Intermittent particle transport with arbitrary distributions of duration of motional phases

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Abstract. Intermittent transport of biological objects, including ballistic and Brownian motion, Brownian motion with drift, occurs universally in various forms and scales. In many instances models of intermittent transport imply that the distribution of duration of motional phases is exponential. However, this is by no means always the case. In this paper we generalize the model of intermittent transport, proposed in Bressloff P C and Newby J M 2013 Rev. Mod. Phys. 85 135–196, to the general case of arbitrary distributions of duration of motional phases. We derive also an asymptotic approximation to the model in the assumption that transitions between the phases are frequent.

1. Introduction
Intermittent transport of biological objects, including ballistic and Brownian motion, Brownian motion with drift, occurs universally in various forms and scales [1–3]. Various models of intermittent transport are presented in Refs. [2,4–10]. In the great majority of instances these models imply that the distribution of duration of motional phases is exponential. However, this is by no means always the case [3,11–15]. In this paper we generalize the model of intermittent transport, proposed in Ref. [9], to the general case of arbitrary distributions of duration of motional phases. We derive also an asymptotic approximation to the model in the assumption that transitions between the phases are frequent.

2. Mean-field model
Particles (molecules, vesicles, organelles, biological individuals, etc.) move in the $d$-dimensional space $\mathbb{R}^d$. They can be in one of $n$ phases, when they diffuse with drift, diffusion coefficients and drift velocities being different in each phase. (This model is not quite realistic, since usually particles either move with some velocity or just diffuse. However, the general model allows treating in a unified manner.) The particles can instantly change the phase. The key feature of the model is that the rates of transition from one phase to another depend in general on the elapsed time from the beginning of the current phase. If the transition rates are constant, the duration of each phase has the exponential distribution, otherwise it has a non-exponential distribution.

Figure 1. An example of the trajectory of a particle.
The exponential distribution is the only continuous distribution, describing memoryless random variables [16]. Recall that a random variable $X$ is memoryless, if $P\{X > \tau' + \tau \mid X > \tau\} = P\{X > \tau\}$ for all $\tau, \tau' \geq 0$. $P(\cdot)$ is the probability, $P(\cdot | \cdot)$ is the conditional probability. In other words (in the current interpretation), for any elapsed time $\tau'$ from the beginning of a phase, the distribution of time $\tau$ left till the end of the phase, does not depend on $\tau'$.

Hence in the case of non-constant transition rates phase-space densities of the particles cannot depend only on the space variable $x$ and time $t$. They depend also on the elapse time from the beginning of a phase, which is denoted $\tau$ and called the age of particles. We assume that each time the particle changes the phase it is born anew.

Let $\xi(x, t, \tau) = (\xi_1(x, t, \tau), \ldots, \xi_n(x, t, \tau))$ be the vector of phase-space densities, where $\xi_i$ is the phase-space density of the particles in the $i$th phase. The densities obey the system of the second-order partial differential equations

$$
\partial_t \xi_i + \partial_{\tau} \xi_i + v_i \cdot \nabla \xi_i - D_i \Delta \xi_i + \gamma_i \xi_i = 0, \quad i = 1, \ldots, n,
$$

where $D_i$, $v_i$ and $\gamma_i \equiv \gamma_i(\tau)$ are the diffusion coefficients, drift velocities and extinction rates, respectively. Eq. (1) is a straightforward modification, taking into consideration diffusion, of a similar equation from Ref. [17], see also Refs. [18, 19]. Note, that the extinction rates are not constant, they depend on the age $\tau$. Eq. (1) is supplemented by the condition for the densities of newly born particles (see Refs. [17, 18])

$$
\xi_i|_{\tau=0} \equiv \eta_i(x, t) = \sum_{j=1}^{n} \kappa_{ij} \int_0^{\infty} \gamma_j(\tau') \xi_j(x, t, \tau') \, d\tau', \quad i = 1, \ldots, n,
$$

where $\kappa_{ij} \equiv \kappa_{ij}(x)$ are probabilities of transition from the $j$th to $i$th phase such that

$$
\kappa_{ij} > 0, \quad i \neq j, \quad \kappa_{ii} = 0 \quad \text{and} \quad \sum_{i=1}^{n} \kappa_{ij} = 1.
$$

The latter condition provides conservation of particles. The phase space densities are subject to the initial conditions

$$
\xi_i|_{t=0} = \vartheta_i(x, \tau), \quad i = 1, \ldots, n,
$$

where $\vartheta_i$ are the initial distributions of the densities. The initial distributions depend on the age of particles.

