Scaling study of diffusion in dynamic crowded spaces

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Abstract. We formulate a scaling theory for the long-time diffusive motion in a space occluded by a high density of moving obstacles in dimensions 1, 2 and 3. Our tracers diffuse anomalously over many decades in time, before reaching a diffusive steady state with an effective diffusion constant \(D_{\text{eff}}\), which depends on the obstacle diffusivity and density. The scaling of \(D_{\text{eff}}\), above and below a critical regime, is characterized by two independent critical parameters: the conductivity exponent \(\mu\), also found in models with frozen obstacles, and an exponent \(\psi\), which quantifies the effect of obstacle diffusivity.

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1. Introduction

Brownian motion in disordered media has long been the focus of much theoretical and experimental work \([1, 2, 3, 4]\). A particularly important application has more recently emerged, due to the progress in imaging and microscopy techniques, namely, transport inside the cell (see, e.g., \([5, 6, 7, 8]\) for some pioneering studies or \([9, 10, 11, 12]\) for more recent overviews). Indeed, it is now possible to track the movement of single molecules or other small particles inside living cells, with sizes ranging from small proteins to viruses, RNA molecules or ribosomes. One generally considers the mean square displacement \(\langle \Delta r^2(t) \rangle\) (MSD, the average of the squared distance traveled by the particle) and tries to fit it to a law of the form \(\langle \Delta r^2(t) \rangle \propto t^\alpha\). Some experiments in prokaryotic cytoplasms \([13, 14]\) have found evidence for this behavior with \(\alpha = 1\), characteristic of the classical Brownian (or diffusive) motion \([15]\). Many other works, however, have found signals of subdiffusive (i.e., \(\alpha < 1\)) transport \([16, 17]\). In eukaryotic cells, where
the intracellular environment is considerably more complex \[18\], heterogeneous \[19\] and crowded, the range of observed behavior is even wider \[20\] \[21\] \[22\].

On the theoretical front, in addition to the general problem of (sub)diffusion, attention has been paid to issues such as first-passage times \[23\] \[24\], driven \[25\] \[26\] \[27\] and active \[28\] \[29\] tracers, different particle shapes and boundary conditions \[30\] \[31\] \[32\]. A celebrated framework to generate anomalous diffusion is the continuum-percolation or “Swiss-cheese” model \[33\]. In it, a large number of interpenetrating obstacles, usually disks or spheres, are randomly distributed throughout the system (see Figure 1). The behavior of tracer particles is controlled by the obstacle density. For low concentration, the long-time behavior is diffusive. When the percolation threshold \[34\] \[35\] is reached, however, the system undergoes a localization transition \[36\] \[37\] \[38\] \[39\] \[40\]. The Swiss-cheese model is successful in generating (transient) anomalous diffusion in a crowded environment. From the point of view of cellular transport, however, it falls short in one crucial respect: cellular interiors are constantly rearranging themselves. This shortcoming can be addressed by considering dynamical obstacles \[41\] \[42\] \[43\] \[44\] \[45\] \[46\]. In this case, the localization transition disappears and normal diffusion is reached at any obstacle density for long times \[47\]. This regime is usually described with the aid of a theory presented by Nakazato and Kitahara \[48\], which is exact in the low- and high-density limits. For intermediate densities, however, the theory of \[48\] offers good quantitative agreement only if the obstacles move relatively fast \[49\] \[50\].

Here we take an alternative approach to the problem by considering a wide range of timescales, from very slow obstacle diffusion to the faster regimes studied by previous authors, with the goal of finding universal critical scaling behavior (see, e.g., \[51\] \[52\] \[53\] \[54\]). Using extensive numerical simulations, we compute an effective diffusion constant, $D_{\text{eff}}$, for a wide range of obstacle concentrations and diffusivities in one, two and three spatial dimensions. Even though no localization transition is observed, we find that the critical percolation point still holds a special importance. In particular, the value of $D_{\text{eff}}$ is controlled by two critical exponents: the conductivity $\mu$ \[55\], which quantifies the approach to the critical density, and an exponent $\psi$, giving the scaling with the obstacle diffusivity.

