Heterogeneity transforms subdiffusion into superdiffusion via ensemble self-reinforcement

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We formulate a subdiffusive master equation in continuous time with random transition probabilities such that the ensemble of random walks exhibits superdiffusion. This counter intuitive result is explained by the ensemble self-reinforcement phenomenon, which emulates conditional transition rates of an underlying discrete random walk with strong memory through a heterogeneous ensemble. We find the ensemble averaged solution of this master equation and the exact equation for the second moment, which exhibits superdiffusion. Ensemble self-reinforcement allows a smooth transition between subdiffusion and superdiffusion depending on a single parameter.

Introduction. — Anomalous diffusion appears in many natural processes in physics, chemistry and biology when measurements of mean squared displacement \(m^{(2)}(t)\) show non-linear dependence on time: \(m^{(2)}(t) \propto t^\mu\) \cite{1, 2, 3}. A variety of models has been suggested for anomalous diffusion including continuous time random walk \cite{4}, fractional Brownian motion \cite{5}, generalized Langevin equation \cite{6, 7} and Lévy walks \cite{8, 9}. The integral feature of all anomalous models is that they involve memory effects. When a stochastic process depends on a series of previous events, it is often referred to as having non-Markovian characteristics or memory. In many natural phenomena, memory is a recurring theme, such as earthquakes \cite{10}, quantum physics \cite{11, 12, 13} intracellular transport \cite{14, 15}, and cell motility \cite{16}. Another direction to model anomalous diffusion is through random walks that account for the whole history of its past, described as strong memory \cite{17, 18}. However, it is difficult to justify why natural processes should exhibit such strong memory effects, especially for inanimate objects such as intracellular organelles. In efficient search strategies \cite{19, 20} that have an essential role in time sensitive biological processes \cite{21}, strong memory has significant effects \cite{22}. More recently, it was shown that strong memory and self-reinforcement can generate superdiffusion in a continuous time and finite velocity strong memory model \cite{23}, even in the presence of rests \cite{24}. However, when including a trapping state, the superdiffusion caused by reinforcement was only transient \cite{25}.

In cellular processes, the movement of organelles is often subdiffusive due to the crowded cytoplasm \cite{26, 27}, which is in direct contrast with the need to efficiently and quickly transport material to specific targets, accomplished by active transport. At the same time, cells are extremely heterogeneous \cite{28, 29} and many biological processes incorporate redundancy \cite{30}. A natural question is: Does heterogeneity provide an advantage for biological processes when trapping is involved? In our paper, we demonstrate, how heterogeneity changes the fundamental characteristic of the fractional master equation, used in modelling many biological processes that exhibit trapping \cite{31, 32}. Moreover, by introducing heterogeneity into subdiffusive random walk models we obtain a surprising result: the fractional master equation generates superdiffusion. For the first time, we show from a random walk perspective the reason behind why heterogeneity is needed in natural phenomena for efficient transport of an ensemble.

Subdiffusive fractional master equation

The subdiffusive movement of particles on a lattice that experience trapping with heavy-tailed waiting times can be described by the fractional master equation \cite{33}

\[
\frac{\partial p}{\partial t} = -i(x,t) + qi(x-a,t) + (1-q)i(x+a,t).
\] (1)

Here \(p\) is the probability to find the particle at position \(x = ka\ (k \in \mathbb{Z})\) and time \(t\). The anomalous escape rate \(i(x,t)\) is defined as

\[
i(x,t) = \tau_0^{-\mu} D^{1-\mu}_t p(x,t), \quad 0 < \mu < 1
\] (2)

and \(D^{1-\mu}_t\) is the Riemann-Liouville derivative

\[
D^{1-\mu}_t p(x,t) = \frac{1}{\Gamma(\mu)} \frac{\partial}{\partial t} \int_0^t \frac{p(x,t')}{(t-t')^{1-\mu}} dt'.
\] (3)