3. Equations for age-independent densities

We define the densities

$$
\psi_i(x, t) = \int_0^{\infty} \xi_i(x, t, \tau) \, d\tau,
$$

independent of the age $\tau$. Eqs. (1) and (2) yield the system of equations

$$
\partial_t \psi_i + v_i \cdot \nabla \psi_i - D_i \Delta \psi_i = \sum_{j=1}^{n} (\kappa_{ij} - \delta_{ij}) \int_0^{\infty} \gamma_j(\tau) \xi_j(x, t, \tau) \, d\tau, \quad i = 1, \ldots, n,
$$

where $\delta_{ij}$ is the Kronecker delta. Note that if the extinction rates $\gamma_i$ are constant (do not depend on the age), Eq. (6) takes the form

$$
\partial_t \psi_i + v_i \cdot \nabla \psi_i - D_i \Delta \psi_i = \sum_{j=1}^{n} (\kappa_{ij} - \delta_{ij}) \gamma_j \psi_j, \quad i = 1, \ldots, n.
$$

To express the right-hand side of Eq. (6) through the densities $\psi_i$ note that the solutions of Eq. (1) are given by

$$
\xi_i(x, t, \tau) = \begin{cases} S_i(\tau) G_i(\tau) \eta_i(x, t - \tau), & \tau \in (0, t), \\ S_i(\tau) G_i(t) \vartheta_i(x, \tau - t), & \tau \in (t, \infty), \end{cases}
$$
where \( S_i(\tau) = \exp \left\{- \int_0^\tau \gamma_i(\tau') \, d\tau' \right\} \) are survival probabilities, and \( G_i \) are propagators given by \( G_i(t_1)f(x,t_2) = \int_{\mathbb{R}^d} G_i(x-y,t_1)f(y,t_2) \, dy \) with the Gaussian kernels \( G_i(x,t) = (2\pi D_i t)^{-d/2} \exp \left\{ -|x-v(t)|^2/4D_i t \right\} \) satisfying the diffusion equation \( \partial_t G_i + v_i \cdot \nabla G_i - D_i \Delta G_i = 0 \).

Eqs. (5) and (7) yield the relation \( \psi_i(x,t) = \int_0^\infty S_i(\tau) \psi_i(x,t-\tau) \, d\tau \). Then \( G_i(\tau) \psi_i(x,t-\tau) = \int_0^\infty S_i(\tau') \psi_i(x,t-\tau') \, d\tau' + \int_0^\infty S_i(\tau-\tau') \psi_i(x,t-\tau') \, d\tau' \). The probability density functions (PDFs) of the age for each phase are given by \( p_i(\tau) = \gamma_i(\tau) S_i(\tau) \equiv \gamma_i(\tau) \exp \left\{- \int_0^\tau \gamma_i(\tau') \, d\tau' \right\} \). The memory kernels \( \phi_i \) are defined by the relations \( p_i(\tau) = \phi_i(\tau') S_i(\tau-\tau') \, d\tau' \) [20]. Then \( \int_0^\infty \gamma_i(\tau) \xi_i(x,t,\tau) \, d\tau = \mathcal{M}_i \psi_i(x,t) + N_i \theta_i(x,t) \), where \( \mathcal{M}_i \psi_i(x,t) = \int_0^t \phi_i(\tau) G_i(\tau) \psi_i(x,t-\tau) \, d\tau \), and \( N_i \theta_i(x,t) = \int_0^\infty \phi_i(\tau) \int_0^\infty S_i(\tau'-\tau') \psi_i(x,t'-t') \, d\tau' \). As a result, the system of equations (6) is recast as

