

Emergence of Lévy Walks from Second-Order Stochastic Optimization

Łukasz Kuśmierz* and Taro Toyozumi†

RIKEN Brain Science Institute, 2-1 Hirosawa, Wako, Saitama 351-0198, Japan

(Received 8 October 2017; published 18 December 2017)

In natural foraging, many organisms seem to perform two different types of motile search: directed search (taxis) and random search. The former is observed when the environment provides cues to guide motion towards a target. The latter involves no apparent memory or information processing and can be mathematically modeled by random walks. We show that both types of search can be generated by a common mechanism in which Lévy flights or Lévy walks emerge from a second-order gradient-based search with noisy observations. No explicit switching mechanism is required—instead, continuous transitions between the directed and random motions emerge depending on the Hessian matrix of the cost function. For a wide range of scenarios, the Lévy tail index is $\alpha = 1$, consistent with previous observations in foraging organisms. These results suggest that adopting a second-order optimization method can be a useful strategy to combine efficient features of directed and random search.

DOI: [10.1103/PhysRevLett.119.250601](https://doi.org/10.1103/PhysRevLett.119.250601)

Many organisms must actively search for resources in order to survive and produce offspring. The foraging theory examines the various search strategies implemented by organisms depending on their abilities and the environments in which they live. In a directed search, the greater involvement of sensory and information processing abilities enable more complicated strategies. In contrast, in the boundary case of a memoryless and senseless forager, the only option is to wander randomly in the environment (random search). Even in this case, however, different strategies exist, depending on the character of the random motion. A natural candidate model for the random strategy is Brownian motion that describes a wide range of natural phenomena, including the movement of inanimate particles under thermal noise. A prominent feature of Brownian motion is the linear growth of the variance of the position with time. However, empirical data indicate that for organisms the observed growth is often faster. Lévy walks (LWs) [1–3] and similar Lévy flights (LFs) [2,4,5] have been successfully applied to fit experimental data obtained from the movement patterns of many organisms and their cells, including T cells [6], microglia [7], starved slime mold (*Dictyostelium discoideum*) [8,9], swarming bacteria [10], fruit flies [11], honey bees [12,13], wandering albatrosses [14,15], marine predators [16], and humans [17–19] (also in a human's gaze [20] and word association [21] trajectories). In many different random search scenarios, LWs and LFs have been shown to be advantageous over normal diffusion [22–32] and alternative superdiffusive models [33]. These observations have led to the so-called Lévy flight optimal foraging hypothesis, which states that LFs (or LWs) represent evolutionary adaptations due to their distinct advantages over other random search strategies [22,34,35].

Recently, this view has been disputed, because none of the mentioned organisms is senseless and all of them are able to

perform some forms of directed search (taxis); for example, T cells and isolated bacteria perform chemotaxis [36–40], whereas fruit flies perform phototaxis [41], geotaxis [42], and chemotaxis [43,44]. Indeed, a number of studies have shown that characteristics of LFs and LWs may emerge naturally on large scales from more realistic case specific models of movement [45], including simple deterministic and semideterministic walks in complex environments [35,46–50], self-avoiding random walks [51–53], diffusion with a time-varying diffusion constant [54–56], and a multiplicative, self-accelerating process [9,57,58]. It has also been suggested that in some species a power-law distribution of lengths of straight line segments of their movement patterns, a hallmark of LWs and LFs, is a consequence of either the Weber-Fechner law in odometry [59], a power-law distribution of switching times between competing activities [60–65], or a so-called aerial lottery [66–68]. Moreover, in some cases the apparent superdiffusive character of the population dynamics may be an artifact of averaging over an ensemble of the diffusive motions of individuals with diverse characteristics [69].

These studies suggest that LWs and LFs naturally arise in many realistic biological settings, but they do not argue why an apparent common behavior is observed across species and environments. Recently, a generalization of the LF optimal foraging hypothesis was proposed that explicitly combines directed and random search strategies. Specifically, an *ad hoc* combination of taxis for choosing a direction and random, heavy-tailed distributed step lengths was shown to be efficient under some search conditions [27,70]. In contrast, here we propose a novel mechanism by which LWs and LFs can emerge from a generic, locally optimal, directed search strategy. In our model, the directed search is realized as a taxis driven by local observations of a cost function (e.g., a repellent

concentration minus an attractant concentration) whose minima correspond to targets. Inspired by the second-order gradient-based optimization techniques known from computer science, we assume that the search is based on noisy gradient and Hessian estimates. As we show below, this generically leads to heavy tails of the step distribution. In contrast to previous models, our model predicts a continuous crossover between random Lévy searches and directed, deterministic taxis depending on the amount of information on the target location provided by observations.

