# The topography of the environment alters the optimal search strategy for active particles 

Giorgio Volpe ${ }^{\text {a, } 1}$ and Giovanni Volpe ${ }^{\text {b }}$<br>a Department of Chemistry, University College London, London WC1H 0AJ, United Kingdom; and bepartment of Physics, University of Gothenburg, 41296 Gothenburg, Sweden

Edited by David A. Weitz, Harvard University, Cambridge, MA, and approved September 18, 2017 (received for review June 26, 2017)


#### Abstract

In environments with scarce resources, adopting the right search strategy can make the difference between succeeding and failing, even between life and death. At different scales, this applies to molecular encounters in the cell cytoplasm, to animals looking for food or mates in natural landscapes, to rescuers during search and rescue operations in disaster zones, and to genetic computer algorithms exploring parameter spaces. When looking for sparse targets in a homogeneous environment, a combination of ballistic and diffusive steps is considered optimal; in particular, more ballistic Lévy flights with exponent $\alpha \leq 1$ are generally believed to optimize the search process. However, most search spaces present complex topographies. What is the best search strategy in these more realistic scenarios? Here, we show that the topography of the environment significantly alters the optimal search strategy toward less ballistic and more Brownian strategies. We consider an active particle performing a blind cruise search for nonregenerating sparse targets in a 2D space with steps drawn from a Lévy distribution with the exponent varying from $\alpha=1$ to $\alpha=2$ (Brownian). We show that, when boundaries, barriers, and obstacles are present, the optimal search strategy depends on the topography of the environment, with $\alpha$ assuming intermediate values in the whole range under consideration. We interpret these findings using simple scaling arguments and discuss their robustness to varying searcher's size. Our results are relevant for search problems at different length scales from animal and human foraging to microswimmers' taxis to biochemical rates of reaction.


optimal search strategy | complex topographies | active particles | Lévy walks | anomalous diffusion

What is the best strategy to search for randomly located resources? This is a crucial question for fields as diverse as biology, genetics, ecology, anthropology, soft matter, computer sciences, and robotics (1,2). To describe and analyze how a searcher browses the search space, many different plausible models have been proposed, including Brownian motion and intermittent search patterns as well as Lévy flights and walks (1-3). In particular, Lévy statistics, among others models (1), have been successfully used to describe the emergence of optimal search strategies in natural systems at different length scales, from molecular entities $(4,5)$ to swimming and swarming microorganisms $(6-$ 8 ) to crawling eukaryotic cells (9) to different species of foraging animals (10-16) to human motion patterns (17-19), although in the field of movement ecology there is some controversy on how universal Lévy searches are (20-25). Lévy statistics have also found applications in science and engineering [e.g., for defining the optimal search strategy for robots (26) and for describing anomalous diffusion and navigation on networks $(27,28)]$.
The strategies based on Lévy statistics can be described under a unified framework, where the searcher is an active particle (29) that performs random jumps (blind search) with lengths $\ell$ that are drawn from a stable distribution $P(\ell)$. The two limiting cases for $\alpha \rightarrow 0$ and $\alpha=2$ correspond to ballistic and Brownian motion, respectively. The intermediate cases combine diffusive (i.e., local exploration) and ballistic (i.e., decorrelating, long-range excursions) steps in different proportions. In particu-
lar, the case for $\alpha=1$ corresponds to a compromise superdiffusive regime, where the searcher explores its surroundings while reducing oversampling compared with a pure Brownian strategy $(2,11,30)$. When resources are plentiful, the most efficient strategy is a Brownian search $(\alpha=2)(11,14,15)$; when resources are sparse, however, a Lévy strategy with $\alpha=1$ performs better over a pure Brownian strategy (2). In general, more ballistic search strategies (i.e., $\alpha \leq 1$ ) have been shown to be optimal in a wide range of situations, with the specific value of the exponent $\alpha$ dependent on, for example, the nature of the encounters with the targets (i.e., destructive or nondestructive) or the presence of memory in the searcher's motion (11, 23, 31-35).
These studies have limited their analysis to landscapes characterized by a barrier-free homogenous topography. However, in realistic scenarios, the environment is often characterized by a more complex topography, where boundaries, barriers, and obstacles play a crucial role in determining the searcher's motion. Examples of complex search spaces include cytoplasm for molecules within cells (36), biological tissue (or soil) for motile bacteria (37), and patchy landscapes for foraging animals (38). This complexity can significantly influence the longterm behavior of the system under study (39). As it has been recently shown, even a small perturbation, such as an external drift, can shift the optimal search strategy toward more Brownian strategies (40).

Here, by considering a searcher performing a blind cruise search for uniformly distributed nonregenerating sparse targets, we show with numerical simulations and simple scaling arguments that the exponent that optimizes the search strategy depends on the topography of the environment. In particular, we show that, different from the homogeneous case where typically $\alpha \leq 1$ optimizes the search process, the optimal search strategy

## Significance

Adopting the right search strategy is of critical importance in a broad range of natural and man-related activities. For example, when foraging in an environment with scarce resources, the search strategy used by animals to look for nourishment is a matter of life or death. It is generally accepted that, under most conditions, the optimal strategy alternates ballistic and diffusive steps. This, however, does not take into account that many search spaces feature complex topographies with boundaries, barriers, and obstacles. Here, we show that the presence of such complexity shifts the optimal strategy toward less ballistic and more diffusive searches.