2. Model and parameters

In our model, which we implement in continuous spaces in spatial dimension $d = 1, 2$ and 3, a volumeless particle undergoes a discrete-time random walk and encounters obstacles that block its path. The obstacles are uniformly-placed possibly-overlapping $d$-balls, an arrangement that has been called the Swiss-cheese model \[33\], see Fig. 1. At each timestep, our tracer particle takes a step in a random direction (chosen isotropically) of length extracted from a Gaussian distribution with standard deviation $\sigma_p$. We set $\sigma_p = 1$ to define the unit length in the system.

The precise form of the interaction between walkers and obstacles seems, at first glance, to be a delicate issue. On second glance, however, the expectation is that it
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Figure 1. A particle traces a discrete-time random walk in two dimensions in green, blocked by frozen obstacles. At each time interval it draws a proposal for its new location from a centered Gaussian distribution. If offered a new position inside a red obstacle, the particle stays put for that timestep and attempts a new move at the following timestep. This arrangement of overlapping circular obstacles is commonly referred to as the Swiss-cheese model [33] in the case of immobile obstacles. Here, we consider the obstacles to be also Brownian particles, diffusing independently from one another.

will affect the short-time dynamics rather than the scaling properties of the asymptotic behavior of the tracers. This assertion can be rigorously motivated by the theory and experimental results on critical phenomena and the renormalization group [51, 53, 52]. Briefly stated, around a critical point, one can identify a small number of scaling variables whose evolution can encode the behavior of a complex system with many degrees of freedom. One then finds that microscopic details cease to matter and, instead, systems can be classified into a small number of universality classes, characterized only by symmetry considerations and other global features, such as the number of spatial dimensions. Hence, all the systems in the same universality class can be understood through the study of their simplest representative. The most celebrated example of this universality is the Ising model, naively a toy representation of magnetic interactions, but which quantitatively explains experimental results not only in ferromagnetic systems, but also for the liquid-gas transition, and for binary fluids [54].

We are motivated to employ this approach here by the known results for diffusion in a static disordered medium. In this case, as we shall explain below, the system experiences a phase transition and, hence, universal scaling behavior as it approaches a percolation limit. This scaling is characterized by a critical conductivity exponent $\mu$, so called because it can account for the behavior of conductivity of conductor/superconductor mixtures as well as for that of random walks in a static,
crowded environment \[56\].

With these considerations in mind, we shall define simple interaction rules. If we then find power-law dependences for the diffusion constant, the resulting critical exponents—or, in other words, our results for the long-time behavior of the diffusivity—will be applicable to systems with more realistic interactions. Therefore, we simply have the particle stop if its proposed new location would be inside one of the obstacles. To avoid situations where the particle can jump over obstacles, we fix the obstacle radius as \(R = 10 \gg \sigma_p\). The obstacles themselves also move, ignoring interactions and always drawing their discrete steps from a Gaussian distribution with standard deviation \(\sigma_{\text{obs}} \leq \sigma_p\). To deal with situations where the void pocket inhabited by a particle becomes entirely squeezed, obstacles can “step on” particles, in which case the particle stops all motion until the obstacle moves off of it.

We are interested in how well the particle can explore the empty space, as measured by the mean square displacement after \(t\) timesteps,

\[
\langle \Delta r^2(t) \rangle = \langle [r(t + t_0) - r(t_0)]^2 \rangle.
\]

As discussed in the introduction, when the MSD grows linearly with time, we say the motion is diffusive and characterize it by a diffusion constant \(D\), defined through the equation \(\langle \Delta r^2(t) \rangle = 2dDt\), where \(d\) is the spatial dimension.