Equation (1) describes a random walk where a particle leaves its current state \(x\) at time \(t\) with rate \(i(x,t)\) and either jumps with constant probability \(q\) or \(1-q\) to \(x+a\) or \(x-a\), respectively \cite{33}. The anomalous rate defined in Eq. (2) characterizes waiting times that are Mittag-Leffler distributed \cite{33}. From (1), by setting \(q = 1/2\) and taking the continuous space limit, one can obtain the fractional diffusion equation \(\partial p/\partial t = D_\mu \partial^2 \partial D^{1-\mu}_t p(x,t)/\partial x^2\), with the fractional diffusion coefficient \(D_\mu = a^2/2\tau_0^\mu\). Equation (1) with \(q = 1/2\) and the fractional diffusion equation produces subdiffusive behavior characterized by the mean-squared displacement (and also the variance since the mean is zero) \(m^{(2)}(t) \sim t^\mu\) where \(0 < \mu < 1\). If \(q\), the probability of jumping one step in the positive direction, is a random variable, should one still expect the mean-squared displacement to be subdiffusive?
Random transition probabilities.— Clearly for many biological processes, such as intracellular transport [14–34], the value of $q$ is heterogeneous across the population of particles. To account for the heterogeneity across a population of particles, consider that $q$ in Eq. (1) is a random variable that is Beta distributed with a probability density function

$$f(q) = \frac{q^{\alpha_{+} - 1}(1 - q)^{\alpha_{-} - 1}}{B(\alpha_{+}, \alpha_{-})}$$

where $B(\alpha_{+}, \alpha_{-})$ is the beta function.

If $q$ becomes random, how does the subdiffusive behavior in Eq. (1) change? In other words, how does the randomness of $q$ change the subdiffusive behavior $m^{(2)}(t) \sim t^{\mu}$ where $0 < \mu < 1$? One might reasonably expect that ensemble fluctuations in $q$ will increase the dispersion of particles leading to randomness of the fractional diffusion coefficient. This idea for standard diffusion has been considered by theories of ‘diffusing diffusivity’ [40–42] and such heterogeneity was demonstrated to be advantageous for biochemical processes triggered by first arrival [29]. Moreover, heterogeneity can be modelled in many ways such as a non-constant diffusion coefficient [43–45] or a non-constant anomalous exponent [37, 39, 46–48].

In this Letter, we show that ensemble heterogeneity in $q$ not only increases the subdiffusive dispersion but leads to a fundamental change in behavior such that the subdiffusive master equation (1) with random $q$ exhibits superdiffusion even for the case when $q$ is distributed symmetrically with mean $\bar{q} = 1/2$. In what follows, we will demonstrate that the randomness of $q$ leads to an effective strong memory orchestrated by the ensemble of particles. We call this new mechanism ensemble self-reinforcement. To show this, we need to find the explicit expression for the ensemble averaged probability distribution $\tilde{p}(x, t)$ in continuous time defined as

$$\tilde{p}(x, t) = \int_{0}^{1} p(x, t|q)f(q)dq,$$

where $p(x, t|q)$ is the solution for the master equation (1) with a single value of $q$. In order to do this, we first consider the underlying discrete time random walk for [1] and then utilize the idea of subordination [13, 49].

**Ensemble self-reinforcement.—** The underlying discrete time random walk for Eq. (1) is described by the difference equation $X_{n+1} = X_n + \xi_{n+1}$ where the random jump $\xi_n = \pm a$ with probability $q$ and $1 - q$ respectively, and $X_0 = 0$. The conditional probability

$$P(x, n|q) = \Pr\{X_n = x\}$$

obeys the master equation

$$P(x, n+1|q) = qP(x - a, n|q) + (1 - q)P(x + a, n|q).$$

The solution [49] is

$$P(x, n|q) = \left(\frac{n}{\frac{1}{2}(n + x/a)}\right)^{2(n + \frac{x}{a})}\left(q^\frac{1}{2}(n + \frac{x}{a})\right)^{1 - q\frac{1}{2}(n + \frac{x}{a})}.$$  

(8)

The particle reaches the point $x$ at time $n$ if it makes $\frac{1}{2}(n + x/a)$ positive jumps and $\frac{1}{2}(n - x/a)$ negative jumps.

