Aging Effects and Population Splitting in Single-Particle Trajectory Averages

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We study time averages of single particle trajectories in scale-free anomalous diffusion processes, in which the measurement starts at some time $t_a > 0$ after initiation of the process at $t = 0$. Using aging renewal theory, we show that for such nonstationary processes a large class of observables are affected by a unique aging function, which is independent of boundary conditions or the external forces. Moreover, we discuss the implications of aging induced population splitting: with growing age t_a of the process, an increasing fraction of particles remains motionless in a measurement of fixed duration. Consequences for single biomolecule tracking in live cells are discussed.

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Recently there is growing interest in the diffusive properties of single molecules or microscopic tracer particles in living biological cells [1,2] since such information provides insight into molecular regulation and signaling underlying cellular biology [3]. Similar particle tracking methods are used to analyze complex fluids [4,5]. This field is opening up new perspectives in nonequilibrium statistical mechanics revealing, in particular, phenomena such as anomalous diffusion, weak ergodicity breaking, and population splitting as discussed in this Letter.

Population splitting is a widely observed phenomenon in single biomolecule experiments where a fraction of the molecules is immobile (or extremely slow) while the complimentary fraction is mobile. Such two-phase dynamics was observed for the motion of lipids in phospholipid membranes [6], single protein molecules in the cell nucleus [7], H-Ras on plasma membranes [8], and of membrane proteins [9]. The immobile fraction is also often found in fluorescence recovery after photobleaching experiments [6]. Here, we come up with a novel single molecule population splitting mechanism which is controlled by the age of the system t_a. This aging population splitting has broad consequences for the way we report statistical properties of single molecule experiments, which can be made either with respect to the total population or with respect to the mobile fraction.

Let us first look at a Brownian particle in water at room temperature. Since the studies of Nordlund [10], experimentalists have tracked individual trajectories of particles and used the information for precise measurements of diffusion constants. Consider a particle, that was immersed in the medium at time $t = 0$ while the experimental observation starts at the "aging time" $t_a \geq 0$. The time averaged mean squared displacement $\overline{\delta^2}$ (TAMSD) is a measure of the diffusivity. It is defined through the trajectory $x(t)$, which is recorded in the time interval $(t_a, t_a + T)$, in terms of

$$\overline{\delta^2} = \frac{1}{T-\Delta}\int_{t_a}^{t_a+T-\Delta}[x(t+\Delta)-x(t)]^2 dt, \qquad (1)$$

with the lag time $\Delta \ll T$. At finite measurement time T the TAMSD (1) is usually averaged over many trajectories to produce the smooth quantity $\langle\overline{\delta^2}\rangle$. In experiments we may have $t_a = 0$, namely the start of measurement coincides with the immersion of the observed particle in the medium. In contrast, the particle may be immersed long before the start of the measurement, and in some cases we may not even know the aging time t_a. Luckily, for Brownian motion, t_a is an irrelevant time scale. Because of the stationary increments of Brownian motion, even if $t_a \gg T$, one finds $\overline{\delta^2} \sim 2K_1\Delta$ where K_1 is the diffusion coefficient of the Brownian motion. We say that no aging occurs since $\overline{\delta^2}$ is t_a independent.

A far more challenging behavior is encountered when the medium is strongly disordered. As originally pointed out by Bouchaud in the context of spin glass dynamics [11], strongly disordered systems may exhibit weak ergodicity breaking [12]. Roughly speaking, this implies nonstationary dynamics, where certain sojourn times t in microstates of the system become asymptotically power-law distributed, $\psi(t) \simeq t^{-(1+\alpha)}$ with $0 < \alpha < 1$, leading to a diverging mean sojourn time (see more details below). This in turn causes the inequivalence of long time and ensemble averages [13–21]. Imagine that at time $t = 0$ we immerse an ensemble of particles in such a disordered system. The particles diffuse in the interval $(0, t_a)$, and some of them get trapped in the associated energy landscape containing deep traps. At time t_a, one starts measuring individual particle trajectories and the TAMSD $\overline{\delta^2}$ is recorded. If the life times of particles in the traps are finite, eventually all particles will exhibit normal behavior, like Brownian particles. If the traps are perfect sinks, i.e., infinitely deep traps, we again get trivial behavior: all particles become localized. However, when we encounter

