Non-Gaussian Normal Diffusion in a Fluctuating Corrugated Channel

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(Dated: February 12, 2022)

A Brownian particle floating in a narrow corrugated (sinusoidal) channel with fluctuating cross section exhibits non-Gaussian normal diffusion. Its displacements are distributed according to a Gaussian law for very short and asymptotically large observation times, whereas a robust exponential distribution emerges for intermediate observation times of the order of the channel fluctuation correlation time. For intermediate to large observation times the particle undergoes normal diffusion with one and the same effective diffusion constant. These results are analytically interpreted without having recourse to heuristic assumptions. Such a simple model thus reproduces recent experimental and numerical observations obtained by investigating complex biophysical systems.

PACS numbers:

I. INTRODUCTION

Recent observations [1–6] of particle diffusion in fluctuating crowded environments manifestly contradict the common belief that normal diffusion is associated with a Gaussian distribution of spatial displacements. Indeed, if for simplicity we restrict ourselves to one dimensional (1D) geometries, the displacement, \( \Delta x(t) = x(t) - x(0) \), of a standard overdamped Brownian particle suspended in a homogeneous Newtonian fluid [7] (i) grows with time according to the Einstein-Stokes law, \( \langle \Delta x^2(t) \rangle = 2Dt \); (ii) is distributed according to a rescaled Gaussian probability density function (pdf), \( p(\Delta x/\sqrt{t}) \) with half-variance \( D \). Under these circumstances, the random variable \( \Delta x(t) \) is said to undergo Gaussian normal (or Fickian) diffusion.

There is no a priori reason why the diffusion of a tracer in a time varying inhomogeneous medium should be Fickian. In real biophysical systems, with increasing the observation time the rescaled displacement distributions, \( p(\Delta x/\sqrt{t}) \), often develop prominent exponential tails, whereas the tracers start diffusing linearly in time. Such transient tails disappear only for asymptotically large observation times (at times hardly accessible to real experiments [1]). When finally the \( \Delta x \) distributions turn Gaussian, as predicted by the central limit theorem, without appreciably changing the underlying diffusion mechanism. Persistent diffusive transients of this type have been detected in diverse experimental setups [1,3,8,10]. Extensive numerical simulations confirmed the occurrence of this remarkable phenomenon in crowded environments consisting of slowly diffusing or changing microscopic constituents (filaments [1,3], large hard spheres [4,9], clusters [11,12], and other heterogeneities [13]).

The current interpretation of picture above postulates the existence of one or more relaxation processes affecting the suspension medium or the confining geometry, where the tagged particle diffuses [1]. As long as the fixed time interval, \( t \), over which \( \Delta x(t) \) is measured is of the order of the relaxation time constant(s), \( \tau \), the particle displacement can obey a non-Gaussian statistics. Through what mechanism, under these conditions the particle’s diffusion retains its normal character, may vary from case to case. To this purpose, a popular paradigm revolves around the heuristic notion of diffusing diffusivity [14], whereas the environmental fluctuations are modeled by means of an ad hoc random particle diffusion constant, \( D(t) \). On assuming that \( D(t) \) is an Ornstein-Ulenbeck process with average \( \bar{D} \) and time constant \( \tau \), the distribution \( p(\Delta x/\sqrt{t}) \) changes from exponential for \( t \ll \tau \) to Gaussian for \( t \gg \tau \). In both time regimes, the displacement diffusion is normal, with \( \langle \Delta x^2(t) \rangle = 2Dt \) [14]. This phenomenological description, together with its more refined variations [15,21], may qualitatively interpret a conspicuous body of diverse experimental observations, but sheds little light on the underlying microscopic mechanisms.

In this paper we investigate both numerically and analytically the directed diffusion of an overdamped Brownian particle in a narrow quasi-1D corrugated channel [22,23] of fluctuating width. Such a time variable geometry is inspired to cell biology [24,25] and models the key ingredient of the phenomenon under study, namely slow environmental fluctuations. The relevant stochastic model is detailed in Sec. III. The simulation results of Sec. III reproduce the essentials of non-Gaussian normal diffusion [14] without having recourse to the paradigm of diffusing diffusion: (1) The distribution of the particle displacements along the channel is Gaussian for observation times either much shorter (local diffusion) or much longer than the correlation time of the channel fluctuation (channel diffusion), and exponential for a rather wide interval of intermediate observation times; (2) A normal
diffusion law with the same channel diffusion constant extends from intermediate to large observation times, thus implying a nontrivial relationship between displacement pdf’s. The compatibility of normal diffusion with different displacement statistics is discussed in Sec. [11] (3). These effects are robust as long as fluctuations randomly open and close the channel constrictions. As remarked in the concluding Sec. [11] the compartmentalization of particle’s diffusion thus emerges as a prerequisite of non-Gaussian normal diffusion.