[^0]tends toward less ballistic and more Brownian cases, corresponding to values for the exponent $\alpha$ in the range (1, 2].

## Results

Search in a Homogenous Topography. We start by analyzing an active particle of radius $R$, blindly searching for targets in an environment with a homogeneous topography (i.e., without any physical obstacles). As the active particle cruises the search space, it continuously captures the targets that come within a capture radius $r_{\mathrm{c}}=2 R$ from its center, as schematically shown in Fig. 1A. The number of targets caught in each run is proportional to the area swept by the capture region surrounding the active particle. We assume the targets to be uniformly distributed, nonregenerating, and scarce (i.e., with density $\rho \ll r_{\mathrm{c}}^{-2}$ ). The latter condition implies that, after an active particle captures a target, the probability of finding a second one is negligible if the particle moves by $\ell \lesssim r_{\mathrm{c}}$.
The active particle performs a run-and-tumble motion (i.e., it has a fixed speed $v$ and changes its orientation $\varphi$ by a nor-


Fig. 1. Optimal search strategy in a homogenous topography. (A) Schematic representation (not to scale) of an active particle of radius $R$ blindly searching for uniformly distributed targets (dots) in a homogenous environment. The particle placed at position $[x, y]$ moves with constant speed $v$ and variable orientation $\varphi$. The capture radius is $r_{c}$ (gray shaded area). (B) The time intervals $t_{n}$ with $n=0,1,2, \ldots$ between changes of orientation $\varphi$ are drawn from a Lévy distribution $P_{\alpha}(t)$ of exponent $\alpha \in[1,2]$. The solid lines represent power laws of exponent $-\mu=-(\alpha+1)$ for the two limiting cases at $\mu=2(\alpha=1)$ and $\mu=3(\alpha=2)$. Note that, for the case $\alpha=2$, the distribution is a Gaussian, which is not a power law asymptotically. (C) Four different 1,000 -s trajectories with a common origin are shown for various values of $\alpha$. The black scale bar corresponds to 1,000 . (D) Average number of caught targets (circles) as a function of $\alpha$ in normalized units (n.u.). The values are averaged over 1,000 1-h trajectories and normalized to the maximum value at $\alpha=1$. The gray shaded area represents one SD around the average values.
mally distributed angle with zero mean and $\mathrm{SD} \sigma_{\varphi}$ at discrete time intervals $t_{n}$ with $\left.n=0,1,2, \ldots\right)(29)$. In the following, we set $v=5 R \mathrm{~s}^{-1}$ and $\sigma_{\varphi}=\pi / 6$. The time intervals $t_{n}$ between changes of direction are drawn from a Lévy distribution $P_{\alpha}(t)$ of exponent $\alpha \in[1,2]$ (Fig. 1B) (2). Asymptotically, this distribution tends to a power law with exponent $-(\alpha+1)$ for $\alpha \in[1,2)(2)$ :

$$
\begin{equation*}
P_{\alpha}(t) \approx A(\alpha) t^{-(\alpha+1)} \text { for } t \rightarrow \infty \tag{1}
\end{equation*}
$$

where $A(\alpha)$ is a normalization constant, such that $\int_{0}^{\infty} P_{\alpha}(t) d t=$ 1 ; for $\alpha=2$, the distribution is a Gaussian, which decays exponentially in $t$. As $v$ is constant, the run lengths $\ell_{h}\left(t_{n}\right)=v t_{n}$ are also distributed according to a Lévy distribution of same index $\alpha$, thus leading the particle to move superdiffusively for $\alpha<2$ and diffusively for $\alpha=2$ at long times (Fig. S1A) (2). Examples of trajectories for various values of $\alpha$ are shown in Fig. 1C: as $\alpha$ decreases from the case of a pure Brownian strategy $(\alpha=2)$, the searchers tend to move ballistically over longer distances before a change in orientation occurs. These different superdiffusive regimes allow the searcher to explore the overall search space, combining ballistic and diffusive steps in different proportions $(2,11,30)$. Fig. $1 D$ plots the average number of caught targets $\left\langle N_{\mathrm{h}}\right\rangle$ obtained from 1,000 simulated 1-h trajectories as a function of $\alpha$. This number decreases as a function of $\alpha$, so that the optimal search strategy is for $\alpha=1$, while the worst is the Brownian ( $\alpha=2$ ), in agreement with foraging theory (2).

Search in a Porous Topography. To understand how the complexity of the environment influences the optimal search strategy, we now consider an active particle looking for targets in a medium with a heterogeneous topography (Fig. 2A). Specifically, the search space is now a 2D porous medium composed of uniformly distributed circular interconnected pores with average radius $R_{\mathrm{p}} \gg r_{\mathrm{c}}$; the characteristic size of a cluster of pores is much bigger than the total particle's displacement within the simulation time. We model the interaction with the pore walls using reflective boundary conditions, so that the particle moves along the walls until its orientation changes to point away from the boundary (41). This scenario is realistic at different length scales, as indeed, both biological and artificial microswimmers and elementary robots behave in a similar way $(29,42)$.