power-law trapping times, a wealth of interesting behaviors emerges. This includes widely investigated phenomena such as anomalous diffusion (namely, $\langle x^2\rangle \simeq t^\alpha$ [22]) and weak ergodicity breaking [13,14,21]. Here we investigate the dependence of $\langle\overline{\delta^2}\rangle$ on the aging time t_a as well as the fingerprint of ergodicity breaking under aging condition, namely, we compute precisely the fluctuations of $\overline{\delta^2}$ showing that they strongly depend on t_a. This yields new perspectives on weak ergodicity breaking since, so far, the effect of aging on time averaged observables has not been investigated. As we show, knowledge of these effects is crucial for a meaningful physical interpretation of single trajectory measurements.

For the TAMSD $\langle\overline{\delta^2}\rangle$, we find a simple relation between the aged ($t_a > 0$) and nonaged ($t_a = 0$) cases,

$$\langle\overline{\delta^2}\rangle = \Lambda_\alpha(t_a/T)\langle\overline{\delta^2}\rangle_{t_a=0}, \quad \text{with} \quad \Lambda_\alpha(z) = (1+z)^\alpha - z^\alpha, \tag{2}$$

in which the multiplicative factor Λ_α carries the entire dependence on the aging time t_a and $0 < \alpha < 1$ is the anomalous diffusion exponent. In Eq. (2), $\langle\overline{\delta^2}\rangle_{t_a=0} = 2K_\alpha\Delta/[\Gamma(1+\alpha)T^{1-\alpha}]$ is the solution for the nonaged case $t_a = 0$ [13,14]. Equation (2) shows an elegant connection between aged and nonaged systems through $\Lambda_\alpha(t_a/T)$, which serves as a clock determining the age of the process. Importantly, we show the universality of this result here, by extension to a wide class of physical observables beyond the TAMSD and for external force fields.

CTRW model.—Anomalous diffusion based on power-law distributions of waiting times $\psi(t)$ is naturally described in the continuous time random walk (CTRW) model. The CTRW model was conceived by Montroll and Weiss [23] and further developed by Montroll, Scher, and Shlesinger [24]. In a CTRW [25], the position coordinate x of the walker is an accumulation of random jump lengths δx_i. After n jumps the walker's position is $x(n) = \sum_{i=0}^{n}\delta x_i$. The δx_i are independent, identically distributed (IID) random variables with zero mean and finite variance σ^2. Jumps are separated by random IID waiting times, drawn from the common distribution $\psi(t)$. This implicitly defines a counting process $n(t)$, the random number of steps up to time t [25]. The statistics of the overall diffusion process $x(t) = x(n(t))$ is derived from both constituents, a method commonly called subordination [26–29]. For a large variety of physical applications of CTRW, see Refs. [22,24]. In particular, CTRW dynamics was identified in single particle tracking in living cells [1]. We first discuss the counting process $n(t)$.

Aging renewal theory.—The effect of the aging time t_a in subdiffusive CTRW is investigated in the framework of aging renewal theory [30,31]. Since waiting times are independent, $n(t)$ is a renewal process, which we assume to start at $t = 0$. Waiting times are power-law distributed, $\psi(t) \sim \tau^\alpha t^{-(1+\alpha)}/|\Gamma(-\alpha)|$ ($0 < \alpha < 1$), with scaling factor τ. In our study of the aging properties of the process, we consider the number of jumps $n_a(t_a, t) = n(t + t_a) - n(t_a)$ in the interval $(t_a, t_a + t)$. In the limit of large times t_a, $t \gg \tau$, the corresponding probability density for n_a in double Laplace space, $(t_a, t) \to (s_a, s)$, becomes [30,32]

$$p(n_a; s_a, s) = \frac{\delta(n_a)}{s}\left[\frac{1}{s_a} - h(s_a, s)\right] + \frac{h(s_a, s)}{s^{1-\alpha}}\tau^\alpha e^{-n_a(s\tau)^\alpha}. \tag{3}$$