II. FLUCTUATING CHANNEL MODEL

The dynamics of an overdamped (or massless) Brownian particle in a channel is modeled by the Langevin equation \( \mathbf{f}(t) = \sqrt{D_0} \mathbf{\xi}(t) \), where \( \mathbf{r} = (x, y) \) are the particle’s coordinates and the translational fluctuations \( \mathbf{\xi}(t) = [\xi_x(t), \xi_y(t)] \) are zero-mean, white Gaussian noises with autocorrelation functions \( \langle \xi_i(t)\xi_j(0) \rangle = \delta_{ij}\theta(t) \), with \( i, j = x, y \). The strength of \( \xi(t) \) is the free-particle diffusion constant, \( D_0 \), which is typically proportional to the temperature of the suspension fluid. Without loss of generality, we considered a two-dimensional (2D) sinusoidal channel with axis oriented along \( x \) and symmetrically confined transverse coordinate, \( |y| \leq w(x,t) \), where

\[
w(x,t) = (y_L/2)[\varepsilon^2 + (1 - \varepsilon^2) \sin^2(\pi x/x_L)].
\]

Here, \( y_L \) and \( x_L \) are respectively the maximum width and the length of the unit channel cell, and \( \varepsilon^2 y_L \) is the fluctuating width of the pores located at \( x = 0 \mod(\pi) \). We assume for simplicity that \( \varepsilon(t) \) obeys the Ornstein-Uhlenbeck equation

\[
\dot{\varepsilon} = - (\varepsilon - \varepsilon_0)/\tau + \sqrt{D_\varepsilon}/\tau \varepsilon \xi(t),
\]

where the noise \( \xi(t) \) has the same statistics of, but is uncorrelated with the thermal noises, \( \xi(t) \). Unless stated otherwise, we set \( \varepsilon_0 = 0 \), so that the average pore width is \( \langle \varepsilon^2 \rangle y_L \) with \( \langle \varepsilon^2 \rangle \equiv \sigma_\varepsilon^2 = D_\varepsilon/\tau \). In order to ignore hydrodynamic effects [22], we addressed the case of pointlike particles in highly viscous suspension fluids. Accordingly, we assumed that, for small channel fluctuations, the varying pressure exerted by the walls on the fluid does not sensibly modulate the particle’s diffusion constant, \( D_0 \), neither in space nor in time. In practice, to modulate the effective width of the channel pores without incurring this difficulty, one can simply apply a tunable external gating potential [22].

We numerically integrated the particle Langevin equation in the free space inside the channel by means of a Milstein algorithm [26]; we imposed reflecting boundary conditions at the channel’s walls, \( y = \pm w(x,t) \), and took stochastic averages over not fewer than \( 10^5 \) particle’s trajectories with random initial conditions.

III. THE CASE OF OPENING-CLOSING PORES

The statistics of the particle displacement, \( \Delta x(t) \), depends on the observation time, \( t \), as shown in Fig. 1, where three different pdf regimes are clearly distinguishable: two distinct Gaussian distributions, \( p(\Delta x/\sqrt{t}) = (4\pi B)^{-1/2} \exp(-\Delta x^2/4Bt) \), at very short and large \( t \) values (insets) and an exponential (or Laplace) distribution, \( p(\Delta x/\sqrt{t}) = (2\alpha)^{-1} \exp(-\Delta x/\alpha \sqrt{t}) \), over an extended intermediate \( t \) range. The short-\( t \) Gaussian regime describes the free Brownian diffusion inside a single channel cell, far from the walls, which occurs for time intervals not larger than \( \tau_L = \min\{x_L^2/8D_0, y_L^2/8D_0\} \). Under these circumstances, the fitting parameter \( B \) turned out to coincide with \( D_0 \), as expected [7].