As it can be seen in Fig. 2B, moving in such a porous environment shifts the optimal search strategy toward a more Brownian strategy ( $\alpha=1.3$ ) from the more ballistic case in the homogenous topography $(\alpha=1)$. This shift can be understood in quantitative terms by looking at the effective probability distribution of the run lengths $P_{\mathrm{p}, \alpha}(\ell)$ in the porous medium (Fig. 2C). This distribution is well-approximated by a power law with an exponential cutoff at $R_{\mathrm{c}}=\lambda R_{\mathrm{p}}$ :

$$
\begin{equation*}
P_{\mathrm{p}, \alpha}(\ell) \approx B(\alpha, v) \ell^{-(\alpha+1)} e^{-\frac{\ell}{R_{\mathrm{c}}}} \text { for } \ell \rightarrow \infty \tag{2}
\end{equation*}
$$

where $B(\alpha, v)$ is a normalization constant, such that $\int_{0}^{\infty} P_{\mathrm{p}, \alpha}(\ell)$ $d \ell=1$, and $\lambda$ is a proportionality constant; $\lambda \approx 2.4$ is estimated by fitting the previous function to the simulated data and in general, depends on the geometrical features of the medium. As a result of this interaction with the boundaries, therefore, the porosity affects longer run lengths more than shorter ones, thus mainly penalizing the more ballistic strategies over the more Brownian ones. In other terms, even if the changes in the particle's orientation are still dictated by the distributions in Fig. $1 B$, the boundaries effectively limit the maximum run length, leading the particles to perform a subdiffusive motion rather than a superdiffusive one as in the homogenous environment (Fig. S1B); this behavior is in accordance with observations on persistent random walkers in the presence of obstacles (43). Qualitatively, this can also be appreciated by looking at some sample trajectories for different values of $\alpha$ (Fig. 2D): when $\alpha$ decreases, the particles tend to spend longer portions of their


Fig. 2. Shift of the optimal search strategy in a porous topography. (A) A sample area of an extended 2D porous medium, where an active particle searches for uniformly distributed targets (dots). The porous medium is composed of circular interconnected pores of average radius $R_{\mathrm{p}}\left(R_{\mathrm{p}} / r_{\mathrm{c}} \approx 12.5\right)$. ( $B$ ) Average number of caught targets $\left\langle N_{p}\right\rangle$ (squares) as a function of $\alpha$ in normalized units (n.u.). The values are averaged over 1,000 1-h trajectories and normalized to the maximum value at $\alpha=1.3$. The gray shaded area represents one SD around the average values. To directly compare with the homogenous case, the trend of Fig. 1D is also shown (circles). (C) Simulated probability distribution of the run lengths $P_{\mathrm{p}, \alpha}(\ell)$ in the porous medium as a function of $\alpha$ (dots). The distributions are fitted to a power law with an exponential cutoff for $\alpha \in\left[1,2\right.$ ) (Eq. 2) (dashed lines). The vertical dashed line represents the cutoff $R_{\mathrm{C}}$. $(D)$ Four different 1,000-s trajectories with a common origin are shown for different values of $\alpha$. All black scale bars correspond to $50 R$.
trajectories at the walls, thus exploring less efficiently the inner area of the pores. It is interesting to note that, at least when the searcher explores the complex topography for a finite time as in our simulations, the average shift in the optimal search strategy depends on the pore characteristic size, while it is largely independent of the density of pores and the local configuration of the explored cluster (Fig. S2).

Scaling Arguments. To formalize the shift in the optimal search strategy caused by the topography of the environment, we define the efficiency $\eta$ of catching targets in the porous medium compared with the homogeneous case as

$$
\begin{equation*}
\eta(\alpha, v)=\frac{\left\langle N_{\mathrm{p}}(\alpha, v)\right\rangle}{\left\langle N_{\mathrm{h}}(\alpha, v)\right\rangle} . \tag{3}
\end{equation*}
$$

Since the mean square displacement of the active particle is of order $t^{3-\alpha}$ in a homogenous topography, self-intersections constitute a negligible fraction of the overall path for $\alpha<2$, which is closely related to the fact that the Hausdorff dimension of a Lévy process in the plane is equal to its exponent $\alpha$ (44); this is also the case in the porous topography for run lengths just below the spatial cutoff (Fig. 2C), which contribute with higher probability to the capture of new targets. As a consequence, to a first approximation, we obtain that the target capture rate is proportional to the average step length for a given topography and a given $\alpha$, so that

$$
\begin{equation*}
\eta(\alpha, v)=\frac{\left\langle\ell_{\mathrm{p}}(\alpha, v)\right\rangle}{\left\langle\ell_{\mathrm{h}}(\alpha, v)\right\rangle}=\beta(v)\left[1-(1-\gamma)\left(\frac{T_{\mathrm{c}}}{t_{\mathrm{c}}}\right)^{-\alpha+1}\right] \tag{4}
\end{equation*}
$$

where $\beta(v) \in[0,1]$ is a function of the particle speed, $\gamma \in[0,1]$ is a constant, $T_{\mathrm{c}}=R_{\mathrm{c}} / v, t_{\mathrm{c}}=r_{\mathrm{c}} / v$, and $\left\langle\ell_{\mathrm{p}}(\alpha, v)\right\rangle$ and $\left\langle\ell_{\mathrm{h}}(\alpha, v)\right\rangle$ are the average step lengths in the porous and homogenous topography, respectively (Materials and Methods discusses their calculation).