Remarkably, the occurrence of the term $\delta(n_a)$ shows that there is a nonzero probability for the particle not to perform any steps at all. To see this, note that the density of waiting times t_1 for the first jump to occur after start of the measurement at t_a is $h(s_a, s_1) = [1 - (s_1/s_a)^\alpha]/(s_a - s_1)$, i.e., $h(t_a, t_1) = [\sin(\pi\alpha)t_a^\alpha]/[\pi t_1^\alpha(t_a + t_1)]$ [30,33,34]. In the limit $\alpha \to 1$, the number of jumps n_a and real time t are equivalent, $p(n_a; t_a, t) = \delta(n_a - t/\tau)$, and τ is the typical time for a single jump to occur. In contrast, for $\alpha < 1$, Eq. (3) shows that n_a is random and varies continuously between 0 and ∞. After Laplace inversion,

$$p(n_a; t_a, t) = [1 - m_\alpha(t/t_a)]\delta(n_a) + m_\alpha(t/t_a)p_m(n_a; t_a, t). \tag{4}$$

Here, m_α is the probability to have a nonzero number of steps during $(t_a, t_a + t)$, for which [33,35]

$$m_\alpha(t/t_a) = B([1 + t_a/t]^{-1}; 1-\alpha, \alpha)/[\Gamma(1-\alpha)\Gamma(\alpha)], \tag{5}$$

with $m_\alpha \sim 1$ for $t_a \ll t$, and $m_\alpha \sim (t/t_a)^{1-\alpha}/[\Gamma(\alpha)\Gamma(2-\alpha)]$ for $t_a \gg t$. $B(z; a, b)$ is the incomplete beta function [36,37]. p_m is the conditional probability for the mobile population, i.e., for $n_a > 0$. For strong aging $t_a \gg t$, it is given in terms of a Fox H-function [37,38],

$$p_m(n_a; t_a, t) \sim \frac{\Gamma(2-\alpha)}{(t/\tau)^\alpha}H^{1,0}_{1,1}\left[\frac{n_a}{(t/\tau)^\alpha}\,\middle|\,\begin{matrix}(2-2\alpha, \alpha)\\ (0, 1)\end{matrix}\right], \tag{6}$$

which is explicitly independent of t_a. Equation (3) defines the average of any function of n_a, e.g., the qth order moment

$$\langle n_a^q(s_a, s)\rangle = \Gamma(q+1)(s_a^\alpha - s^\alpha)/[\tau^{\alpha q}s_a^\alpha(s_a - s)s^{1+\alpha q}], \tag{7}$$

used below. After dual Laplace inversion we obtain

$$\langle n_a^q(t_a, t)\rangle = \Gamma(q+1)/[\Gamma(\alpha)\Gamma(1+\alpha q-\alpha)] \times [(t+t_a)/\tau]^{\alpha q}B(t/[t+t_a]; 1+\alpha q-\alpha, \alpha). \tag{8}$$

Thus, the number of steps during a time interval t is not stationary: the moments for the period $[0, t]$ clearly differ from those for $[t_a, t_a + t]$. $\langle n_a^q(t_a, t)\rangle$ scales as $\simeq t^{\alpha q}$ at $t_a = 0$, and vanishes as $\simeq t_a^{\alpha-1}t^{1-\alpha+\alpha q}$ for $t_a/t \gg 1$.

Equations (4)–(6) show a twofold effect of aging: (i) in an ensemble of CTRW particles a finite fraction always stays immobilized during $(t_a, t_a + t)$. Only at $t_a = 0$, this effect is negligible and $p(n_a; 0, t) \equiv p_m(n_a; 0, t)$. With increasing age t_a, the population splits into two, and the mobile fraction m_α decreases algebraically towards 0 as t_a grows. (ii) Even if we solely consider the mobile

fraction, their stepping statistics, and thus p_m, change with growing t_a. Both effects have to be considered carefully when interpreting diffusion data.