For longer observation times the particle becomes sensitive to confinement [22]. The escape from one cell into the adjacent ones requires diffusing through narrow pores, a mechanism that takes relatively long waiting times. On extending the approximate techniques of Ref. [27] to the case of fluctuating pores, one estimates a characteristic mean-first exit time (MFET)

\[
\tau_0 = \frac{x_L^2}{8D_0 \langle |\varepsilon| \rangle} = \frac{x_L^2}{8D_0} \sqrt{\frac{\pi \tau}{2D_\varepsilon}}.
\]

Here, \( \tau_0 \) is the time the particle takes to diffuse from inside a cell up to the center of its left or right exit pore. Accordingly, the time constant of the corresponding discrete intercell jumping process is \( 2\tau_0 \) and the channel


A defining property of channel diffusion is featured in Fig. 2. One normal diffusion law with the same diffusion constant, \( D \), fits all numerical data for \( \langle \Delta x^2(t) \rangle \) with \( t \geq 2\tau_0 \), i.e., in correspondence with both the Laplace and the asymptotic Gaussian distributions. To assess the Gaussian nature of the normal diffusion for \( t \to 0 \) and \( t \to \infty \), we explicitly computed a few higher moments \( \langle \Delta x^n(t) \rangle \) with \( n \geq 1 \), also reported in Fig. 2. We checked that in both limits \( \langle \Delta x^{2n}\rangle^{1/n} = [(2n-1)!!]^{1/n}\langle \Delta x^2 \rangle \), as expected for Gaussian \( \Delta x \) distributions. Instead, for the Laplace pdf’s fitted in Fig. 4 one would expect \( \langle \Delta x^{2n}\rangle^{1/n} = [(2n!)^{1/n}\langle \Delta x^2 \rangle \). The agreement between these latter estimates and the actual diffusion data in the intermediate \( t \) domain is qualitative good, only, which we attributed to the deviations from the Laplace distributions, apparent at \( \Delta x/\sqrt{t} \ll \alpha \).

On the other hand, the Laplace and the large-\( t \) Gaussian fitting pdf curves introduced above, yield the same channel diffusion constant, \( D \), only under the condition \( \alpha^2 = B \). However, the inset of Fig. 2 shows that, for the parameters of Fig. 1, \( 0.8 < \alpha/\sqrt{B} < 0.9 \). The ratio \( \alpha/\sqrt{B} \) thus serves as a measure of the exponential character of the displacement statistics across the normal diffusion transient dominated by channel fluctuations. An estimate of this ratio is obtained in Sec. IV.

The role of the time scale \( \tau \) is further illustrated in Fig. 3. As the MFET of Eq. (4) increases like \( \tau^{1/2} \), for large \( \tau \) the diffusion curves \( \langle \Delta x^2(t) \rangle \) develop a plateau in the range \( \tau_L \ll t \ll \tau_0 \). During this time interval, the diffusing particle “fills up” the 2D channel cell where it was initially injected, attaining a temporary maximum displacement \( \langle \Delta x^2 \rangle \sim \bar{x}^2 \), where \( \bar{x} = \pi/4 \) is the average half-width of the cell \( w(x) \), Eq. (1), for \( \sigma_\tau \to 0 \). This diffusion plateau is represented in Fig. 2 by a horizontal line.

The numerical estimates of the channel diffusion constant, \( D \), for \( t \gtrsim 2\tau_0 \) and the fitting parameter \( B \) of the Gaussian \( \Delta x \) pdf for \( t \gg 2\tau \) were anticipated to coincide. Simulation data, like those reported in Fig. 2, confirmed our expectations, within the statistical error, for all choices of the simulation parameters. Moreover, on combining Eqs. (3) and (4), one expects that \( D/D_0 = (2D_c/\pi \tau)^{1/2} \), also in fair close agreement with the numerical data plotted in the inset of Fig. 3(b).

Finally, we notice that on lowering \( \tau \) the slopes of the normal diffusion branches for \( t < \tau_L \) and \( t \gtrsim 2\tau_0 \) tend to coincide, that is \( D \) (and \( B \)) tend to \( D_0 \). This is due to the fact that the average pore width, \( \langle x^2 \rangle y_L \), grows like \( D_2/\tau \). As a result, for \( \langle x \rangle \gtrsim 1 \) the effective channel bottlenecks are no longer located at \( x = 0 \) mod{\( \pi \)}, but rather at \( x = \pi/2 \) mod{\( \pi \)}, and have fixed width, \( y_L \). Accordingly, from Eq. (3), \( \tau_0 = x^2/8D_0 \) and the channel diffusion constant of Eq. (4) is \( D = D_0 \).
and (ii) the same normal diffusion law holds for any $D$, for different $\tau_p$ curves, whereas the solid lines in (a) are the corresponding Gaussian curves, $p(\Delta x/\sqrt{t})$, defined in the text, with $B = D$. For short $t$, all curves in (b) collapse on one linear branch with diffusion constant $D_0$, also denoted by a straight line. Inset: $D$ vs. $\tau$ for different $D_c$ (see legend). All other simulation parameters are as in the main panel.