Next, we obtain the master equation for

$$\tilde{P}(x, n) = \int_{0}^{1} P(x, n|q)f(q)dq$$

by averaging (7) using $f(q)$ from (4). Then,

$$\tilde{P}(x, n+1) = u_{n}^+ (x-a)\tilde{P}(x-a, n) + u_{n}^- (x+a)\tilde{P}(x+a, n)$$

(10)

where the transition probabilities $u_{n}^+(x)$ and $u_{n}^-(x)$ are defined as follows

$$u_{n}^+(x) = \int_{0}^{1} P(x, n|q)f(q)dq, \quad u_{n}^-(x) = 1 - u_{n}^+(x).$$

(11)

Transition probabilities (11) follow from averaging (7) with respect to $f(q)$. By using the solution (5) we find

$$u_{n}^\pm (x) = \frac{\alpha_{\pm} + \frac{1}{2}(n \pm \frac{x}{a})}{\alpha_{+} + \alpha_{-} + n}.\quad (12)$$

Surprisingly, randomness of the parameter $q$ generates effective transition probabilities, $u_{n}^\pm (x)$, which describes the ensemble self-reinforcement phenomenon. It follows from (12) that the probability to step in the positive or negative direction increases as more steps in those directions are made in the past, which is known as self-reinforcement. In what follows, we demonstrate the link between Eqs. (10) with (12) and random walks with transition probabilities dependent on the entire history of its past, a property called strong memory. Furthermore, we provide an explanation to how these two concepts are linked despite the difference in the underlying mechanism.

**Effective random walk with strong memory.—** The aim of this subsection is to show that Eq. (10) describes a random walk with strong memory. Let $X_n$ be the position of this random walk. The master equation (10) for $P(x, n) = \Pr\{X_n = x\}$, where $X_{n+1} = X_n + \xi_{n+1}$. The conditional transition probability for the discrete steps, $\xi_n$, depends on its entire history such that

$$\Pr\{\xi_{n+1} = \pm a | \xi_1, \ldots, \xi_n \} = \frac{\alpha_{\pm} + n_{\pm}}{\alpha_{+} + \alpha_{-} + n}.$$  

(13)

Here $n_{\pm}$ is the number of steps taken in the positive and negative directions, respectively. Equation (13) can be obtained from the transition probabilities [12] by combining the current position $x = a(n_+ - n_-)$ and the total number of steps $n = n_+ + n_-$. The transition probabilities (13) depend on the entire history because $n_{\pm}$ counts
the number of steps taken in the positive and negative directions up to time \( n \). This dependence of the conditional transition probability on the entire history of the random walk is known in the literature as strong memory effects [10]. The conditional transition probability on the entire history of \( \xi \) is Mittag-Leffler distributed [50]. Using subordination [6, 49], we can write

\[
\bar{p}(x,t) = \sum_{n=0}^{\infty} \bar{P}(x,n)Q\_\mu(n,t)
\]

where \( \bar{P}(x,n) \) is defined in [9] and \( Q\_\mu(n,t) = \text{Prob}\{N\_\mu(t) = n\} \). From the master equation [10] or by averaging the solution (8) as shown in (9), one can obtain

\[
\bar{P} = \left( \frac{n}{\frac{1}{2}(n + \frac{\tau}{a})} \right) \frac{B\left(\frac{1}{2}(n + \frac{\tau}{a}) + \alpha_+ + \frac{1}{2}(n - \frac{\tau}{a}) + \alpha_-\right)}{B(\alpha_-, \alpha_+)}.
\]

The probability \( Q\_\mu(n,t) \) is given by [50],

\[
Q\_\mu(n,t) = \left( \frac{t}{\tau_0} \right)^{\mu n} \sum_{k=0}^{\infty} \frac{(k+n)!}{n!} \frac{(-\frac{\tau}{a})^k}{\Gamma(\mu(k+n)+1)}.
\]

Fig. 1 illustrates the solution (15) obtained by Monte Carlo simulations for the symmetrical case \((\alpha_+ = \alpha_-)\). One can see the unusually strong dispersion for the subdiffusive master equation, which is a result of the interaction between ensemble self-reinforcement described by \( \bar{P}(x,n) \) and heavy-tailed waiting times with divergent mean described by \( Q\_\mu(n,t) \). Next, we will show the analytical relationship for the second moment and variance that is generated by the interaction of these two components.

Superdiffusion generated by ensemble self-reinforcement. — Now, we will show that superdiffusion can arise from a subdiffusive master equation with ensemble self-reinforcement. To do this, we need to find the moments corresponding to the discrete case of (15)

\[
M\_m(n) = \sum_{x=-\infty}^{\infty} x^m \bar{P}(x,n), \quad m \in \{1, 2, \cdots \}.
\]
We define the parameter \( k = \mu = \alpha / 2 \). However, the results that follow are still valid for the asymmetrical case. In the absence of advection is emphasised in Fig. 1 which shows symmetric distributions for different values of \( \mu \). Figure 1 also shows that in the limit of large \( \alpha \), the distribution reverts back to the distribution typical for the subdiffusive regime. In what follows, we show this analytically.