The first control parameter in this model is the dimensionless obstacle density, \(\hat{n} = nR^d\), where \(n\) is the number density of obstacle centers. In previous works, in which the obstacles are frozen, at low obstacle densities the MSD is governed by three different behaviors at varying time scales \[37, 39\]. These time scales have also been observed empirically in biological systems \[57\].

In these cases, at microscopic time scales, particles do not encounter obstacles and diffuse freely. This gives us another characteristic parameter: the short-term diffusivity of the tracers, \(D_p = \sigma_p^2/2d\). If there were no obstacles at all, we would recover \(\langle \Delta r^2(t) \rangle = 2dD_p t\).

At intermediate time scales, the system experiences subdiffusive motion, meaning \(\langle \Delta r^2(t) \rangle \sim t^\alpha, \alpha < 1\). Finally, for long times, the central limit theorem causes the MSD to revert to linear growth, \(\langle \Delta r^2(t) \rangle \sim 2dD_{\text{eff}} t\) with \(D_{\text{eff}} \ll D_p\) \[11\].

In frozen models, this third window of diffusive motion recedes as \(\hat{n}\) approaches a critical value, \(\hat{n}_c\), at which point it disappears entirely. This localization transition takes place at the percolation point \(\hat{n}_c\) of the obstacles, when an infinite cluster partitions space into finite, disconnected pockets \[34, 35\]. The critical scaling of \(D_{\text{eff}}\) is controlled by a conductivity exponent \(\mu\) \[35, 50, 37\]

\[
D_{\text{eff}} \propto (\hat{n}_c - \hat{n})^\mu,
\]

with \(D_{\text{eff}} = 0\) in the supercritical regime \(\hat{n} \geq \hat{n}_c\). For \(d = 2\) and \(3\), the critical density has been calculated to be \(\hat{n}_c = 0.359\) \[58, 59\] and \(0.839\) \[60\], respectively. We also see that \(\hat{n}_c = 0\) trivially in \(d = 1\), because localization occurs once a single frozen obstacle appears.
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Figure 2. Time-dependent diffusion coefficient $D(t)$, eq. (3), in $d = 2$ at approximately critical obstacle density for various obstacle diffusivities. Diffusivities are shown in units of the characteristic particle diffusivity $D_p$. In this representation, diffusive motion is characterized by a constant $D(t)$. Such a regime is always reached for long times in our model, no matter the obstacle density, defining an effective diffusion constant $D_{eff}$. The inset shows a closeup of the approach to this steady-state behavior for $D_{obs}/D_p = 10^{-2.4}$. All curves in this plot are averaged over 24 independent simulations, each with 360 tracer particles.

In our model with moving obstacles, as has been observed [41, 44], particles never become localized because the obstacles themselves will eventually move out of the way. We expect, thus, to find these three time windows at all obstacle densities, matching the biological observations. As we shall demonstrate, however, $n_c$ still carries a special significance, so we continue to refer to $n < n_c$ ($n > n_c$) as the subcritical (supercritical) regime.

The second control parameter is the diffusivity of the obstacles, $D_{obs}$. This will generally be much lower than $D_p$ (otherwise, with our rules, the tracers’ movement would become enslaved to the obstacles). To optimize our simulations, we only move the obstacles every 10 time steps, giving us $D_{obs} = \sigma_{obs}^2/20d$. As $D_{obs} \to 0$ we recover the frozen models [4].

3. Results in $d = 2$

We use a simulation box of linear size $L = 1000$ with periodic boundary conditions. Given the annealed nature of our disorder, this is more than enough to avoid finite-size effects (see Appendix A). Since we are interested in the asymptotic behavior, we

‡ We have checked this explicitly by computing fits to (2) and confirming that our $\mu$ is compatible with the values in the literature.
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We need to follow our tracers for very long times in order to obtain good statistics; we use $1.2 \times 10^9$ time steps. The MSD for each tracer is calculated according to eq. \(1\), for values of \textit{t} chosen as powers of 2 and with \textit{t}_0 ranging over multiples of $10^6$. Thus we averaged the distance traveled by a single particle across a shifting time window, with each $10^6$ steps as a different starting time. We gave the system a $10^7$ timestep “burn-in” period, in which data was not collected to allow the system to converge to its stationary distribution. We further improved our estimate of $\langle \Delta r^2(t) \rangle$ by launching 360 independent tracers in a single simulation, and ran 24 separate simulations for each pair of $\sigma_{obs}, \hat{n}$ values, so that the configuration and motion of obstacles can vary from system to system.