**IV. EXPONENTIAL NORMAL DIFFUSION**

In Sec. III we showed that on increasing the observation time larger than twice the MFET, (i) the displacement distribution evolves from Laplacian to Gaussian, and (ii) the same normal diffusion law holds for any $t$. A simple argument, first introduced in Ref. [14], can be generalized to support these conclusions.

Let us model a particle trajectory in the $x$ direction as the sum of random small steps, $\Delta x_i$, taken at discretized times, $t_i = i \Delta t$, where $i = 1, \ldots N$ and $\Delta t = 1$, for simplicity. The position of the particle at time $N$ is, therefore, $x_N = \sum_{i=1}^{N} \Delta x_i$. Accordingly,

$$\langle x_N^2 \rangle = \sum_{i=1}^{N} \langle \Delta x_i^2 \rangle + 2 \sum_{i \neq j} \langle \Delta x_i \Delta x_j \rangle,$$

where $\sum_{i \neq j} \langle \Delta x_i \Delta x_j \rangle$ stays for $\sum_{i=1}^{N-1} \sum_{j=1}^{N} \langle \Delta x_i \Delta x_j \rangle$, contrary to the standard model of Brownian random walker [7], normal diffusion at time $N$ sets in under the generic condition that the step directions are uncorrelated, $\langle \Delta x_i \Delta x_j \rangle = 0$, that is for mirror-symmetric distributions, $p(\Delta x_i)$, with variances, $\langle \Delta x_i^2 \rangle$, possibly different, but of the same order.

Following the authors of Ref. [14], one can further assume that during each unit time step the particle’s diffusion is normal with time-dependent constant, $D_i$, i.e.,

$$p(\Delta x_i) = (4\pi D_i)^{-1/2} \exp(-\Delta x^2_i/4D_i),$$

with unspecified $D_i$ distribution, $p(D_i)$. It follows immediately that

$$\langle x_N^2 \rangle = 2\langle D \rangle N,$$

and

$$\langle x_N^2 \rangle - 3\langle x_N^2 \rangle^2 = 12(\langle D^2 \rangle - \langle D \rangle^2)N + 24\sum_{i \neq j} (\langle D_i D_j \rangle - \langle D_i \rangle \langle D_j \rangle),$$

where $\langle D \rangle \equiv \langle D_i \rangle$ for the relevant choice of $p(D_i)$.

Suppose now that two particle steps, $\Delta x_i$ and $\Delta x_j$, are statistically uncorrelated, i.e., $\langle D_i D_j \rangle = \langle D_i \rangle \langle D_j \rangle$, only for $|i - j| > \tau$. We then distinguish two limiting cases, (i) $N \gg \tau$, where

$$\mu_x = \frac{\langle x_N^2 \rangle - 3\langle x_N^2 \rangle^2}{\langle x_N^2 \rangle^2} = \frac{3\mu_D}{N} \to 0,$$

with $\mu_D = (\langle D^2 \rangle - \langle D \rangle^2)/\langle D \rangle^2$. A vanishing $\mu_x$ hints at a Gaussian $x_N$ distribution as obtained from numerical simulation;

(ii) $N \ll \tau$, where

$$\mu_x = \frac{\langle x_N^2 \rangle - 3\langle x_N^2 \rangle^2}{\langle x_N^2 \rangle^2} \simeq 3\mu_D.$$

$\mu_N = 3$ would correspond to an exponential distribution of $x_N$; the coefficient $\mu_D$ is thus a measure of the deviation of the actual $x_N$ distribution from the ideal Laplace distribution.