Aging CTRW.—We now add the position coordinate to our description. For IID jump lengths δx_i, the jump process $x(n)$ converges to free Brownian motion in the large-n limit. The anomalous diffusion process $x(t) = x(n(t))$ inherits the aging properties of the counting process $n(t)$. Thus, consider the qth order TA moment

$$\overline{\delta^q} = \frac{1}{T-\Delta}\int_{t_a}^{t_a+T-\Delta} |x(t+\Delta) - x(t)|^q dt, \qquad (9)$$

useful to characterize experimental data [39]. For free Brownian motion $x(n)$, we know that $\langle |x(n_2) - x(n_1)|^q \rangle = 2^{1-q/2}\Gamma(q)\sigma^q |n_2 - n_1|^{q/2}/\Gamma(q/2)$. Since $x(n)$ and $n(t)$ are independent, by help of Eq. (8) the qth order TA moment becomes

$$\langle \overline{\delta^q} \rangle \simeq \frac{\Lambda_\alpha(t_a/T)\Gamma(q+1)[K_\alpha \Delta^\alpha]^{q/2}}{\Gamma(\alpha+1)\Gamma(2-\alpha+\alpha q/2)}\left(\frac{\Delta}{T}\right)^{1-\alpha} \qquad (10)$$

at $\Delta \ll T$. Here $K_\alpha = \sigma^2/(2\tau^\alpha)$ [22]. Interestingly, t_a effects only enter the prefactor $\Lambda_\alpha(t_a/T)$, generalizing Eq. (2) to arbitrary order moments. Moreover, even when t_a of different trajectories is random, the Δ scaling of $\overline{\delta^2}$ remains unaffected, only the prefactor is changed.

However, when extracting quantitative information from time series such as the diffusion constant K_α, we need to account for the population splitting. Figure 1 shows simulations results for the TAMSD, Eq. (1). For $t_a = 0$, individual $\overline{\delta^2}$ scatter around the ensemble average $\langle \overline{\delta^2} \rangle$, Eq. (10). In contrast, for the aged process ($t_a \gg T$), $\langle \overline{\delta^2} \rangle$ appears much lower than the shown individual trajectories. This is due to the fact that a significant fraction $1 - m_\alpha$ of particles do not move during the measurement. These trajectories are naturally not visible in a logarithmic plot. In an experiment, diffusivities can solely be extracted from data on the mobile particles.

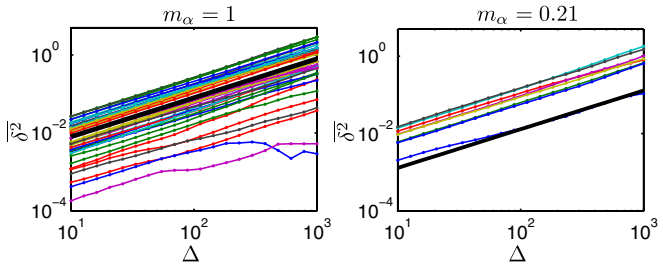

FIG. 1 (color online). TAMSD $\overline{\delta^2}$ for individual free CTRW trajectories (symbols) and theoretical mean Eq. (10) (bold black lines). Each panel is based on 40 trajectories. Left: Nonaged case, $t_a = 0$, $m_\alpha = 1$. Right: Aged process, $t_a = 1.75 \times 10^7$ arb. units: the immobile fraction $1 - m_\alpha \approx 80\%$ of trajectories are absent in the log-log plot. We chose $\alpha = 1/2$, $\tau = \sigma^2 = 1$, and $T = 2 \times 10^6$. Note that the average over the full population $\langle \overline{\delta^2} \rangle$ is not representative of the average over the mobile population.

