

Being Heterogeneous Is Advantageous: Extreme Brownian Non-Gaussian Searches

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Redundancy in biology may be explained by the need to optimize extreme searching processes, where one or few among many particles are requested to reach the target like in human fertilization. We show that non-Gaussian rare fluctuations in Brownian diffusion dominates such searches, introducing drastic corrections to the known Gaussian behavior. Our demonstration entails different physical systems and pinpoints the relevance of diversity within redundancy to boost fast targeting. We sketch an experimental context to test our results: polydisperse systems.

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With the discovery [1] of Brownian non-Gaussian (BnG) diffusion—a stochastic motion with a mean squared displacement linearly increasing in time (Brownian or Fickian behavior) and a non-Gaussian probability density function (PDF) for the displacements—the expectation has been raised [2] that the excess of probability for rare large fluctuations might dominate first-passage processes, leading to unexpected phenomena. While BnG behavior found numerous experimental [2–20] and molecular dynamics [21–23] confirmations, at odds with expectation theoretical analyses showed that typical Gaussian searches turn out to be more effective than non-Gaussian ones [24–26]. In a companion paper [27], where full references about the available theoretical models for BnG diffusion are provided, we give a detailed account of this basic issue, showing that for the large class of subordination processes [28,29] the typical timescale for one searcher to reach the target—e.g., the mean first passage time (MFPT)—is indeed shorter in Gaussian than in non-Gaussian motion.

In the last years, however, an upsurge of studies and commentaries [30–41] has pointed out that in many situations such as fast activation processes in chemistry and cellular responses in biology, the relevant timescale is actually not the time spent by a given single searcher to reach the target, but rather the time at which the first few searchers, out of many, perform this task. A paradigmatic example is human reproduction, in which a single sperm cell out of $M \sim 10^8$ finds and fertilizes the egg. The computation of this time scale is a typical extreme statistics problem that justifies the presence of redundancy in some

biological processes but that, so far, has been mainly studied for normal Brownian motion.

In this Letter, we investigate the role that BnG motion, and in general the class of subordination processes may have on the extreme targeting problems. In particular, by focusing on the diffusing diffusivity (DD) model [42], and polydisperse polymer ensembles—equilibrium grand canonical [43,44] and quenched [45]—we show that the *extreme*-MFPT for non-Gaussian diffusion may become orders of magnitude shorter than the Gaussian one. This finding reveals a drastically different scenario with respect to the ordinary MFPT problem, identifying extreme targeting as a natural setting in which the non-Gaussianity makes a substantial difference.

Before going into the details of the calculations let us provide a qualitative argument for our findings. As we articulate in Ref. [27], models for BnG diffusion display an excess of probability both in the central part and in the tails, when compared with a Gaussian PDF of the same width (see Fig. 1). The excess of probability in the central part of the PDF, associated with a slower diffusion, is shown in [27] to be responsible for the lower effectiveness of non-Gaussian searches in ordinary targeting problems, when one looks at the typical timescale for a particle to reach the target. At a glance, this conclusion [24–26] frustrates expectations [2] of novel phenomena in diffusion-limited reactions driven instead by the “tail effect.” Yet, if one considers the class of problems in which reactions are activated by the first (or the first few) successful searchers among many, the corresponding targeting timescale, the

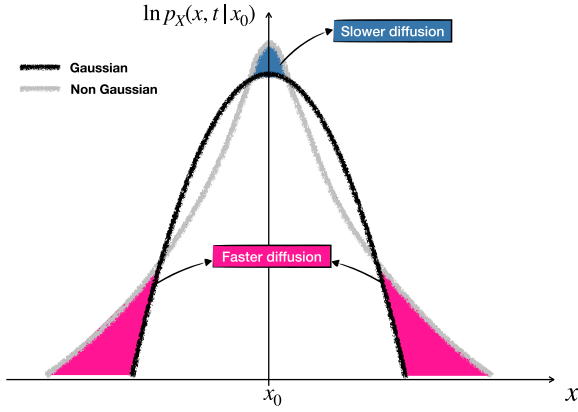


FIG. 1. Comparison between Gaussian and non-Gaussian PDFs for subordination processes. The two PDFs share the same mean and standard deviation but the non-Gaussian one has an excess probability both in the tails and in the center part. The non-Gaussian PDF is obtained from the FSP model with $p = 0.99$ (see text).

extreme-MFPT, is governed by rare trajectories which are the few among the many to follow a quasigeodesic path to the target [31,41]. Here we argue that through the tail effect non-Gaussianity adds to these rare events the possibility for the searcher to diffuse faster (see Fig. 1) and hence it impacts dramatically the *extreme*-MFPT, as we detail below.