\[
\partial_t \psi + \mathcal{L}\psi + \mathcal{D}\psi = (T - I) \left( \mathcal{M}\psi + N\theta \right),
\]

where \( \psi = (\psi_1, \ldots, \psi_n) \), the drift operator \( \mathcal{L} \) is given by \( \mathcal{L}\psi = (L_1\psi_1, \ldots, L_n\psi_n) \), \( L_i\psi_i = v_i \cdot \nabla \psi_i \), the diffusion operator \( \mathcal{D} \) is given by \( \mathcal{D}\psi = (D_1\psi_1, \ldots, D_n\psi_n) \), \( D_i\psi_i = -D_i \Delta \psi_i \), and \( \mathcal{T} \equiv T(x) = (\kappa_{ij})_{i,j=1}^n \) is the transition matrix, \( I \) is the identity matrix, the memory operator \( \mathcal{M} \) is given by \( \mathcal{M}\psi = (\mathcal{M}_1\psi_1, \ldots, \mathcal{M}_n\psi_n) \), and the operator \( \mathcal{N} \) is given by \( \mathcal{N}\psi = (\mathcal{N}_1\psi_1, \ldots, \mathcal{N}_n\psi_n) \). The initial conditions (4) yield the initial conditions for the system (8)

\[
\psi\big|_{t=0} = \int_0^\infty \vartheta(x,\tau) \, d\tau,
\]

where \( \vartheta = (\vartheta_1, \ldots, \vartheta_n) \).

4. Asymptotic solution

In this section we obtain an asymptotic approximation to the model in the assumption that transitions between the phases are frequent, i.e., the mean age in each phase is small. We suppose here that the first and second moments of the PDFs of the age for each phase are finite.

4.1. Assumptions

The mean age in each phase is small of order \( \varepsilon \), in this case the transition rates \( \gamma_i \) are represented in the form \( \gamma_i(\tau) = \varepsilon^{-1} \tilde{\gamma}_i(\tau/\varepsilon) \), where \( \tilde{\gamma}_i \) do not depend on \( \varepsilon \), see Ref. [18]. This implies representations for the survival probabilities, PDFs and memory kernels in the form \( S_i(\tau) = \tilde{S}_i(\tau/\varepsilon) \), \( p_i(\tau) = \varepsilon^{-1} \tilde{p}_i(\tau/\varepsilon) \), \( \phi_i(\tau) = \varepsilon^{-2} \tilde{\phi}_i(\tau/\varepsilon) \), respectively, where \( \tilde{S}_i \), \( \tilde{p}_i \) and \( \tilde{\phi}_i \) do not depend on \( \varepsilon \). In this case the asymptotic expansions of the memory kernels are given by

\[
\varepsilon \phi_i(\tau) = \frac{1}{\varepsilon} \tilde{\phi}_i(\frac{\tau}{\varepsilon}) \sim \tilde{\phi}_i,0 \delta(\tau) + \tilde{\phi}_i,1 \delta'(\tau) \varepsilon + \tilde{\phi}_i,2 \delta''(\tau) \varepsilon^2 + \ldots \quad \text{as} \quad \varepsilon \to 0
\]

(see Ref. [18]) with the coefficients \( \tilde{\phi}_i,0 = 1/\langle \tau_i \rangle \) and \( \tilde{\phi}_i,1 = \langle \tau_i^2 \rangle/2\langle \tau_i \rangle^2 - 1 \), where \( \langle \tau_i \rangle = \int_0^\infty \tau \tilde{p}_i(\tau) \, d\tau \) and \( \langle \tau_i^2 \rangle = \int_0^\infty \tau^2 \tilde{p}_i(\tau) \, d\tau \) are the first moments (mean values) of the densities \( \tilde{p}_i \) and their second moments, respectively. The diffusion coefficients \( D_i \) are supposed to be small of order \( \varepsilon \), i.e., \( D_i = \varepsilon D_i \), where \( D_i \) do not depend on \( \varepsilon \).