We account for this categorization by considering the mobile fraction only, which we denote by $\langle \cdot \rangle_m$. Compare $\langle \overline{\delta^q} \rangle = \Lambda_\alpha(t_a/T)\langle \overline{\delta^q} \rangle_{t_a=0} \sim \alpha(T/t_a)^{1-\alpha}\langle \overline{\delta^q} \rangle_{t_a=0}$, where $\sim$ holds for the limit $t_a \gg T$, with the mobile average

$$\langle \overline{\delta^q} \rangle_m = \frac{\Lambda_\alpha(t_a/T)}{m_\alpha(T/t_a)}\langle \overline{\delta^q} \rangle_{t_a=0} \sim \frac{\alpha(1-\alpha)\pi}{\sin(\alpha\pi)}\langle \overline{\delta^q} \rangle_{t_a=0}. \qquad (11)$$

We see that the average over the complete ensemble ultimately indicates a suppression $\simeq (T/t_a)^{1-\alpha}$ of dynamic activity, whereas the restriction to the fraction of mobile particles significantly softens the dampening effect of aging. In the limit $t_a \gg T$, the time averages (11) are expected to be reduced merely by a constant factor compared with the nonaged case $t_a = 0$.

If we consider ratios of TA moments of the form [39]

$$\frac{\langle \overline{\delta^q} \rangle}{\langle \overline{\delta^p} \rangle} = \frac{\langle \overline{\delta^q} \rangle_m}{\langle \overline{\delta^p} \rangle_m} = \frac{a_q}{a_p}(K_\alpha \Delta^\alpha)^{(q-p)/2}, \qquad (12)$$

with $a_q = \Gamma(q+1)/\Gamma(2-\alpha+\alpha q/2)$, these are bare of any dependence on t_a or T, or restriction to mobile particles. With Eq. (12), one can experimentally determine K_α and α without having to care about aging effects.

In a biological cell, the diffusive motion of a tracer particle is spatially confined. To address such systems we determine the TAMSD in the presence of an external potential. As a generic example, we consider the harmonic potential $\lambda x^2/2$. The Langevin equation for $x(n)$ is $dx/dn = -\lambda x(n) + \xi(n)$, $\xi(n)$ being white Gaussian noise with $\langle \xi(n_1)\xi(n_2) \rangle = \sigma^2 \delta(n_2 - n_1)$ [40]. Thus, $x(n)$ is a stationary Ornstein-Uhlenbeck process. Its increments are Gaussian variables of variance $\langle [x(n_2) - x(n_1)]^2 \rangle = \sigma^2[1 - \exp(-\lambda|n_2 - n_1|)]/\lambda$. From above subordination approach, we find

$$\langle \overline{\delta^2} \rangle = \frac{\Lambda_\alpha(t_a/T)}{\Gamma(1+\alpha)}\frac{2K_\alpha \Delta}{T^{1-\alpha}} E_{\alpha,2}(-\lambda_\alpha \Delta^\alpha), \qquad (13)$$

with the generalized Mittag-Leffler function $E_{\alpha,2}$ (see the Supplemental Material [37]) and $\lambda_\alpha = \lambda/\tau^\alpha$. Asymptotically, $\langle \overline{\delta^2} \rangle \simeq \Delta$ for $\Delta \ll \lambda_\alpha^{-1/\alpha}$ and $\simeq \Delta^{1-\alpha}$ for $\Delta \gg \lambda_\alpha^{-1/\alpha}$ [21]. Despite the introduction of the intrinsic time scale $\lambda_\alpha^{-1/\alpha}$, the TAMSD for $t_a > 0$ is simply multiplied by Λ_α.

In fact, this is a general feature of the TA of a large class of observables $F(x_2, x_1)$,

$$\langle \bar{F} \rangle = \frac{1}{T-\Delta}\int_{t_a}^{t_a+T-\Delta} \langle F(x(t+\Delta), x(t)) \rangle dt, \qquad (14)$$

where the random quantity F may represent moments $[F(x_2, x_1) = |x_2 - x_1|^q]$ or correlation functions. We only require that F fulfill $\langle F(x(n_2), x(n_1)) \rangle = f(|n_2 - n_1|)$. Thus, $f(n) = \sigma^2 n$ for the second moment of unbounded motion [cf. (1)], or $f(n) = \sigma^2[1 - \exp(-\lambda n)]/\lambda$ in a harmonic potential. In these cases we find [35]