Let us first briefly recall the theoretical context behind the *extreme*-MFPT problem. Given $M \gg 1$ independent (i.e., noninteracting) searchers, each with its own random arrival time τ_i , the arrival time of the fastest one is defined as $T_M = \min\{\tau_1, \tau_2, \dots, \tau_M\}$. (More generally one can consider $T_{k,M}$, namely, the time at which the k -fastest searches have reached the target [40,41]; clearly, $T_M \equiv T_{1,M}$.) We now include a possible heterogeneity for the diffusing particles, assuming that their diffusion coefficients are characterized either by a discrete steady-state probability mass function $p_D^*(D_n)$ ($n = 1, 2, \dots$) or continuous PDF $p_D^*(D)$, with average $\mathbb{E}[D] \equiv D_{\text{av}}$. Since the searchers are independent, the statistics of T_M can be computed from the one of a single particle. Denoting by $0 \leq P(\tau_i > t) \leq 1$ the one-particle survival probability, and by $\mathcal{S}_{D_n}(t)$ the survival probability of a generic particle with diffusion coefficient D_n , the probability associated with the extreme statistics is $P(T_M > t) = \prod_{i=1}^M P(\tau_i > t) = \prod_n (\mathcal{S}_{D_n}(t))^{M_n}$, where, by the law of large numbers, $M_n = M p_D^*(D_n)$ is the number of searchers with diffusion coefficient D_n . The *extreme*-MFPT, $\mathbb{E}[T_M] = \int_0^\infty dt P(T_M > t)$ is thus

$$\mathbb{E}[T_M] = \int_0^\infty dt \exp\left(M \sum_n p_D^*(D_n) \ln \mathcal{S}_{D_n}(t)\right). \quad (1)$$

Here and below, are the substitutions $\sum_n \mapsto \int dD$, $D_n \mapsto D$ understood if p_D^* is a PDF instead of a probability mass function. Note that by choosing $p_D^*(D) = \delta(D - D_{\text{av}})$,

Eq. (1) recovers the ordinary approach, appropriate for a Gaussian diffusion in which all particles share the same diffusion coefficient D_{av} . Despite the hypothesis of independent searchers enormously simplify the computation of $P(T_M > t)$, the full explicit expression of $\mathcal{S}_{D_n}(t)$ is often unknown and approximations are needed. The assumption $M \gg 1$ suggests that the computation of $P(T_M > t)$ can be approximated by the short-time behavior of $\mathcal{S}_{D_n}(t)$, where $\mathcal{S}_{D_n}(t) \simeq 1$. This is usually done by solving explicitly the boundary problem of the associated Fokker-Planck equation and taking the small time approximation of the corresponding survival probability [31,32,46,47]. For several targeting processes with varying space dimensions, boundaries, and shape of the target (if small enough), most results have been shown to fall into a universal category of extreme events statistics. This is due to the fact that the most effective rare trajectories almost follow a geodesic path to the target [31,41] of length ℓ , which is a straight line in a homogeneous and isotropic environment. It is thus paradigmatic to address the one-dimensional case for which

$$\mathcal{S}_{D_n}(t) = \text{erf}\left(\frac{\ell}{\sqrt{4D_n t}}\right) \underset{t \rightarrow 0^+}{\simeq} 1 - \frac{e^{-\frac{\ell^2}{4D_n t}} \sqrt{4D_n t}}{\sqrt{\pi \ell}}, \quad (2)$$

implying

$$\mathbb{E}[T_M] = \int_0^\infty dt \exp\left(-M \left[\sum_n p_D^*(D_n) \frac{e^{-\frac{\ell^2}{4D_n t}} \sqrt{4D_n t}}{(\sqrt{\pi \ell})} \right]\right). \quad (3)$$

For large M this integral can be approximated [30] as $\mathbb{E}[T_M] \simeq \int_0^{t_0} dt = t_0$, with t_0 solution of

$$M \sum_n p_D^*(D_n) \left(e^{-\frac{\ell^2}{4D_n t_0}} / \left(\frac{\sqrt{\pi \ell}}{\sqrt{4D_n t_0}} \right) \right) = 1. \quad (4)$$

It is convenient at this point to define

$$\tau_{\text{av}} \equiv \frac{\ell^2}{2D_{\text{av}}}, \quad (5)$$

which represents the characteristic time for a particle with an average diffusion coefficient D_{av} to travel over the distance ℓ . As outlined in the Supplemental Material [48], taking $p_D^*(D) = \delta(D - D_{\text{av}})$ in Eq. (4) yields the standard Gaussian result [30,49–51]

$$\mathbb{E}[T_M] / \tau_{\text{av}} \underset{M \gg 1}{\simeq} 1 / (2 \ln M) \quad (\text{Gaussian}), \quad (6)$$

which highlights how a large number of searchers M reduces the extreme MFPT with respect to the typical time taken by a particle to diffuse over the distance ℓ .