To apply the argument above to the model under study, the time step $\Delta t$ has to be taken not shorter than $\tau_0$, i.e., the argument does not hold for the intracell diffusion. The corresponding coefficient $\mu_P$ can be estimated analytically by adapting the procedure of Ref. [27] to the case of a fluctuating channel, namely

$$\mu_D \simeq \frac{\langle \epsilon^2 \rangle - \langle \epsilon \rangle^2}{\langle \epsilon \rangle^2} = \frac{\pi}{2} - 1.$$
\[ \frac{dx}{dt} = \frac{\theta}{\tau} (\varepsilon - \varepsilon_0) \]  

Walls: \( w_t = y_L \left[ \varepsilon + (1 - \varepsilon^2) \sin^2 x \right] / 2 \), \( w_b = -w_t \).

\[ D/D_0 = \varepsilon^2 + \varepsilon_0^2 \]  

The dashed line is the analytical prediction \( \varepsilon_B = \mu/2 \) and \( \sigma_B = 2 \varepsilon_0 \).

The dependence of \( D \) on \( \varepsilon_0 \) in the absence and presence of channel fluctuations is compared in the inset of Fig. 4. For \( \varepsilon_0 > \sigma_z \) the diffusion constant grows insensitive to the fluctuation strength, \( D_z \). The obvious conclusion is that non-Gaussian normal diffusion only occurs when the fluctuations of the channel walls are strong enough to actually open and close the pores. Note that in the absence of channel fluctuations, \( D_z = 0 \), our data for \( D \) are well fitted by Eq. (4), with \( \tau \) given by the first Eq. (3) upon replacing \( \langle \varepsilon \rangle \) with \( \varepsilon_0 \).

The results of Fig. 4 illustrate the importance of diffusion compartmentalization during intermediate observation time intervals, \( 2 \tau_0 \leq t \leq 2 \tau \). For \( \varepsilon_0 > \sigma_z \), the tagged particle diffuses along the channel at all times, with only weakly correlated open-pore crossings; hence a Gaussian displacement distribution. In sharp contrast, for \( \varepsilon_0 < \sigma_z \), the pore crossings of the trapped particle grow more and more time correlated; hence the exponential tails of \( p(\Delta x/\sqrt{t}) \) discussed in Sec. IV. This description is consistent with the subordination mechanism advocated in Ref. [20].

The microscopic model investigated in this paper, despite its simplicity, was proven to reproduce most of the intriguing properties of the phenomenon known as non-Gaussian normal diffusion. Such a phenomenon has emerged as ubiquitous in soft matter physics, which suggests a number of promising generalizations of the present model by incorporating additional sources of randomness, for instance, by decorrelating channel's pore spacing and fluctuations or exciting size and configurational fluctuations of the diffusing particles, each on a suitably long time scale. Their combined action is expected to make the conclusions of the present study even more robust.

V. CONCLUSIONS

So far, by setting \( \varepsilon_0 = 0 \) in Eq. (2) we assumed that the fluctuations of the channel cause the opening and closing of its pores. Of course, in most cases the pores remain open at all times, with \( \varepsilon_0 > 0 \) and slightly fluctuating cross-section. Therefore, we investigated how the non-Gaussian normal diffusion mechanism depends on \( \varepsilon_0 \). In the main frame of Fig. 4 we plotted the rescaled displacement pdf’s at \( t = 2 \tau \) for the simulation parameters of Fig. 1 except that \( \varepsilon_0 \) is increased from 0 up to well above \( \sigma_z \). One sees immediately that on widening the pores, the rescaled pdf’s change from exponential at \( \varepsilon_0 = 0 \), see Fig. 1 to Gaussian with \( B = D \), for \( \varepsilon_0 > \sigma_z \).

On the other hand, on adopting the Laplace distribution \( p(\Delta x/\sqrt{t}) \) for \( x_N \) and the normal diffusion law, \( \langle \Delta x^2 \rangle = 2Dt \), instead of Eq. (6), that is, \( \langle D \rangle = D = B \), numerator and denominator of \( \mu_x \) can be calculated explicitly to obtain

\[ \mu_x = 3\alpha^4 / B^2. \]  

Finally, on comparing Eqs. (9)-(11), one estimates \( \alpha/B^{1/2} \approx 0.86 \), in fairly close agreement with the numerical data reported in the inset of Fig. 2.

ACKNOWLEDGEMENTS

Y.L. is supported by the NSF China under grant No. 11875201. P.K.G. is supported by SERB Start-up Research Grant (Young Scientist) No. YSS/2014/000853 and the UGC-BSR Start-Up Grant No. F.30-92/2015. D.D. thanks CSIR, New Delhi, India, for support through a Junior Research Fellowship.

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