$$\langle \bar{F} \rangle = C + \frac{\Lambda_\alpha(t_a/T)}{\Gamma(1+\alpha)} \frac{g(\Delta/\tau)}{(T/\tau)^{1-\alpha}}, \tag{15}$$

for $\Delta \ll T$, with the constant $C = f(0)$. The function g is defined as $g(s) = s^{2\alpha-2}\mathcal{L}\{f(n) - f(0); n \to s^\alpha\}$ in Laplace space [32]. In the limit $\Delta \to 0$, the TA (15) reduces to the constant C, the expectation value of the observable when measured at identical positions. For example, if we study correlations in an equilibrated process, $F(x_2, x_1) = x_2 x_1$, then $C = \langle x^2 \rangle$ is the thermal value of x^2. Conversely, C naturally vanishes for TA moments of displacements, $F(x_2, x_1) = |x_2 - x_1|^q$, so it did not appear previously. We observe that the lag time dependence enters exclusively through the multiplicative function $g(\Delta/\tau)$. For example, for $f(n) \sim n^q$, $C = 0$, and we recover the previous result (10). Finally, the factor Λ_α only depends on the ratio t_a/T and the parameter α, and due to a factor $T^{\alpha-1}$ any TA converges to the constant C as $T \to \infty$. Note that this dependence on t_a and T is universal in the sense that it is indifferent to the specific choice of the observable F or model of the jump process $x(n)$, but directly follows from the nature of the aging counting process $n(t)$. In the Brownian limit $\alpha = 1$, Eq. (15) reduces to $\langle \bar{F} \rangle = f(\Delta/\tau)$, restoring the equivalence of ensemble and time averages and the stationarity.

Distribution of TAMSD.—Due to the scale-free nature of the distribution $\psi(t)$ of waiting times all TAs of physical observables, e.g., $\overline{\delta^2}$, remain random quantities, albeit with a limiting distribution $\phi(\xi)$ for the dimensionless ratio $\xi = \overline{\delta^2}/\langle \overline{\delta^2} \rangle$ [9,17,41]. As contributions to TAs of the form (1) occur at time instants when the particle performs a jump, we expect that in the sense of distributions both $\overline{\delta^2}$ and n_a should be equivalent, $\overline{\delta^2} \overset{d}{=} c n_a$, for some nonrandom, positive c. In other words,

$$\xi = \overline{\delta^2}/\langle \overline{\delta^2} \rangle \overset{d}{=} n_a(t_a, T)/\langle n_a(t_a, T) \rangle, \tag{16}$$

for $\Delta \ll T$. We may thus deduce the statistics directly from the underlying counting process. In the Supplemental Material [37] we provide numerical evidence for this argument.

The distribution $\phi(\xi)$ for $t_a = 0$ is related to a one-sided stable law [13]. For $t_a \gg T$, Eqs. (16), (4), and (6), in the limit $\Delta \ll T$ yield

$$\phi(\xi) \sim [1 - m_\alpha(T/t_a)]\delta(\xi) + m_\alpha(T/t_a)\Gamma(2-\alpha) \times \frac{(T/t_a)^{1-\alpha}}{\Gamma(\alpha)} H^{1,0}_{1,1}\left[\xi \frac{(T/t_a)^{1-\alpha}}{\Gamma(\alpha)} \middle| \begin{matrix} (2-2\alpha, \alpha) \\ (0, 1) \end{matrix} \right]. \tag{17}$$

The probability $1 - m_\alpha(T/t_a)$ for not moving during the measurement ($\xi = 0$) approaches one as $\simeq (T/t_a)^{1-\alpha}$. Figure 2 shows excellent agreement of Eq. (17) with simulations and demonstrates the qualitative changes in the probability density with growing age of the process.