Let us now focus on classes of subordination processes $X(t)$ displaying BnG diffusion. These can be introduced via the stochastic differential equation

$$dX(t) = \sqrt{2D(t)}dB(dt), \quad (7)$$

where $B(t)$ is a Wiener process (Brownian motion) and $D(t)$ describes the fluctuations in time of the diffusion coefficient. By defining the *subordinator* as $S(t) \equiv 2 \int_0^t dt' D(t')$, Eq. (7) can be reformulated in the random path or subordination representation $dX(t) = dB(dS)$ [42,52–54]. Depending on the statistical properties of $D(t)$, and hence of the subordinator $S(t)$, several stochastic processes can be described by Eq. (7). For example, if $D(t) = Y^2(t)$ and $Y(t)$ is a d_Y -dimensional Ornstein-Uhlenbeck process ($d_Y = 1, 2, 3, \dots$), we have the DD model [42]. In the context of financial markets, under the name of stochastic volatility models they are used to correct the Black-Scholes theory for non-Gaussian effects [55,56]. Another possibility [52–54] is $D(t) = D_1/N^\alpha(t)$, with $\alpha > 0$ and $N(t) \geq 1$ a birth-death process (N only changes by ± 1) [57]. In this case Eq. (7) describes the motion of the center of mass of polymers of size N exchanging monomers with a chemostat [43,44], namely, grand canonical polymers (GCP), and D_1 is the diffusion coefficient of a single monomer in solution. Taking $\alpha = 1$ one has the Rouse approximation, whereas for the Zimm model $\alpha = \nu$ [58], ν being equal to $1/2$ for ideal, and $0.588\dots$ for self-avoiding chains [43]. This model introduces the concept of critical fluctuations in the diffusion coefficients, inherited by those of the polymer size $N(t)$ close to the critical point [43,44].

Distinctive properties of the stochastic process $D(t)$ are its stationary distribution p_D^* , and the autocorrelation time τ . For the DD model τ is a free parameter; in the GCP model τ is determined by the reaction rate constants of the birth-death process and it diverges at criticality (critical slowing down). Consider a situation in which the diffusion coefficients of the heterogeneous particles are initially distributed according to p_D^* . For time $t \ll \tau$ each diffusing particle retains its initial diffusion coefficient, and the behavior of the system is described by a statistical average over p_D^* . In the literature, such a superposition of statistics has been named *superstatistics* (SS) [2,17,59,60]. During the SS regime, $p_X(x, t|x_0)$ presents non-Gaussian features like those reported in Fig. 1. On the other hand, as $t \gg \tau$, the probability of the scaled subordinator $S(t)/t$ concentrates around its average value $2D_{\text{av}}$, the central part of $p_X(x, t|x_0)$ becomes Gaussian, and as time passes by non-Gaussianity is relegated to lesser and lesser probable fluctuations. This regime is thus associated with a large deviation (LD) principle [61], and the extreme-MFPT tends to the behavior in Eq. (6). The comparison between τ and $\mathbb{E}[T_M]$ determines whether the extreme search involves or not BnG features: The analysis of the extreme-MFPT within the SS (LD) approximation is applicable to situations where $\mathbb{E}[T_M] \ll \tau$ ($\mathbb{E}[T_M] \gg \tau$).