While Eq. 4 explicitly depends on the particle's speed $v$ through $\beta(v)$, the normalized efficiency $\eta^{*}$ defined as

$$
\begin{equation*}
\eta^{*}(\alpha)=\frac{\eta(\alpha, v)}{\max (\eta \mid v)} \approx \frac{\eta(\alpha, v)}{\beta(v)}=1-(1-\gamma)\left(\frac{T_{\mathrm{c}}}{t_{\mathrm{c}}}\right)^{-\alpha+1} \tag{5}
\end{equation*}
$$

is a universal curve that does not directly depend on $v$. Interestingly, from this equation, the geometrical meaning of $\gamma$ is apparent as the percentage of time that the particle spends running instead of being stuck at a boundary above the spatial cutoff $R_{\mathrm{c}}$.
Using Eq. 5, we can, therefore, estimate the shift in the optimal search strategy caused by the topography of the environment by finding the maximum of $\eta^{*}(\alpha)\left\langle N_{\mathrm{h}}(\alpha)\right\rangle$ [i.e., only based on geometrical parameters $\left(t_{\mathrm{c}}, T_{\mathrm{c}}\right.$, and $\gamma$ ) and the knowledge of the particle's behavior in a homogenous topography $\left.\left\langle N_{\mathrm{h}}(\alpha)\right\rangle\right]$. As shown in Fig. 3A, Eq. 5, where $y$ is the only fitting parameter, reproduces very well the simulated data, and allows us to predict correctly the optimal value for the capture rate in the porous medium from $\left\langle N_{\mathrm{h}}(\alpha)\right\rangle$ (Fig. 3B). By comparing model predictions (Fig. 3C) with simulated data (Fig. 3D), Fig. $3 C$ and $D$ shows how, after $\gamma$ is known, this simple model based on scaling arguments predicts correctly the optimal strategy in the porous medium at any particle speed. Fig. 3 shows that, for a given $\gamma$, the speed at which the particle moves within the environment also has an effect on the optimal search strategy: for low values of speed, the optimal search strategy shifts toward the more ballistic case $(\alpha=1)$, as the particle tends to interact with the boundaries only at very long times, thus mostly moving as in an effectively homogenous environment; however, when $v$ increases, the optimal search strategy shifts more and more toward the Brownian case ( $\alpha=2$ ), since this case is the one that minimizes the interaction with the boundaries over time.
For additional confirmation of the fact that the shift in optimal search strategy is caused by the upper spatial cutoff introduced by the topography of the environment, we now consider a porous medium with a convex topography instead of the concave topography considered previously (Fig. 2A). In this topography, the particle searches for uniformly distributed targets within an interconnected space containing convex obstacles where there is no upper cutoff (i.e., $R_{\mathrm{c}} \rightarrow \infty$ ) (Fig. $4 A$ ). Also, in this case, the average radius of the obstacles $R_{\mathrm{p}}$ is chosen, so that $R_{\mathrm{p}} / r_{\mathrm{c}} \approx$ 12.5 . As expected, the optimal search strategy remains at $\alpha=1$ (Fig. $4 B$ ) as for a particle searching in a homogenous space (Fig.


Fig. 3. Influence of the topography on the optimal search strategy: comparison between simulated data and model. (A) Normalized efficiency $\eta^{*}$ : simulations (circles) and fit to Eq. 5 (dashed line). (B) Average number of caught targets in the porous environment $\left\langle N_{p}\right\rangle$ as a function of $\alpha$ : simulations (circles) and fit to the model (dashed line). (C) Model prediction and ( $D$ ) simulated data of the average number of caught targets in the porous environment $\left\langle N_{\mathrm{p}}\right\rangle$ in normalized units (n.u.) as a function of $\alpha$ and normalized speed $v / R(\gamma=0.47)$.
$1 D)$. In qualitative terms, these results can be interpreted by observing sample trajectories for various values of $\alpha$ (Fig. 4C): in fact, as can be appreciated from these trajectories, the convex porosity does not prevent the particles from moving ballistically over long distances when the value of $\alpha$ is decreased.

Search in the Presence of Brownian diffusion. The results shown so far apply to most length scales as long as properly rescaled to the particle's radius $R$. However, when $R$ approaches the microand nanoscales, Brownian diffusion starts playing a significant role in the translational and rotational motions of an active particle $(29,41)$. In particular, while the translational diffusion of a particle scales with its inverse linear dimension $\left(\propto R^{-1}\right)$, its rotational diffusion scales with its inverse volume $\left(\propto R^{-3}\right)$. As a consequence of this volumetric scaling, as $R$ decreases, Brownian rotation randomizes any persistence in the particle's orientation caused by the Lévy strategy. Brownian diffusion then becomes an important parameter to consider when determining the optimal search strategy in a nontrivial topography for microscopic active particles, such as biological and artificial microswimmers [e.g., motile bacteria (6-8) and manmade micro- and nanorobots (45)] moving in complex and disordered environments ( $29,39,46,47$ ). Fig. $5 A$ shows how the optimal search strategy (i.e., the optimal value of $\alpha$ ) varies as a function of the particle's radius (i.e., of the strength of the particle's translational and rotational Brownian diffusion coefficients). We focus again on the environment of Fig. 2A, as it shows a clear deviation from the homogenous case (Fig. 1). For a given $v / R$ (e.g., for $v / R=5 \mathrm{~s}^{-1}$ ), when $R$ is above a certain threshold value (e.g., $R \geq 5 \mu \mathrm{~m}$ for $v / R=5 \mathrm{~s}^{-1}$, corresponding to a sufficiently weak rotational diffusion), the optimal strategy is the same as the one predicted in Fig. 3C (Fig. $5 A$ and $B$ ). However, when $R$ decreases (entailing a stronger rotational diffusion), the optimal search strategy shifts toward $\alpha=1$ (Fig. $5 A$ and $C$ ). This shift happens, because the increased rotational diffusion leads to a reduction of the time that the particle spends at the boundaries. This effectively reduces the penalization that boundaries have on more ballistic strategies, thus allowing for the exploration of a greater inner area of the porous structure compared with more diffusive strategies. Reducing $R$ further, the optimal search strategy remains at $\alpha=1$, although the relative efficiency over other $\alpha$ values decreases (Fig. 5D). Finally, for even smaller values of $R$ (e.g., $R \leq 0.1 \mu \mathrm{~m}$ for $v / R=5 \mathrm{~s}^{-1}$ ), the search process becomes effectively insensitive to the value of $\alpha$ (Fig. $5 E$ ), as the increase in rotational diffusion makes persistent motion negligible (29).