This Letter is organized as follows. First, we fix the notation and introduce a one-dimensional version of our model. Next, we list different scenarios in which we are able to prove the existence of the heavy tails. We then discuss how the tails are affected by the landscape and the observation methods. Finally, we discuss a multidimensional generalization of the model followed by concluding remarks.

Let $(x_n)_{n=0}^{\infty}$ be a sequence generated by the Newton optimization rule

$$x_{n+1} = x_n + \Delta_n, \quad (1)$$

with

$$\Delta_n = -\frac{f'(x_n) + \xi_G^{(n)}}{f''(x_n) + \beta + \xi_H^{(n)}}, \quad (2)$$

where the cost function $f: \mathbb{R} \rightarrow \mathbb{R}$ is to be minimized. The rule with $\beta = \xi_G^{(n)} = \xi_H^{(n)} = 0$ performs a gradient descent or a gradient ascent on f , depending on its curvature. A positive constant β (damping) is added to the denominator in order to turn this algorithm into a minimizer. Note that the steepest descent method

$$\tilde{\Delta}_n = -\frac{f'(x_n) + \xi_G^{(n)}}{\beta} \quad (3)$$

is recovered from (2) in the limit of $\beta \rightarrow \infty$ if f has a bounded second derivative. Terms $\xi_G^{(n)}$ and $\xi_H^{(n)}$ account for noise: If the optimization is to be performed in the physical world, derivatives of f are based on noisy measurements. Similarly, in many optimization problems solved on a computer, especially in machine learning, a function to be optimized is estimated with finite precision. With these definitions, the sequence $(x_n)_{n=0}^{\infty}$ denotes a one-dimensional discrete-time random walk.

Trajectories of LWs consist of linear segments (or instantaneous jumps in the case of LFs) Δ_n , which are independent and identically distributed random variables (hence we omit the time index n in the discussion of distributions and write simply Δ). The probability density function (PDF) of Δ is characterized by heavy tails, i.e., for large $|z|$

$$\rho_{\Delta}(z) \sim |z|^{-1-\alpha}, \quad (4)$$

where the tail index $0 < \alpha < 2$. In the following, we show that for a wide range of scenarios the random walk defined by (1) and (2) is equivalent to a (possibly inhomogeneous) LW or LF (depending on how it is mapped into a continuous time process [71]) with $\alpha = 1$. We shall first analyze the case when $\beta = 0$ and $f(x) = \text{const}$, so that only noise is sampled. Assuming that the noise is Gaussian and that both f' and f'' are measured independently and without bias, we can write

$$\Delta = -\frac{\xi_G}{\xi_H}, \quad (5)$$

where ξ_G and ξ_H are independent Gaussian variables with zero mean and standard deviations σ_G and σ_H . The reader can easily verify that Δ is in this case characterized by the Cauchy distribution

$$\rho_{\Delta}(z) = \frac{1}{\pi} \frac{\gamma}{\gamma^2 + z^2}, \quad (6)$$

where $\gamma = (\sigma_G/\sigma_H)$. Comparing (6) with (4), we see that in our case $\alpha = 1$. More generally, let us assume that the numerator X_G and denominator X_H in (2) are independent random variables with PDFs ρ_{X_G} and ρ_{X_H} , respectively. This is the case if ξ_G and ξ_H are conditionally independent given the current position of the walker. The asymptotic form of the PDF of $\Delta = -X_G/X_H$ is given by

$$\begin{aligned} \rho_{\Delta}(z) &= \int_{-\infty}^{\infty} dz_1 \rho_{X_G}(z_1) \int_{-\infty}^{\infty} dz_2 \rho_{X_H}(z_2) \delta\left(z + \frac{z_1}{z_2}\right) \\ &= \frac{1}{z^2} \int_{-\infty}^{\infty} dz_1 \rho_{X_G}(z_1) \rho_{X_H}\left(-\frac{z_1}{z}\right) |z_1| \\ &= \frac{\langle |X_G| \rangle \rho_{X_H}(0)}{z^2} + o(z^{-2}), \end{aligned} \quad (7)$$