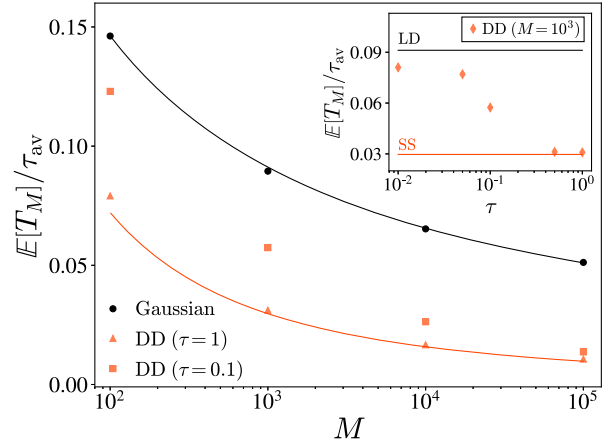


FIG. 2. Extreme-MFPT for the DD model (orange or gray in the gray scale version) and the Gaussian one (black) vs M . Note that the ratio $\mathbb{E}[T_M]/\tau_{\text{av}}$ does not depend on ℓ and D_{av} . Symbols refer to numerical simulations, while solid lines are theoretical estimations from Eqs. (S8) (black) and (S16) (orange or gray in the gray scale version) of the Supplemental Material [48]. Simulations are with $d_Y = 1$ and for different values of τ (details are reported in the Supplemental Material [48]). Inset: Crossover between the SS and the LD regime, attained upon changing τ at fixed M .

In the Supplemental Material [48] it is reported the steady-state PDF $p_D^*(D)$ for the DD model in arbitrary dimension d_Y . Within the SS approximation, we show that

$$\mathbb{E}[T_M]/\tau_{\text{av}} \underset{M \gg 1}{\simeq} d_Y/(\ln M)^2, \quad (\text{DD model}). \quad (8)$$

Note that the $1/\ln(M)$ dependence of Eq. (6) is here replaced by $1/[\ln(M)]^2$. On the contrary, if $\mathbb{E}[T_M] \gg \tau$, Eq. (6) applies. We thus appreciate that the extra probability for rare large fluctuations associated with the non-Gaussian tails of the DD model in the SS regime drastically reduces the extreme MFPT with respect to Gaussian searches performed with the average diffusion coefficient. Such a reduction is particularly visible in Fig. 2 for $\tau = 1$, where the relation $\mathbb{E}[T_M] \ll \tau$ is satisfied for the whole range of M and simulations of the DD model are nicely in agreement with the full theoretical estimate for the SS regime reported in Eq. (S16) of the Supplemental Material [48]. When $\tau = 0.1$, as M decreases a crossover occurs from the SS regime $\sim (\ln M)^2$ to the LD one $\sim \ln M$. This is highlighted also in the inset of Fig. 2, by keeping M fixed and varying τ .

The SS regime for the GCP model has a simple, practical experimental implementation: A polydisperse sample produced in a step-growth polymerization [62]. Whereas for GCPs the polymerization or depolymerization process continuously occurs over time while system and chemostat exchange monomers, in the polydisperse case polymerization terminates after the initial outgrowth and the sample constantly remains in the SS regime with D a static random variable. Taking for simplicity chains with exactly one

reaction center in the end, one can equivalently address the SS regime of GCPs considering a heterogeneous sample distributed according to the Flory-Schulz size distribution [45] $p_N^*(n) = (1-p)p^{n-1}$, where $0 \leq p \leq 1$ is the polymerization extent. We will refer to this as Flory-Schulz polydisperse (FSP) model. As $p \rightarrow 1^-$, the average polymer size $\mathbb{E}[N] = 1/(1-p)$ diverges and the system becomes critical [43,44,53]. Correspondingly, D_{av} tends to zero and τ_{av} diverges. The analysis reported in the Supplemental Material [48] for Rouse polymers yields

$$\frac{\mathbb{E}[T_M]}{\tau_{\text{av}}} \underset{M(1-p) \gg 1}{\simeq} \frac{(1-p)\ln(1-p)}{2p\ln[(1-p)M]} \quad (\text{FSP model}), \quad (9)$$

where, in consistency with our approximations, we have assumed a sufficiently large number of searchers such that $M \gg (1-p)^{-1}$. In the LD regime, the extreme MFPT of GCPs is again described by Eq. (6). Comparison of Eq. (9) with Eq. (6) reveals that while Gaussian searches take an infinite time to be accomplished as the system approaches criticality and τ_{av} diverges, non-Gaussian ones are still realized within a finite time. This means that wild fluctuations in the polymer size induce such heavy tail effect in $p_X(x, t|x_0)$ to keep the extreme-MFPT finite, eluding the critical slowing down for this kind of search. One might argue that since this analysis applies to the center of mass of the polymer which is an immaterial point in space, is of limited practical relevance. However, our results indicate that the instances which reach the target under non-Gaussian heterogeneous conditions are precisely those fast diffusers responsible for the tail effect. These are the polymers with a small size, for which the Rouse time of the chain [58] is very small, and hence their center-of-mass dynamical timescale corresponds to that of any monomer unit acting in practice as a ligand. We may add that this example shows that heterogeneity supplements to extreme searches the concept of *fitness*: In a heterogeneous sample not only the geodesic path to the target is followed in extreme searches, but the successful searcher happens to belong to the fittest subset (in our case, the fastest, small-size polymers). In analogy with the previous plots, simulations in Fig. 3 confirm our analytical predictions for the FSP model.