4.2. Asymptotic solution

Taking into account the assumptions we recast Eq. (8) in the form

\[
\varepsilon \partial_t \psi + \varepsilon \mathcal{L}\psi + \varepsilon^2 \mathcal{D}\psi = (T - I) \left[ \mathcal{M}\psi + \mathcal{N}\vartheta \right],
\]

where the diffusion operator \( \mathcal{D} \) is given by \( \mathcal{D}\psi = (D_1\psi_1, \ldots, D_n\psi_n) \), \( D_i\psi_i = -D_i \Delta \psi_i \), the memory operator \( \mathcal{M} \) is given by \( \mathcal{M}\psi = (M_1\psi_1, \ldots, M_n\psi_n) \), \( M_i\psi_i(x,t) = \int_0^\infty S_i(\tau) \psi_i(x,t-\tau) \, d\tau \), and \( \mathcal{N}\psi = \int_0^\infty S_i(\tau) \psi_i(x,t-\tau) \, d\tau \).
\[ f_0^t \frac{1}{\tau} \phi_i(\frac{\tau}{\varepsilon}) G_i(\tau) \psi_i(x, t - \tau) \, d\tau, \] and the operator \( \hat{N} \) is given by \( \hat{N} \theta = (\hat{N}_1 \theta_1, \ldots, \hat{N}_n \theta_n) \),

\[ \hat{N}_i \theta_i(x, t) = \int_0^\infty \varepsilon^{-1} \phi_i(\tau/\varepsilon) \int_0^\infty S_i(\tau' - \tau) G_i(t) \theta_i(x, \tau' - t) \, d\tau' \, d\tau. \]

To find the asymptotic solution to the problem (11), (9) we represent the densities in the form

\[ \psi(x, t) = \psi^0(x, t^\prime) + \psi^0(x, t^\circ), \]

where \( t^\prime = t/\varepsilon \) and \( t^\circ = \varepsilon t \) are fast and slow time, respectively, \( \psi^0 \) and \( \psi^0 \) are inner and outer solutions, respectively. The inner solution is negligible outside of the initial layer \( 0 < t \lesssim O(\varepsilon) \) and tends in the layer to zero exponentially with \( t \). The outer solution approximates \( \psi \) outside of the initial layer.

### 4.3. Outer solution and diffusion approximation

Substituting the outer solution into Eq. (11) yields the system of equations

\[ \varepsilon^2 \partial_{t^0} \psi^0 + \varepsilon \mathcal{L} \psi^0 + \varepsilon^2 \bar{\mathcal{D}} \psi^0 = (T - I) \left[ \hat{\mathcal{M}} \psi^0 + \hat{N} \theta \right]. \tag{12} \]

Taking into account the asymptotic expansions (10) of the memory kernels we obtain the expansions of the memory operators \( \hat{M}_i \psi^0(x, t^\circ) = \int_{t^\circ}^{t^\circ / \varepsilon} \varepsilon^{-1} \phi_i(\tau/\varepsilon) G_i(\tau) \psi_i(x, t^\circ - \varepsilon \tau) \, d\tau = \{ \hat{\phi}_i, \phi_i(\varepsilon \cdot \nabla) + \hat{\phi}_i, \phi_i \} \psi_i(x, t^\circ), \]

where diagonal matrices \( \hat{\phi}_i \) are given by \( \hat{\phi}_i = \text{diag}(\hat{\phi}_i) \). The asymptotic expansions (10) of the memory kernels implies the asymptotic behavior

\[ \hat{N}_i \theta_i(x, t^\circ) \sim 0 \quad \text{as} \quad \varepsilon \rightarrow 0. \tag{14} \]

We assume that the outer solution \( \psi^0 \) has the asymptotic expansion \( \psi^0 \sim \psi_0^0 + \psi_0^1 \varepsilon + \psi_0^2 \varepsilon^2 + \ldots \)

\[ \psi_0^0 = \psi_0^0(x, t^\circ) = \rho(x, t^\circ) w, \tag{16} \]

where the vector \( w \) is given by \( w = \hat{\phi}_0^{-1} \varphi \) (\( \varphi \) is a positive vector such that \( (T - I) \varphi = 0 \)), and the function \( \rho \) is to be determined. We impose the condition \( \sum_{i=1}^n w_i = 1 \). In this case \( \rho = \sum_{i=1}^n \psi_0^0 \), i.e., \( \rho \) is the approximation of the particle density.