We describe the motion of the particle over time with a time-dependent diffusion coefficient,

\[
D(t) = \frac{\langle \Delta r^2(t) \rangle}{2dt\phi}.
\]

This definition is similar to that of \[39\], with one key difference: because some particles are trapped under obstacles at any given moment and therefore not moving, time must be rescaled by the proportion of particles that are free, or $\phi = e^{-\pi\hat{n}}$ in $d = 2$. A similar argument was made in \[61, 62\]. This allows us to recover $D(t) \approx D_p$ for very small $t$, and also allows our results to approach the proper values in the limit of $D_{obs} \to 0$.

Figure 2 displays the evolution of $D(t)$ over time for simulations at $\hat{n} \approx \hat{n}_c$ (similar plots in the sub- and supercritical regime are included in Appendix B). We are interested in the asymptotic value $D_{\text{eff}} = \lim_{t \to \infty} D(t)$, which, as discussed above, can be reached for any $\hat{n}$.

We estimate $D_{\text{eff}}$ by fitting $\langle \Delta r^2(t) \rangle$ to a constant for $t \geq 229$. Error bars are computed with a bootstrap method \[63\]. The resulting values are plotted in Figure 3–left. For $\hat{n} < \hat{n}_c = 0.359$, as $D_{obs} \to 0$, $D_{\text{eff}}$ must eventually plateau at the values found by the frozen-obstacle models. On the other hand, for $\hat{n} \geq \hat{n}_c$, $\lim_{D_{obs} \to 0} D_{\text{eff}} = 0$. As a consequence, in our log-log plots, curves for $\hat{n} < \hat{n}_c$ are concave and those for $\hat{n} > \hat{n}_c$ are convex. Remarkably, at precisely $\hat{n}_c$, $D_{\text{eff}}$ follows a power law

\[
D_{\text{eff}} \propto D_{\text{obs}}^\psi, \quad \hat{n} = \hat{n}_c.
\]

A fit to eq. \(4\) (see inset to Figure 3) yields $\psi = 0.274(2)$ with and excellent goodness-of-fit value of $\chi^2$/d.o.f. = $6.42/6$ [d.o.f. = degrees of freedom]. Our numerical finding of a power-law behavior for $D_{\text{eff}}$ suggests that our model could exhibit critical scaling even in the case of moving obstacles, with the addition of a critical exponent $\psi$ that encodes the dependence on obstacle diffusivity just as $\mu$ encodes the effect of obstacle density.

Combining eq. \(4\) with eq. \(2\), we can formulate the following ansatz for the critical scaling in our model:

\[
\frac{D_{\text{eff}}}{D_p} \simeq |\epsilon|^\mu g_\pm \left[ (D_{\text{obs}}/D_p) |\epsilon|^{-\mu/\psi} \right],
\]

\(\S\) Equivalently, $\phi = e^{-2\hat{n}}$ in $d = 1$ and $\phi = e^{-4\pi\hat{n}}$ in $d = 3$. 