where the last equality holds if $\langle |X_G| \rangle \equiv \int \rho_{X_G}(z) |z| dz < \infty$ and $0 < \rho_{X_H}(0) = \lim_{z \rightarrow 0^{\pm}} \rho_{X_H}(z) < \infty$. The condition $\langle |X_G| \rangle < \infty$ is equivalent to the statement that the tails of $\rho_{X_G}(z)$ decay faster than z^{-2} . If this condition is not fulfilled, the appearance of heavy tails in the distribution of Δ is trivial. In our case, however, the heavy tails of ρ_{Δ} appear due to a nonzero probability of X_H being arbitrarily close to zero. The described mechanism is very general, as it does not assume that the noise distribution has heavy tails. Intuitively, the division in (2) takes the role of a noise amplifier. Clearly, first-order methods, such as the steepest descent (3), do not involve a division by a random variable and therefore do not generically lead to heavy tails.

In the case of correlated X_G and X_H , the presence of heavy tails cannot be ensured, in general. For instance, if $X_G = -YX_H$ for some random variable Y , then the resulting Δ has the same distribution as Y . However, as we will now show, the heavy tails are still present in the generic case of the bivariate normal distribution of X_G and X_H :

$$\rho_X(\mathbf{x}) = \frac{|\mathbf{P}|^{1/2}}{2\pi} \exp \left[-\frac{1}{2} (\mathbf{x} - \boldsymbol{\mu})^\top \mathbf{P} (\mathbf{x} - \boldsymbol{\mu}) \right], \quad (8)$$

where $\mathbf{X} = \begin{pmatrix} X_G \\ X_H \end{pmatrix}$ is a two-dimensional Gaussian random vector, $\boldsymbol{\mu} = \begin{pmatrix} \mu_G \\ \mu_H \end{pmatrix}$ is a vector of its expected values, $\mathbf{P} = \begin{pmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{pmatrix}$ is a symmetric, positive-definite precision matrix, and $|\mathbf{P}|$ is its determinant. The PDF of Δ can be calculated as $\rho_\Delta(z) = \int d^2\mathbf{x} \rho_X(\mathbf{x}) \delta[z + (x_1/x_2)]$ and in the special case of $\mu_G = \mu_H = 0$ simplifies to the shifted Cauchy distribution

$$\rho_\Delta(z) = \frac{1}{\pi} \frac{|\mathbf{P}|^{1/2}}{P_{22} - 2P_{12}z + P_{11}z^2}. \quad (9)$$

In general, ρ_Δ takes the form

$$\rho_\Delta(z) = \frac{|\mathbf{P}|^{1/2}}{2\pi z^2} \int_{-\infty}^{\infty} dx |x| \exp \left[-\frac{1}{2} (\tilde{\mathbf{x}} - \boldsymbol{\mu})^\top \mathbf{P} (\tilde{\mathbf{x}} - \boldsymbol{\mu}) \right] = \frac{I(z)}{z^2}, \quad (10)$$

where $\tilde{\mathbf{x}} = \begin{pmatrix} x \\ -x/z \end{pmatrix}$. Since $0 < \lim_{z \rightarrow \infty} I(z) < \infty$, we see that yet again $\rho_\Delta(z) \sim 1/z^2$ for large z .

It may now seem like the second-order methods should always lead to LFs or LWs given noisy observations, which might prevent them from being an efficient search strategy. However, this is not the case if the regularization factor β and curvature $f''(x)$ in the denominator strongly temper heavy tails in (2). For example, in the case of independent Gaussian ξ_G and ξ_H , the large z limit of the cumulative distribution of the step size in (7) is given by

$$P(|\Delta| > z) \approx \frac{2 \langle |X_G| \rangle \rho_{\xi_H}[-\beta - f''(x)]}{z} = \frac{2 \langle |X_G| \rangle}{\sqrt{2\pi} \sigma_H z} e^{-(c^2/2)} \quad (11)$$

with $c = (\beta + f''(x))/\sigma_H$. Namely, heavy tails are still present, but they are suppressed by the exponential factor $e^{-c^2/2}$. Thus, for $|\beta + f''(x)| \gg \sigma_H$ the probability of large random displacements is extremely low. Equation (11) provides a hint as to why the noisy second-order search may be efficient: If β and σ_H are chosen such that $c \approx 0$ at the maxima, where f'' is negative, and $c \gg 1$ at the minima, where f'' is positive, heavy tails are present in the vicinity of the maxima facilitating fast escapes, whereas around the minima heavy tails are strongly suppressed, allowing for an effective local exploration.