The solvability condition for Eq. (15b) (see Appendix A) due to the representation (16) and condition (3) takes the form \( 1 \cdot [\mathcal{L} \psi_0^0 + (I - T) \hat{\phi}_1 \mathcal{L} \psi_0^0] = 1 \cdot \mathcal{L} (\rho w) = \langle \rho \rangle \cdot \nabla \rho = 0 \), where \( \langle \rho \rangle = \sum_{i=1}^n w_i \rho_i \) is the average velocity with respect to the weights \( w \). This condition is met if the average velocity is zero: \( \langle \rho \rangle = 0 \).

In general the condition \( \langle \rho \rangle = 0 \) may not be satisfied. If it is violated, one can apply the transformation \( \psi_i(x, t) = \psi_i(x, t) \), \( \bar{x} = \bar{x} - \langle \nu \rangle t \). The densities \( \psi_i \) satisfy Eq. (6) with the velocities \( \bar{v}_i = v_i - \langle \nu \rangle \) instead of \( v_i \), and the velocities \( \bar{v}_i \) meet the condition \( \langle \bar{v} \rangle = 0 \). Hereafter we assume that the transformation has been applied if needed, and the condition \( \langle \nu \rangle = 0 \) is met. We leave the original designations for the densities and space variables!

If the solvability condition is met, the solution of Eq. (15b) is given by \( \psi_0^1 = c w - \hat{\phi}_0^{-1} A \langle I + (I - T) \hat{\phi}_1 \rangle \mathcal{L} (\rho w) \), where \( A = \langle I - T \rangle |_{\text{span}(\varphi)}^{-1} \), and \( c(x, t) \) is an arbitrary function (see Appendix A).
Substituting $\psi^i_0$ into Eq. (15c) and using the solvability condition yields the diffusion equation for the density $\rho$

$$\partial_t \rho - \langle \hat{D} \rangle \Delta \rho - \nabla \cdot \{ V \Phi_0^{-1} A [I + (I - T)\Phi_1] W V^T \nabla \rho \} = 0 \tag{17}$$

(note that $1 \cdot \mathcal{L}(\mathbf{w}) = 0$), where $\langle \hat{D} \rangle = \sum_{i=1}^n w_i \hat{D}_i$ is the average diffusion coefficient with respect to the weights $\mathbf{w}$, the matrices $V$ and $W$ are given by $V = (v_1 \ldots v_n)$ and $W = \text{diag}(w_1, \ldots, w_n)$. Multiplying Eq. (17) by $\varepsilon$ yields the diffusion equation $\partial_t \rho - \nabla \cdot (D^{\text{eff}} \nabla \rho) = 0$, where the effective diffusion tensor is given by $D^{\text{eff}} = \langle D \rangle I + V \Phi_0^{-1} A [I + (I - T)\Phi_1] W V^T$.

Applying the inverse transformation to the diffusion equation (and leaving the designations unchanged) one obtains the anisotropic diffusion equation with drift

$$\partial_t \rho - \nabla \cdot (D^{\text{eff}} \nabla \rho) + \langle \mathbf{v} \rangle \cdot \nabla \rho = 0.$$

### 4.4. An example

Suppose that the particles move in the one-dimensional space $\mathbb{R}$. They can be in one of two phases ($n = 2$, $\kappa_{12} = \kappa_{21} = 1$), moving right and left with the same velocity: $v_1 = v$, $v_2 = -v$, $D_1 = D_2 = 0$. We consider two distributions of duration of the phases: exponential $p_i(\tau) = \gamma_i e^{-\gamma_i \tau}$ and power-law-like $p_i(\tau) = \gamma_i \nu/(\nu - 1) \nu_{\text{pow}}(\nu - 1)^{-1}(1 + \gamma_i \tau/(\nu - 1))^{-(\nu + 1)}$, see Fig. 2.