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Figure 3. Left: Effective diffusion coefficient against the diffusion coefficient of the obstacles for many obstacle densities in \(d=2\). The percolation density is \(\bar{n}_c \approx 0.359\). Right: Scaling behavior in \(d=2\) of \(D_{\text{eff}}\) around the critical point, \(\bar{n}_c \approx 0.359\), according to eq. (5). We take our value of the conductivity exponent, \(\mu = 1.31\), from [56]. The dynamic exponent \(\psi\) is computed with a critical fit to \(D_{\text{eff}} \propto D_{\text{obs}}^{\psi}\) at \(\bar{n} = \bar{n}_c\) (inset), yielding \(\psi = 0.274(2)\) with \(\chi^2/\text{d.o.f.} = 6.42/6\). Using these exponents, the data collapse in the main panel, with separate branches for the supercritical and subcritical regimes, is achieved without adjustable parameters.

Figure 4. As in Figure 3 but in \(d=3\). Now \(\bar{n}_c \approx 0.84\) and \(\mu \approx 2.88\) [64, 57]. Our critical fit results in \(\psi = 0.520(3)\), with \(\chi^2/\text{d.o.f.} = 7.87/5\).

where \(\epsilon = (\bar{n} - \bar{n}_c)/\bar{n}_c\) and \(g_{\pm}(x)\) are the scaling functions that describe the behavior in the sub- and supercritical regimes. Asymptotically, we expect \(g_{\pm}(x) \sim x^\psi\) as \(x \to \infty\), and \(g_{\pm}(x) \sim \text{const.}\) as \(x \to 0\). Thus, in the subcritical regime, we recover eq. (2) as in studies with frozen obstacles. Using \(\mu = 1.3100(11)\) [56] and our previously computed \(\psi\), eq. (5) collapses all our data without any adjustable parameters, see Figure 3 right.

4. Results in \(d=3\)

We ran analogous simulations in \(d=3\). To keep the wall-clock time of our runs under control, we reduced the simulation box to \(L = 200\), and launched 320 tracers in each system. To avoid finite-size effects, we further slowed the obstacles by only moving...
them once every 100 steps. We follow the same procedure as in $d = 2$ to compute $\psi = 0.520(3)$, see Figure 4.

One difference between $d = 2$ and $d = 3$ is that in the latter case, universality breaks down between lattice and continuum percolation models, so $\mu \neq \mu_{\text{lat}}$ [33]. There is, hence, some disagreement on the value of $\mu$ in $d = 3$. Following the analysis in [64, 37] we have used $\mu = 2.88$, which produces an excellent collapse of our data (see Figure 4).

5. Results in $d = 1$

The one-dimensional case has considerable theoretical interest. Now tracers become localized at $n_c = 0$, so there is no subcritical regime. For our non-frozen model, particles are not localized because they can follow the obstacles as they move, or let an obstacle pass over them. We see, therefore, that $\psi = 0$ trivially.

In order to understand the scaling of $D_{\text{eff}}$ in $d = 1$, we begin by considering several limits. First, when $\hat{n} \to 0$, $D_{\text{eff}} \to D_p$. Second, when $D_{\text{obs}} \to 0$ we approach the frozen limit with $D_{\text{eff}} = 0$. Finally, $\lim_{\hat{n} \to \infty} D_{\text{eff}} = D_{\text{obs}}$. The latter is because, for dense enough obstacles, the tracer’s motion is entirely governed by how quickly the obstacles let it through. With these in mind, and remembering that $\phi = e^{2\hat{n}}$, we propose the following ansatz: $D_{\text{eff}} = D_{\text{obs}}D_p/[D_p(1 - \phi) + D_{\text{obs}}]$. This is equivalent to using a different scaling variable than was used in $d = 2$ and $d = 3$, namely $\epsilon_{\phi} = (\phi - \phi_c)/\phi_c = \phi - 1$, and writing

$$D_{\text{eff}}/D_p = g[(D_{\text{obs}}/D_p) |\epsilon_{\phi}|^{-1}], \quad g(x) = \frac{x}{1 + x}. \quad (6)$$

Figure 5 shows that eq. (6) is an excellent match to our data over a very wide range of $\phi$.