## Discussion

Our results show the critical role played by the topography of the environment in determining the optimal search strategy for
an active particle with run lengths that are drawn from a Lévy distribution. In particular, the presence of physical boundaries, barriers, and obstacles can introduce a cutoff on the distribution of steps that can penalize more ballistic strategies over more Brownian ones depending on different geometrical parameters connected to the topography of the environment and its interaction with the particle's motion.

In our model, we assumed that the particle is performing a cruise search with continuous visibility for targets and perfect hitting probabilities. While we do not expect imperfect hitting probabilities to affect the optimality of the search strategy in our case as long as they affect all $\alpha$ values equally, other search scenarios might influence the optimal search strategy in a complex topography (1): for example, in the case of intermittent search strategies, where there is an alternation between phases of slow motion that allow the searcher to detect the targets and phases


Fig. 4. Convex vs. concave porous topography. (A) A sample area of an extended 2D convex porous medium, where an active particle searches for uniformly distributed targets (dots). The porous medium is made up of the space surrounding circular convex obstacles of average radius $R_{\mathrm{p}}$ ( $R_{\mathrm{p}} / r_{\mathrm{c}} \approx 12.5$ ). ( $B$ ) Average number of caught targets $\left\langle N_{\mathrm{p}}\right\rangle$ (triangles) as a function of $\alpha$ in normalized units (n.u.). The values are averaged over 1,000 1-h trajectories and normalized to the maximum value at $\alpha=1$. The gray shaded area represents one SD around the average values. To directly compare with the homogenous and concave porous cases, the trends of Figs. 1D and $2 B$ are also shown as circles and squares, respectively. (C) Four different 1,000-s trajectories with a common origin are shown for different values of $\alpha$. All black scale bars correspond to $50 R$.


Fig. 5. Optimal search strategy in the presence of Brownian diffusion. (A) Optimal value of $\alpha$ as a function of the particle's radius $R$ for different values of $v: v=5 R \mathrm{~s}^{-1}$ (circles), $v=10 R \mathrm{~s}^{-1}$ (squares), and $v=20 R \mathrm{~s}^{-1}$ (triangles). The dashed horizontal lines represent the optimal values in the absence of Brownian noise (Fig. 3). ( $B-E$ ) Shift of the optimal search strategy as a function of $\alpha$ in normalized units (n.u.) at the sample speed $v=5 R \mathrm{~s}^{-1}$ with decreasing values of the particle's radius $R$ : (B) $R=5 \mu \mathrm{~m},(C) R=1 \mu \mathrm{~m}$, (D) $R=0.5 \mu \mathrm{~m}$, and $(E) R=0.1 \mu \mathrm{~m}$. All values are averaged over 10,000 1-h trajectories. The gray shaded area represents one SD around the average values.
of fast motion, during which targets cannot be detected, or in the case of a search strategy with in-built delays, so that, after a target is caught, some time must elapse before the following target can be caught.
Another aspect that can influence the optimal search strategy is the interaction between the searcher and the obstacles encoded in the boundary conditions. In this work, we have implemented reflective boundary conditions, which imply that the searcher stays at the boundary until a random reorientation event makes it point away from the obstacle. This scenario is realistic at the macroscopic and microscopic scales, as, for example, both elementary robots and microswimmers (biological and nonbiological) have been reported to behave in this way $(29,42)$. Alternatively, different responses can be considered in the presence of boundaries, when information obtained from sensing the surroundings, for example, leads to a voluntary switch in the strategy adopted by the searcher.
As the search time is generally a limiting factor in many realistic search scenarios (1), the searcher was allowed to explore the search space for a finite time in our simulations. Nevertheless, from a fundamental point of view, it would be interesting to study how the optimal search strategy is influenced by the topography of the environment in the limit of infinite search times. In the case of infinite searches, interesting behaviors could emerge as a result of the interplay between the fractal dimensionality of the searcher's trajectory and that of the environment in a porous topography at the percolation threshold or in a network of channels.
Our findings are mostly scale-invariant and only partially break down at the nanoscopic scale ( $R \leq 1 \mu \mathrm{~m}$ ) when rotational diffusion becomes predominant. One important implication of this is that different search strategies (i.e., different values of $\alpha$ ) will lead to similar outcomes for nanoscopic particles, such as biomolecules and molecular motors moving in a 2D space (Fig. $5 E$ ). This issue can be overcome by reducing the dimensionality of the environment: for example, by introducing a preferential direction of motion with molecular rails. In fact, Lévy-type statistics emerge for molecular motors performing searches on polymer chains, such as DNA (4), or on 1D molecular rails, such as microtubules (5). Similarly, increasing the dimensionality of the system to a 3D space will alter the probability that the searcher goes back to the same point compared with a 2D space, and thus, its optimal search strategy in a complex 3D environment can also be affected.

