some κ there exists a sequence $\sigma_n \to 0$ such that

$$d(w_{\sigma_n,\kappa}, r_{\sigma_n,\kappa}) \ge 1/\kappa.$$

Since $w_{\sigma_n,\kappa}$ and $r_{\sigma_n,\kappa}$ are solutions of the problems (83) and (85), we have

$$-\sigma_n\langle w_{\sigma_n,\kappa}, \varphi_{xx}/\eta\rangle + \langle w_{\sigma_n,\kappa}, \varphi + \kappa b\varphi_x\rangle = \langle R_{\sigma_n,\kappa}, \varphi\rangle, \tag{87}$$

$$\langle r_{\sigma_n,\kappa}, \varphi + \kappa b\varphi_x\rangle = \langle R_{\sigma_n,\kappa}, \varphi\rangle, \tag{88}$$

for any $\varphi \in C^2[0,1]$, $\varphi_x(0) = \varphi_x(1) = 0$. Since the sequences $w_{\sigma_n,\kappa}$ and $r_{\sigma_n,\kappa}$ lie in the space of probability measures, which is weakly-* compact, without loss of generality there exist their weak-* limits w_κ and r_κ. Clearly,

$$d(w_\kappa, r_\kappa) \geq 1/\kappa. \tag{89}$$

On the other hand, taking the difference of (87) and (88), and passing to the limit, we find $\langle w_\kappa - r_\kappa, \varphi + \kappa b\varphi_x\rangle = 0$, so $w_\kappa = r_\kappa$ by Lemma 4.1, and we arrive at a contradiction. ■

Lemma 4.4. *For each κ there exists $\epsilon_\kappa > 0$ so that the corresponding solutions of* (20) *have the following properties:*

$$\lim_{\kappa\to+\infty,\ \sigma\leq\epsilon_\kappa} \sup_{0\leq x\leq 1} |P(x) - Q(x)| = 0, \tag{90}$$

$$\lim_{\kappa\to+\infty,\ \sigma\leq\epsilon_\kappa} \widehat{p}_i = \frac{\widehat{(\nu Q)}_i}{\eta(a)}. \tag{91}$$

Proof: The pair $(w_{\sigma,\kappa}, R_{\sigma,\kappa}) = (\eta p, \nu P)$ satisfies (83), so, by Lemma 4.3, for every κ there exists $\epsilon_\kappa > 0$ such that

$$\lim_{\kappa\to+\infty,\ \sigma\leq\epsilon_\kappa} d(\eta p, \sum_{i=1}^{k} \widehat{(\nu P)}_i \delta_{a_i}) = 0. \tag{92}$$

Multiplying the second equation in (20) by P and integrating, we find

$$\int_0^1 \nu(x)P^2(x) - \varsigma P_{xx}(x)P(x)\,dx = \int_0^1 \eta(x)p(x)P(x)\,dx, \tag{93}$$

whence

$$\inf_{0\leq x\leq 1} \nu(x) \int_0^1 P^2(x)\,dx + \varsigma \int_0^1 P_x^2(x)\,dx \leq \sup_{0\leq x\leq 1} P(x). \tag{94}$$

Hence,

$$\|P\|^2_{W_2^1(0,1)} \leq C\|P\|_{C[0,1]} \leq C\|P\|_{W_2^1(0,1)} \leq C. \tag{95}$$

Assume that (90) is not true, i.e. there exist $\delta > 0$ and sequences $\kappa_n \to \infty$ and $\sigma_n \le \epsilon_{\kappa_n}$ such that for the corresponding solutions $(p_n, P_n) = (p_{\sigma_n,\kappa_n}, P_{\sigma_n,\kappa_n})$ to (20) we have $\|P_n - Q\|_{C[0,1]} > \delta$. Since the embedding $W_2^1(0,1) \subset C[0,1]$ is compact, without loss of generality we may assume that P_n converges to some limit P_0 in $C[0,1]$. Obviously,

$$\|P_0 - Q\|_{C[0,1]} \ge \delta. \tag{96}$$

Passing to the limit in the second, forth and the last equations in (20) — the combination of the first two is understood in the weak sense (8) — and remembering (92), we find

$$\nu P_0 - \varsigma (P_0)_{xx} = \sum_{i=1}^{k} \widehat{(\nu P_0)}_i \delta_{a_i},$$

$$(P_0)_x(0) = (P_0)_x(1) = 0,$$

$$\int_0^1 \nu(x) P_0(x)\, dx = 1.$$

By Theorem 3.1, P_0 coincides with Q, which contradicts (96).

From (92) we deduce

$$\lim_{\kappa\to+\infty,\ \sigma\le\epsilon_\kappa} d\left(p, \sum_{i=1}^{k} \frac{\widehat{(\nu P)}_i \delta_{a_i}}{\eta(a_i)}\right) = 0. \tag{97}$$

Due to (90) and $1/k$-periodicity of η, (97) implies that

$$p \to \sum_{i=1}^{k} \frac{\widehat{(\nu Q)}_i \delta_{a_i}}{\eta(a)}. \tag{98}$$

weakly-* as $\kappa \to +\infty,\ \sigma \le \epsilon_\kappa$. Taking test functions which are equal to 1 in one of the wells and are zero at the minima of the potential located outside of that well, we derive (91) from (98). ■

Proof: (Theorem 2.1) Inequality (35) yields

$$\frac{\widehat{(\nu Q)}_i}{\eta(a)} \ge \frac{\widehat{(\nu Q)}_{i+1}}{\eta(a)} + C,\ i = 1, \dots, k-1. \tag{99}$$

Therefore, (14) and (16) are direct consequences of Theorem 3.1 and Lemmas 3.1 and 4.4. ■

5. Discussion

The randomly flashing ratchet model for motor proteins is investigated. The Brownian particles which carry a motor protein are considered to be sensitive to a chemically-induced periodic potential. The motor-free ones diffuse normally. The switch between the two states happens when a particle loses or seizes a motor protein, and the probabilities of these events are prescribed. Mathematically, the model is a pair of weakly coupled reaction-diffusion and Fokker-Planck equations with Neumann boundary conditions. It is shown that unidirectional transport of mass occurs when the diffusion of the potential-sensitive particles is strongly dominated by the influence of the potential. The direction of transport is unambiguously determined by a certain interrelation between the asymmetries of the potential and of the probability of transition from the potential-insensitive to the potential-sensitive state: in particular, at least one of them should be asymmetric to secure the transport effect.

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