Using \cite{50}, we can rewrite \cite{18} as

\[
M^{(m)}(n) = \int_0^1 \left[ \sum_{x=-\infty}^{\infty} x^n P(x, n|q) \right] f(q) dq. \tag{19}
\]

Recognizing that the summation in \cite{19} is simply the \( m \)th moment of the discrete random walk, \( X_n \), governed by \cite{7} for any fixed value of \( q \), we find

\[
M^{(m)}(n) = \int_0^1 \mathbb{E}[(X_n)^m] f(q) dq. \tag{20}
\]

First, we find the conditional moments of the underlying random walk for fixed \( q \): \( \mathbb{E}(X_n) = G'(1) \) and \( \mathbb{E}(X_n^2) = G''(1) + G'(1) \), where \( G(z) = [qz^\alpha + (1-q)z^{-\alpha}]^{\nu} \) is the probability generating function \cite{51}. Performing this calculation, we obtain

\[
\mathbb{E}(X_n) = an(2q - 1) \tag{21}
\]

and

\[
\mathbb{E}(X_n^2) = a^2 (2q - 1)^2 n^2 - a^2 (2q - 1)^2 n + a^2 n \tag{22}
\]

It is clear that when \( q = 1/2 \), the mean \cite{21} is zero and the variance \cite{22} is proportional to \( n \). However, when we take the ensemble average over \( q \) using the symmetric Beta distribution, the mean remains zero but the variance is proportional to \( n^2 \).

Then from \cite{20}, \cite{21} and \cite{22}, it is straightforward to find that

\[
M^{(1)}(n) = 0, \quad M^{(2)}(n) = \frac{a^2}{1 + \alpha} n^2 + \frac{a^2 \alpha}{1 + \alpha} n. \tag{23}
\]

From \cite{23}, one can see that the variance is proportional to \( n^2 \) and this is due to ensemble self-reinforcement expressed by the transition probabilities in \cite{12}, which leads to a greater dispersion of particles over time compared to standard random walks. Note that this result can be obtained by also finding the moments through a recursion relation from the master equation \cite{10, 25}.

For the continuous time case, one can find the first and second moments from \cite{23} and \cite{15} as \( m^{(1)}(t) = \int_{-\infty}^{\infty} x \bar{P}(x, t) dx = 0 \) and

\[
m^{(2)}(t) = \int_{-\infty}^{\infty} x^2 \bar{P}(x, t) dx = \frac{a^2}{1 + \alpha} \bar{\eta}^2(t) + \frac{a^2 \alpha}{1 + \alpha} \pi(t) \tag{24}
\]

where \( \bar{\eta}^2(t) \) and \( \pi(t) \) are derived from the fractional Poisson process \cite{50} as

\[
\pi(t) = \frac{1}{\Gamma(\mu + 1)} \left( \frac{t}{\tau_0} \right)^\mu \tag{25}
\]

and

\[
\bar{\eta}^2(t) = \frac{1}{\Gamma(\mu + 1)} \left( \frac{t}{\tau_0} \right)^\mu + \frac{A_\mu}{\Gamma(\mu + 1)} \left( \frac{t}{\tau_0} \right)^{2\mu}, \tag{26}
\]

where \( A_\mu = \frac{\sqrt{\pi} \Gamma(\mu + 1/2)}{2^{\mu + 1/2} \Gamma(\mu + 1)} \). Finally, the second moment in continuous time is

\[
m^{(2)}(t) = \frac{a^2}{\Gamma(\mu + 1)} \left[ \left( \frac{t}{\tau_0} \right)^\mu + \frac{A_\mu}{1 + \alpha} \left( \frac{t}{\tau_0} \right)^{2\mu} \right] \tag{27}
\]

Equation \cite{27} demonstrates that ensemble self-reinforcement generates superdiffusion even when particles have heavy-tailed waiting times with divergent mean. The appearance of superdiffusion is demonstrated by numerical simulations in Figs. 2 and 3. Both \( m^{(2)}(t) \) and \( \bar{V} = m^{(2)}(t) - \left[ m^{(1)}(t) \right]^2 \) are super-linear but sub-ballistic in proportion to time. Since the first moment is zero for the symmetric Beta distribution, the variance is equal to the second moment. Figure 2 demonstrates numerically the relation in \cite{27} since for values of \( \mu < 0.5 \), \( m^{(2)}(t) \) shows subdiffusion and for values \( \mu > 0.5 \) shows superdiffusion. Moreover for \( \mu = 0.5 \), \( m^{(2)}(t) \) is exactly diffusive.