Our results are relevant for all random search problems where the searcher explores complex search spaces. Examples at various length scales include the rate of molecular encounters in the cytoplasm of cells, the localization of nutrients by motile bacteria in tissue or soil, and the foraging of animals in patchy landscapes as well as search and rescue operations in ruins after natural disasters. Furthermore, similar dynamics could also be applied to optimize navigation in topologically complex networks (27, 28).

## Materials and Methods

Numerical Simulations. In our numerical model, we consider active particles of radius $R$ performing a 2D run-and-tumble motion according to the following equations:

$$
\left\{\begin{array}{l}
\frac{d}{d t} x(t)=v \cos \varphi_{n} \\
\frac{d}{d t} y(t)=v \sin \varphi_{n}
\end{array}\right.
$$

where $[x(t), y(t)]$ is the particle's position, $v$ is the particle's speed, and $\varphi_{n}$ is the particle's orientation during the $n$th time interval, where $n=0,1,2, \ldots$. The time intervals $t_{n}$ between changes of direction are drawn from a Lévy distribution $P_{\alpha}(t)$ of exponent $\alpha \in[1,2]$; only the absolute value of the number is considered. At the end of each time interval, the particle orientation changes by a random angle according to a normal distribution with zero mean and SD $\sigma_{\varphi}=\pi / 6$. The initial position for the trajectory was randomly chosen within the medium according to a uniform distribution. The positions of the targets were randomized for each trajectory. Interactions with the walls were modeled using the boundaries conditions described in ref. 41. In the data in Fig. 5, translational and rotational Brownian motions are included by adding three independent white noise processes ( $W_{x}, W_{y}$, and $W_{\varphi}$ ) to the equations of motion (41); in this set of simulations, the active particles are moving in an aqueous environment ( $\eta=0.001 \mathrm{Nsm}^{-2}$, $T=300 \mathrm{~K}$ ) .

Calculation of the Average Run Length in a Homogenous Topography. The average run length in a homogenous environment $\left\langle\ell_{h}(\alpha)\right\rangle$ is

$$
\begin{gathered}
\left\langle\ell_{\mathrm{h}}(\alpha)\right\rangle=\int_{0}^{\infty} \ell_{\mathrm{h}}(t) P_{\alpha}(t) d t \\
=\int_{0}^{t_{\mathrm{c}}(v)} \ell_{\mathrm{h}}(t) P_{\alpha}(t) d t+\int_{t_{\mathrm{c}}(v)}^{\infty} \ell_{\mathrm{h}}(t) P_{\alpha}(t) d t
\end{gathered}
$$

where $t_{c}(v)=r_{c} / v$ represents the time that it takes for an active particle to travel a distance equal to its capture radius $r_{\mathrm{c}}$. Neglecting the first integral, because it gives a small contribution to the average run length, we obtain

$$
\left\langle\ell_{\mathrm{h}}(\alpha)\right\rangle \approx \int_{t_{\mathrm{c}}(v)}^{\infty} \ell_{\mathrm{h}}(t) P_{\alpha}(t) d t
$$

which using the asymptotic analytical form for $P_{\alpha}(t)$ in Eq. 1, can be calculated to be

$$
\left\langle\ell_{\mathrm{h}}(\alpha)\right\rangle \approx v A(\alpha) \int_{t_{\mathrm{c}}(v)}^{\infty} t^{-\alpha} d t=v \frac{A(\alpha)}{\alpha-1} t_{\mathrm{c}}^{-\alpha+1}
$$

Calculation of the Average Run Length in a Porous Topography. The average run length in a porous environment $\left\langle\ell_{\mathrm{p}}(\alpha)\right\rangle$ is

$$
\begin{gathered}
\left\langle\ell_{\mathrm{p}}(\alpha)\right\rangle=\int_{0}^{\infty} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t \\
=\int_{0}^{t_{c}(v)} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t+\int_{t_{\mathrm{c}}(v)}^{T_{\mathrm{c}}(v)} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t+\int_{T_{\mathrm{c}}(v)}^{\infty} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t
\end{gathered}
$$

where the integral has been divided into three parts delimited by the time cutoff at $t_{c}$ and by that at $T_{c}=R_{c} / v$ calculated using the spatial cutoff introduced by the porous medium (Fig. 2C). As for the homogenous case, the first integral gives a small contribution on the average run length, as it is smaller than $r_{c}$. As such, it can be neglected, so that

$$
\left\langle\ell_{\mathrm{p}}(\alpha)\right\rangle \approx \int_{t_{\mathrm{c}}(v)}^{T_{\mathrm{c}}(v)} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t+\int_{T_{\mathrm{c}}(v)}^{\infty} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t
$$