It is interesting to point out that, at variance with the DD model, the extreme-MFPT for the polydisperse polymers displays the same $1/\ln(M)$ dependence of the Gaussian case. This is to be ascribed to the sharp large-value cutoff at $D_n = D_1$ of the $p_D^*(D_n)$ distribution. To clarify this point, we have analyzed a class of generalized gamma distributions [63] $p_D^*(D) \underset{D \rightarrow \infty}{\sim} \exp\{-[A(\nu, \eta)D/D_{\text{av}}]^\eta\}$, with the parameter η characterizing different tail behaviors. The same procedure used for the other models gives

$$\frac{\mathbb{E}[T_M]}{\tau_{\text{av}}} \underset{M \gg 1}{\simeq} [D(\nu, \eta)/\ln(M)]^{\frac{(\eta+1)}{\eta}} \quad (\text{gen Gamma model}), \quad (10)$$

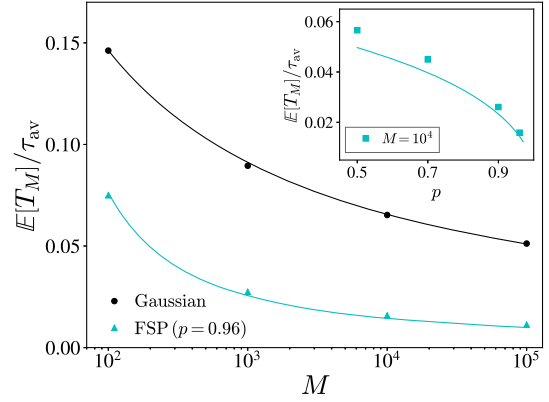


FIG. 3. Extreme-MFPT for FSP model (cyan or gray in the gray scale version). In analogy to Fig. 2, symbols refer to numerical simulations, while solid lines are theoretical estimations from Eqs. (S8) (black) and (S23) (cyan or gray in the gray scale version) of the Supplemental Material [48]. Inset: behavior with respect to p at fixed M ; the solid line indicates the theoretical trend from Eq. (9). Simulation details are reported in [48].

where the full expression of the coefficient $D(\eta, \nu)$ is provided in the Supplemental Material [48]. On the one hand, for $\eta = 1$ (exponential tail) we recover the DD result, namely, $1/[\ln(M)]^2$. On the other hand, in the limit $\eta \rightarrow \infty$ for which the tail of $p_D^*(D)$ drops sharply approaching the step function decay of the FSP model, we recover the $1/\ln(M)$ dependence. The result in Eq. (10) shows explicitly that (a) There is no universal behavior in M when we move outside of the Gaussian regime; (b) For random diffusivity model it is the tail of the diffusivity distribution that decides such a trend.

The origin of non-Gaussianity that we have addressed is amenable to the heterogeneity of the ensemble of diffusers and/or of the environment [64]. Such heterogeneity implies both an excess of probability in the central part and in the tails of the displacements distribution, when compared with the Gaussian one [27]. We have shown that a higher probability for few, faster diffusers (tail effect) influences extreme searches, pointing out that a redundant information stored in *diverse searchers* strongly enhances the fast targeting of the first few instances. Non-Gaussianity is both disadvantageous [27] and advantageous. It is disadvantageous when the activation of a biological function needs a large percentage of ligands to bind receptors; it is advantageous when only a few searchers, among many, are required to reach the target. The latter is the typical situation in which diffusing particles are carriers of information, like in human reproduction. For this kind of search, diversity appears to be an efficient strategy to be recognized in evolutionary examples, and exploited in the design of efficient deliveries. A straightforward setup for experimental confirmation of our results is that of polydisperse polymers.

More broadly, we expect this investigation to open prospects in understanding the role of heterogeneity in

diffusion transport phenomena, for instance in models where the BnG behavior has been discovered [2–19], and likewise in the world of anomalous processes where the mean squared displacement grows nonlinearly in time. Indeed, recent single-particle tracking experiments in crowded environments—such as those of biological cells—show that heterogeneity manifests itself not only in the variability of transport coefficients [65], but also in fluctuations of the anomalous diffusion exponent [66–76].

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