6. Conclusions

We have performed a comprehensive investigation of diffusion in the void space of a dynamic version of the Swiss-cheese model in dimensions one through three. We have characterized the critical point governing the anomalous diffusion using two exponents, one of which is the traditional conductivity exponent $\mu$, and the other of which we call $\psi$. The latter exponent describes scaling of the effective diffusivity at precisely the critical obstacle density. For dimensions one through three we find $\psi = 0$, $\psi = 0.274(2)$ and $\psi = 0.520(3)$, respectively.

Together, $\mu$ and $\psi$ can be used to encode the quantitative behavior of the system for a wide range of obstacle densities and diffusivities. The physics of critical phenomena and the renormalization group suggests that this scaling, which covers several orders of magnitude in the mobility of the obstacles, will be universal, so our results should be directly relevant to the interpretation of cellular transport and other experiments on crowded spaces.

Our scaling theory may have implications for a very different kind of system: the low-temperature phase of spin ice [65, 66]. These compounds produce emergent magnetic
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Figure 5. Effective diffusion constant in $d = 1$. We plot our $D_{\text{eff}}$ rescaled according to eq. (6). Notice that now all densities $\hat{n} > 0$ are supercritical. The inset shows the unscaled data.

monopoles [67] whose dynamical behavior leads to an anomalous noise spectrum [68,69], characterized by a scaling as $1/f^{1.5}$, different from the $1/f^{2}$ of a paramagnetic system. For the case of Dy$_2$Ti$_2$O$_7$, this spectrum has been explained through the presence of a subset of spins with a near-vanishing transverse field, whose flips are forbidden, which severely constrains the movement of the monopoles [70]. The resulting percolation picture maps onto the problem of diffusion of a particle in a space of static obstacles. Other spin-ice compounds, such as those based on holmium, can generate very different transverse-field distributions. In these cases, the timescale of the slow spins can no longer be taken to infinity [70,71] and has to be explicitly considered in the scaling. The scaling theory presented here for a dynamic crowded space can provide such a quantitative description.

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Appendix A. Finite-Size Effects

Our model does not suffer from strong finite-size effects, probably thanks to the annealed nature of the disorder. Therefore, our simulations for $L = 1000$ should be representative of the large-$L$ limit. We have, nevertheless, explicitly checked against finite-size effects by repeating our $\hat{n} = \hat{n}_c$ simulations for a smaller system size ($L = 500$) and verifying that we get the same $D(t)$ curve as in Figure 2. This is shown in Figure A1. For all $D_{\text{obs}}$ the resulting $D_{\text{eff}}$ is the same in the $L = 500$ system, but the data is noisier. Moreover, ultimately the strongest proof for the absence of finite-size effects is the fact that the power-law fits in Figures 3 and 4 satisfy a $\chi^2$ test.

Appendix B. Time evolution in the sub- and supercritical regimes

Figure 2 shows $D(t)$ for many obstacle diffusivities at $\hat{n} \approx \hat{n}_c$. In Figure B1 we reproduce the same plot for a subcritical density ($\hat{n} = 0.2$) and a supercritical one ($\hat{n} = 0.4$). The resulting plots are qualitatively the same as Figure 2. Notice in particular that, even in the supercritical case, above the percolation point, the diffusive regime is eventually reached.

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Figure A1. Same as Figure 2 but adding data for a smaller system size ($L = 500$). Since the curves for $L = 1000$ and $L = 500$ are identical for the whole $t$ range, we have only plotted most of the small simulations up to $t = 2^{26}$ for visualization purposes. The exception is $D_{\text{obs}}/D_p = 10^{-2.4}$, enlarged in the inset. The $L = 500$ curve are noisier for long $t$ where there are few $t_0$ to compute the MSD.
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Figure B1. Left: Same as Figure 2 but for a subcritical obstacle concentration ($\hat{n} = 0.2$). Right: Same as Figure 2 but for a supercritical obstacle concentration ($\hat{n} = 0.4$). The inset shows that the long-time diffusive regime [constant $D(t)$] is clearly reached.

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