We can now treat these two integrals using the fact that, because of the interaction with the boundaries, $\left\langle\ell_{\mathrm{p}}(t)\right\rangle \leq\left\langle\ell_{\mathrm{h}}(t)\right\rangle$ at any given time $t$ taken from the distributions of Eq. 1 (Fig. $1 B$ ). In general, $\left\langle\ell_{\mathrm{p}}(t)\right\rangle=C(t, \alpha, v)\left\langle\ell_{\mathrm{h}}(t)\right\rangle$, where $C \in[0,1]$ is a multivariable function. To simplify the analysis, we introduce the following approximation: $C(t, \alpha, v)=\beta(v)$ for $t \in\left[t_{c}, T_{c}\right]$ and $C(t, \alpha, v)=\gamma \beta(v)$ for $t \in\left[T_{c}, \infty\right)$, where $\beta \in[0,1]$ is a speed-dependent constant and $\gamma \in[0,1]$ is a prefactor related to the topography of the environment. This approximation allows us to determine the decrease of the average run length in the porous environment over the homogenous case by estimating the decrease of the area of the integral before and after the time cutoff at $T_{c}$ (Fig. $2 C$ ) and thus, to treat differently the distribution of the run lengths in the porous environment $P_{\mathrm{p}, \alpha}(\ell)$ (Eq. 2) in the two time intervals. We, therefore, obtain for the two integrals

$$
\int_{t_{\mathrm{c}}(v)}^{T_{\mathrm{c}}(v)} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t \approx \beta(v) v \frac{A(\alpha)}{\alpha-1}\left(t_{\mathrm{c}}^{-\alpha+1}-T_{\mathrm{c}}^{-\alpha+1}\right)
$$

and

1. Bénichou O, Loverdo C, Moreau M, Voituriez R (2011) Intermittent search strategies. Rev Mod Phys 83:81-129.
2. Viswanathan G, da Luz M, Raposo E, Stanley H (2011) The Physics of Foraging: An Introduction to Random Searches and Biological Encounters (Cambridge Univ Press, New York).
3. Shlesinger MF, Klafter J (1986) On Growth and Form, eds Stanley HE, Ostrowsky N (Springer, Dordrecht, The Netherlands).
4. Lomholt MA, Ambjörnsson T, Metzler R (2005) Optimal target search on a fast-folding polymer chain with volume exchange. Phys Rev Lett 95:260603.
5. Chen K, Wang B, Granick S (2015) Memoryless self-reinforcing directionality in endosomal active transport within living cells. Nat Mater 14:589-593.
6. Ariel G , et al. (2015) Swarming bacteria migrate by Lévy walk. Nat Commun 6:8396.
7. Korobkova E, Emonet T, Vilar JMG, Shimizu TS, Cluzel P (2004) From molecular noise to behavioural variability in a single bacterium. Nature 428:574-578.
8. Tu Y, Grinstein $G$ (2005) How white noise generates power-law switching in bacterial flagellar motors. Phys Rev Lett 94:208101.
9. Harris TH, et al. (2012) Generalized levy walks and the role of chemokines in migration of effector cd8+ t cells. Nature 486:545-548.
10. Viswanathan GM, et al. (1996) Levy flight search patterns of wandering albatrosses. Nature 381:413-415.
11. Viswanathan GM, et al. (1999) Optimizing the success of random searches. Nature 401:911-914.
12. Atkinson RPD, Rhodes CJ, MacDonald DW, Anderson RM (2002) Scale-free dynamics in the movement patterns of jackals. Oikos 98:134-140.
13. Ramos-Fernández G , et al. (2004) Lévy walk patterns in the foraging movements of spider monkeys (ateles geoffroyi). Behav Ecol Sociobiol 55:223-230.
14. Sims DW, et al. (2008) Scaling laws of marine predator search behaviour. Nature 451:1098-1102.
15. Humphries NE, et al. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066-1069.
16. de Jager M, Weissing FJ, Herman PMJ, Nolet BA, van de Koppel J (2011) Lévy walks evolve through interaction between movement and environmental complexity. Science 332:1551-1553.
17. Brockmann D, Hufnagel L, Geisel T (2006) The scaling laws of human travel. Nature 439:462-465.
18. Gonzalez MC, Hidalgo CA, Barabasi AL (2008) Understanding individual human mobility patterns. Nature 453:779-782.
19. Raichlen DA, et al. (2014) Evidence of Lévy walk foraging patterns in human huntergatherers. Proc Natl Acad Sci USA 111:728-733.
20. Edwards AM, et al. (2007) Revisiting levy flight search patterns of wandering albatrosses, bumblebees and deer. Nature 449:1044-1048.
21. Mashanova A, Oliver TH, Jansen VAA (2010) Evidence for intermittency and a truncated power law from highly resolved aphid movement data. J R Soc Interface 7: 199-208.
22. Petrovskii S, Mashanova A, Jansen VAA (2011) Variation in individual walking behavior creates the impression of a Lévy flight. Proc Natl Acad Sci USA 108:8704-8707.
23. Humphries NE, Weimerskirch H, Queiroz N, Southall EJ, Sims DW (2012) Foraging success of biological Lévy flights recorded in situ. Proc Natl Acad Sci USA 109: 7169-7174.
24. Jansen VAA, Mashanova A, Petrovskii S (2012) Comment on "Lévy walks evolve through interaction between movement and environmental complexity". Science 335:918.

$$
\int_{T_{\mathrm{c}}(v)}^{\infty} \ell_{\mathrm{p}}(t) P_{\alpha}(t) d t \approx \gamma \beta(v) v \frac{A(\alpha)}{\alpha-1} T_{\mathrm{c}}^{-\alpha+1} .
$$