Deviations from ergodic behavior are quantified by the ergodicity breaking parameter, $\mathrm{EB} = \langle \overline{\delta^2}^2 \rangle / \langle \overline{\delta^2} \rangle^2 - 1$, which is zero for an ergodic processs. Its magnitude

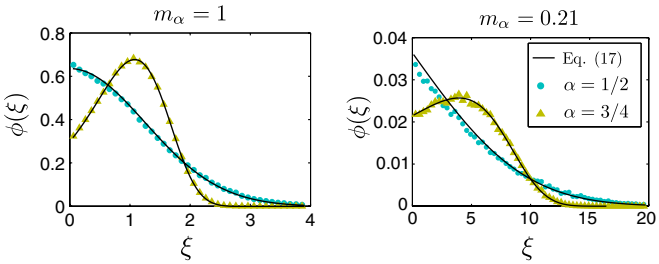

FIG. 2 (color online). Scatter density $\phi(\xi)$ for different α and m_α. Lines: Eq. (7) from Ref. [13] (Left) and Eq. (17) (Right). Symbols: Simulations of free CTRW. Note that the area under the curves for the aged process (Right) is not unity, since the fraction $1 - m_\alpha$ of immobile events is not shown. We used $\sigma^2 = \tau = 1$ arb. units, $\Delta = 100$, $T = 2 \times 10^6$, and $t_a = 1.75 \times 10^7$.

drastically depends on whether we focus on the mobile population or not. For the full ensemble we find

$$\mathrm{EB} = 2\alpha \frac{B([1 + t_a/T]^{-1}; 1+\alpha, \alpha)}{[1 - (1 + T/t_a)^{-\alpha}]^2} - 1, \tag{18}$$

while for the mobile fraction $\mathrm{EB}_m = m_\alpha(T/t_a)\mathrm{EB} - (1 - m_\alpha(T/t_a))$. If $t_a = 0$, then $0 \le \mathrm{EB} = \mathrm{EB}_m \le 1$ reduces to the bounded result of Ref. [13]. In contrast, in the strongly aged regime $t_a \gg T$, EB diverges as $\mathrm{EB} \sim 2(t_a/T)^{1-\alpha}/[\alpha(1+\alpha)]$, indicating huge fluctuations. This is mainly due to the fundamentally different dynamics of the two populations; concentrating solely on the mobile group, we find that $0 < \mathrm{EB}_m \le 1$ stays finite in the limit $t_a/T \to \infty$. Figure 3 shows the behavior of EB.

Conclusions.—We investigated the effects of aging on TAs of physical observables. Previous calculations of TAs tacitly neglect the fact that often the preparation of the system and start of the measurement do not coincide. While this does not cause any problems for ergodic systems with rapid memory loss of the initial conditions, in general this cannot be taken for granted in anomalous diffusion processes. Here we showed for the case of CTRW dynamics with scale-free waiting times that TAs of arbitrary physical observables carry the common factor Λ_α. This factor is universal in the sense that it only depends on the process age t_a and the measurement

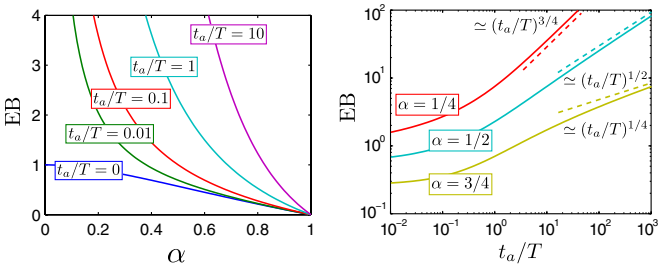

FIG. 3 (color online). Ergodicity breaking parameter (18) as function of α (Left) and t_a/T (Right). Note that the nonergodic fluctuations become larger with increasing t_a.

time T. When deducing solely the Δ scaling of the TAs from data, aging effects are of minor impact. The aging of the process, however, has a pronounced statistical effect, the population splitting into mobile (m_α) and immobile ($1 - m_\alpha$) fractions. This effect occurs despite the *a priori* identical nature of the particles in our model system. It is a direct consequence of the absence of a characteristic sojourn time in microstates, which prohibits the onset of steady state dynamics. Biological experiments [7] indeed report a complex, nonstationary mechanism for the splitting of protein mobility populations. Future studies of population splitting and its relation to the process age might therefore be worthwhile both analytically and experimentally.

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