The distributions have the same mean $1/\gamma_i$. The effective diffusion coefficients, corresponding to the distributions, are $D^{\text{eff}}_{\text{exp}} = 4\gamma_1 \gamma_2 \nu^2/(\gamma_1 + \gamma_2)^3$ and $D^{\text{eff}}_{\text{pow}} = D^{\text{eff}}_{\text{exp}} \nu/(\nu - 2)$. The average drift velocity is $\langle \mathbf{v} \rangle = v(\gamma_2 - \gamma_1)/(\gamma_1 + \gamma_2)$. Fig. 3 shows solutions to the problem

$$\partial_t \rho - D^{\text{eff}}_{\text{exp}} \partial_x^2 \rho + \langle \mathbf{v} \rangle \partial_x \rho = 0, \quad x \in \mathbb{R}, \quad \rho|_{t=0} = \delta(x), \tag{18}$$

with the diffusion coefficients $D^{\text{eff}}_{\text{exp}}$ and $D^{\text{eff}}_{\text{pow}}$, where $\gamma_1 = 10$, $\gamma_2 = 20$, $\nu = 2.5$ and $v = 1$. If $\nu = 2.5$, the diffusion coefficient $D^{\text{eff}}_{\text{pow}}$ is more than $D^{\text{eff}}_{\text{exp}}$ by a factor of five. Fig. 3 demonstrates the significant difference between the solutions.

![Figure 2](image1.png)  
**Figure 2.** The exponential and power-law-like distributions with the same mean.

![Figure 3](image2.png)  
**Figure 3.** The solutions to the initial value problem (18) with the diffusion coefficients $D^{\text{eff}}_{\text{exp}}$ and $D^{\text{eff}}_{\text{pow}}$.

### 5. Concluding remarks

If the distribution of duration of motional phases is exponential then it is enough to estimate the expectation of life of particles in each phase, all the other moments of the distribution are expressed through its mean. (Recall that each time the particle changes the phase it is born anew.) However, if the distribution is not exponential, a model based only on the expectation may lead to incorrect results.

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Appendix A. The linear system \((T - I)\zeta = f\)

In this section dependence of vectors and matrices on \(x\) and \(t\) is omitted.

The solvability of the non-homogeneous linear system

\[
(T - I)\zeta = f, \quad (A.1)
\]

where \(T\) is the transition matrix and \(I\) is the identity matrix, is described by the finite-dimensional analogs of Fredholm’s theorems, in particular, the Fredholm alternative, see, e.g., Ref. [21]. The system (A.1) is solvable if and only if \(f\) is orthogonal to any nontrivial solution of the homogeneous adjoint system

\[
(T^T - I)\nu = 0. \quad (A.2)
\]

The condition (3) means that the vector \(1 = (1 \ldots 1)^T\) is the eigenvector of the transposed matrix \(T^T\), and the corresponding eigenvalue is equal to 1. Positivity of the matrix \(T\) (i.e., positivity of its elements \(\kappa_{ij}\)) implies that the eigenvalue 1 is simple and largest in magnitude [22]. This means that the vector \(1\) is the only solution (within a constant factor) of the system (A.2). Therefore the necessary and sufficient solvability condition for the system (A.1) is \(f \cdot 1 = 0\).

The homogeneous system

\[
(T - I)\zeta = 0 \quad (A.3)
\]

and the adjoint system (A.2) have the same number of linearly independent solutions. Positivity of the matrix \(T\) implies [22] that any solution of the system (A.3) has the form \(\zeta = c\varphi\), where the vector \(\varphi\) is positive (i.e., all its elements are positive), and \(c\) is an arbitrary constant.

If the solvability condition is met, any solution of the system (A.1) is given by \(\zeta = \zeta' + c\varphi\), where \(\zeta'\) is a particular solution of the system (A.1). The solution can also be represented in the form \(\zeta = \zeta_0 + c\varphi\), where \(\zeta_0\) is the unique solution of the system (A.1), such that \(\zeta_0 \cdot \varphi = 0\). The unique solution \(\zeta_0\) can be represented as \(\zeta_0 = [(T - I)\|\text{span}(\varphi)\|]^{-1} f\).

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