Summing these two integrals, we obtain

$$
\begin{aligned}
\left\langle\ell_{\mathrm{p}}(\alpha)\right\rangle & \approx \beta(v) v \frac{A(\alpha)}{\alpha-1}\left(t_{\mathrm{c}}^{-\alpha+1}-T_{\mathrm{c}}^{-\alpha+1}\right)+\gamma \beta(v) v \frac{A(\alpha)}{\alpha-1} T_{\mathrm{c}}^{-\alpha+1} \\
& =\beta(v) v \frac{A(\alpha)}{\alpha-1} t_{\mathrm{c}}^{-\alpha+1}\left[1-(1-\gamma)\left(\frac{T_{\mathrm{c}}}{t_{\mathrm{c}}}\right)^{-\alpha+1}\right]
\end{aligned}
$$

ACKNOWLEDGMENTS. We thank Jan Wehr for useful discussions on the mathematical part of the manuscript and Erçağ Pinçe, Mite Mijalkov, Geet Raju, and Sylvain Gigan for useful discussions in the initial stages of the project. We also acknowledge the COST (European Cooperation in Science and Technology) Action MP1305 "Flowing Matter" for providing several meeting occasions. Giorgio Volpe acknowledges funding from the Wellcome Trust [204240/Z/16/Z]. Giovanni Volpe acknowledges funding from European Research Council Starting Grant ComplexSwimmers Grant 677511.
25. Reynolds A (2015) Liberating Lévy walk research from the shackles of optimal foraging. Phys Life Rev 14:59-83.
26. van Dartel M, Postma E, van den Herik J, de Croon G (2004) Macroscopic analysis of robot foraging behaviour. Connect Sci 16:169-181.
27. Riascos AP, Mateos JL (2012) Long-range navigation on complex networks using Lévy random walks. Phys Rev E 86:056110.
28. Guo Q, Cozzo E, Zheng Z, Moreno Y (2016) Levy random walks on multiplex networks. Sci Rep 6:37641.
29. Bechinger C, et al. (2016) Active particles in complex and crowded environments. Rev Mod Phys 88:045006.
30. Lomholt MA, Tal K, Metzler R, Joseph K (2008) Lévy strategies in intermittent search processes are advantageous. Proc Natl Acad Sci USA 105:11055-11059.
31. Bartumeus F, Catalan J, Fulco UL, Lyra ML, Viswanathan GM (2002) Optimizing the encounter rate in biological interactions: Lévy versus brownian strategies. Phys Rev Lett 88:097901.
32. Raposo EP, et al. (2003) Dynamical robustness of Lévy search strategies. Phys Rev Lett 91:240601.
33. James A, Plank MJ, Brown R (2008) Optimizing the encounter rate in biological interactions: Ballistic versus Lévy versus Brownian strategies. Phys Rev E 78: 051128.
34. Raposo E , et al. (2011) How landscape heterogeneity frames optimal diffusivity in searching processes. PLoS Comp Biol 7:e1002233.
35. Ferreira A, Raposo E, Viswanathan G, da Luz M (2012) The influence of the environment on Lévy random search efficiency: Fractality and memory effects. Physica $A$ 391:3234-3246.
36. Barkai $E$, Garini $Y$, Metzler $R$ (2012) Strange kinetics of single molecules in living cells. Phys Today 65:29-35.
37. Kim MK, Ingremeau F, Zhao A, Bassler BL, Stone HA (2016) Local and global consequences of flow on bacterial quorum sensing. Nat Microbiol 1:15005.
38. Boyer D, et al. (2006) Scale-free foraging by primates emerges from their interaction with a complex environment. Proc $R$ Soc B Biol Sci 273:1743-1750.
39. Pinçe E , et al. (2016) Disorder-mediated crowd control in an active matter system. Nat Commun 7:10907.
40. Palyulin VV, Chechkin AV, Metzler R (2014) Lévy flights do not always optimize random blind search for sparse targets. Proc Natl Acad Sci USA 111:29312936.
41. Volpe G, Gigan S, Volpe G (2014) Simulation of the active Brownian motion of a microswimmer. Am J Phys 82:659-664.
42. Dimidov C, Oriolo G, Trianni V (2016) Random Walks in Swarm Robotics: An Experiment with Kilobots, eds Dorigo M, et al. (Springer International, Cham, Switzerland), pp 185-196.
43. Chepizhko O, Peruani F (2013) Diffusion, subdiffusion, and trapping of active particles in heterogeneous media. Phys Rev Lett 111:160604.
44. Blumenthal RM, Getoor RK (1960) A dimension theorem for sample functions of stable processes. III J Math 4:370-375.
45. Haeufle DFB, et al. (2016) External control strategies for self-propelled particles: Optimizing navigational efficiency in the presence of limited resources. Phys Rev E 94:012617.
46. Chepizhko O, Altmann EG, Peruani F (2013) Optimal noise maximizes collective motion in heterogeneous media. Phys Rev Lett 110:238101.
47. Reichhardt C, Olson Reichhardt CJ (2014) Active matter transport and jamming on disordered landscapes. Phys Rev E 90:012701.


[^0]:    Author contributions: Giorgio Volpe designed research; Giorgio Volpe performed research; Giorgio Volpe and Giovanni Volpe analyzed data; and Giorgio Volpe and Giovanni Volpe wrote the paper.
    The authors declare no conflict of interest.
    This article is a PNAS Direct Submission.
    Published under the PNAS license.
    ${ }^{1}$ To whom correspondence should be addressed. Email: g.volpe@ucl.ac.uk.
    This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10 1073/pnas.1711371114/-/DCSupplemental