Furthermore, from this new, heterogeneous population model we are able to achieve smooth transition between subdiffusion and superdiffusion. This is evident by increasing the value of \( \alpha \to \infty \). This is intuitive as the symmetric Beta distribution approaches a delta function centered at \( q = 1/2 \) as \( \alpha \to \infty \) and so we recover the standard fractional master equation and the resulting subdiffusion. However when \( \alpha \sim 1 \) and \( \mu > 1/2 \), we obtain superdiffusion in the long-time limit. This transition
between superdiffusion and subdiffusion is demonstrated using computational simulations in Fig. 3.

This result is completely different from the case when an external force combines with the subdiffusive master equation where the first moment is $m^{(1)}(t) \sim t^\mu$ and so the second moment becomes $m^{(2)}(t) \sim t^{2\mu}$. For examples considered in this paper, $m^{(1)}(t) = 0$. The superdiffusion caused in this new process is a result of a heterogeneous population of particles and this generates ensemble self-reinforcement demonstrated by (12).

Discussion.— Given that a heterogeneous population of random walkers emulates strong memory, this opens a new avenue for modelling biological processes that display strong memory properties and yet are ensembles of inanimate objects, like organelles and micromolecules. Might it be that nature has developed a mechanism like ensemble self-reinforcement that we demonstrated in (12) as a proxy for strong memory? Such questions have plagued the field of intracellular transport for decades where brainless membrane-bound vesicles seemingly engage in random walks that appear to have correlations caused by strong memory effects [18, 20]. For example, a high value of $q$ might represent a higher affinity to attach to the dynein family of motor proteins and therefore the particle moves very directionally towards the cell nucleus whereas a low value of $q$ would be a higher affinity to attach to kinesin which moves towards the cell periphery. A value of $q \sim 1/2$ would imply that a particle may have equal chance to move in either direction. Ensemble self-reinforcement enables the organization of directional movement as an ensemble effect from heterogeneity. Furthermore, we showed that ensemble self-reinforcement can generate superdiffusion from trapped particles with waiting times that have a divergent mean.

This finding also fits nicely with the emerging theory that, in biological processes, the first arrival times of a signal to a cell (or neuron) influence the subsequent system behavior far more than the average arrival times [30]. With ensemble self-reinforcement the cell can organize the movement of these particles such that it maintains efficiency of transport and overcomes the trapping that occurs in the crowded cytoplasm. We hypothesise that ensemble self-reinforcement is a way that the cell efficiently transports vesicles in a heavily crowded intracellular environment, which has been shown to be subdiffusive [19, 37].

Although there is vast literature on strong memory effects in statistical physics [22, 27, 31, 32], many models lack the mechanism of how the strong memory is produced by seemingly inanimate objects such as the cell, intracellular vesicles and proteins. With this new result, we demonstrate that strong memory can be generated by a heterogeneous population of subdiffusive particles and that, particularly for intracellular transport, such a population experiencing trapping with divergent mean can emulate the efficient transport properties of superdiffusion.

Summary.— This Letter demonstrates that heterogeneous populations of subdiffusive random walks can achieve effective transition probabilities describing strong memory, which we call ensemble self-reinforcement. Of greater importance and novelty, we find that such heterogeneous populations overcomes heavy-tailed waiting times with divergent mean to exhibit ensemble superdiffusion thus revealing an intrinsic advantage of heterogeneity. Moreover, this provides a new mechanism through which seemingly unintelligent systems can exhibit strong memory. Notably, the second moment has a continuous transition from subdiffusion to superdiffusion depending on the beta distribution which governs the heterogeneous population. Not only do these results advance statistical physics, they will ultimately apply broadly to the natural sciences where models of fractional processes are increasingly applied.

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