We now address the question of how the method of estimating f' and f'' from noisy measurements of f can influence our results. The simplest possible model in 1D consists of three observations. Let us assume that the observations are performed at $x_0 - \delta x$, x_0 , and $x_0 + \delta x$, resulting in the following noisy measurements: $y_- = f(x_0 - \delta x) + \xi_-$, $y_0 = f(x_0) + \xi_0$, and $y_+ = f(x_0 + \delta x) + \xi_+$, where ξ_i represent multivariate Gaussian noise. If we assume that δx is small enough, we can write the following

formulas for the maximum likelihood estimates of the first two derivatives:

$$\begin{aligned} \hat{f}'(x_0) &= \frac{y_+ - y_-}{2\delta x} \approx f'(x_0) + \xi_G, \\ \hat{f}''(x_0) &= \frac{y_- + y_+ - 2y_0}{\delta x^2} \approx f''(x_0) + \xi_H, \end{aligned} \quad (12)$$

where $\xi_G = (\xi_+ - \xi_-)/2\delta x$ and $\xi_H = (\xi_+ - 2\xi_0 + \xi_-)/\delta x^2$. Hence, ξ_G and ξ_H are two jointly Gaussian random variables. As shown in (9), this generally yields the LW or LF with $\alpha = 1$. This reasoning is still valid in scenarios with more measurements, whenever the desired estimates are based on linear combinations of noisy observations. Note that the more measurements used in the estimators, the better the Gaussian model of noise.

Finally, we turn our attention to the multidimensional case. For simplicity, we assume that the search space is \mathbb{R}^D with $D \in \mathbb{N}$. The jump vector, in analogy to (2), takes the following form (as before, since we focus on a single step, we omit the step index):

$$\Delta = -\mathbf{A}^{-1} \nabla \hat{f}(\mathbf{x}) = -[\mathbf{H}f(\mathbf{x}) + \beta \mathbf{I} + \boldsymbol{\xi}_H]^{-1} [\nabla f(\mathbf{x}) + \boldsymbol{\xi}_G], \quad (13)$$

where $\mathbf{H}f(\mathbf{x})$ denotes the Hessian of f , $\boldsymbol{\xi}_G$ is a noise vector, and $\boldsymbol{\xi}_H$ is a symmetric noise matrix. Under mild conditions, in the limit of $D \rightarrow \infty$ the noise eigenvalues $\lambda(\boldsymbol{\xi}_H)$ follow the Wigner semicircle distribution [72–75]. If the curvature and damping are much weaker than the noise, they can influence the distribution only insignificantly, so that $0 < \rho_{\lambda(\mathbf{A})}(0) < \infty$ still holds. Let \mathbf{Q} be an orthogonal matrix diagonalizing \mathbf{A} . The k th component of $\mathbf{Q}^T \Delta = -\mathbf{Q}^T \mathbf{A}^{-1} \mathbf{Q} \mathbf{Q}^T \nabla \hat{f}(\mathbf{x})$ is proportional to $1/\lambda(\mathbf{A})_k$, and thus, according to (7), its distribution has the heavy tail $1/z^2$. We can thus conclude [76,77] that the distribution of $\|\Delta\|$ also has the heavy tail $1/z^2$. In the continuous time limit, this leads to a superdiffusive, multidimensional LW or LF [76,78–82]. Note that the components of Δ are not independent and the spectral measure [76,81] takes a nontrivial form, which will be the subject of future studies. In contrast, if the shift of the eigenvalue distribution related to the curvature and damping factor is strong enough, the tails can be cut off completely, due to the bounded support of the Wigner semicircle distribution. In this case, the continuous time limit process corresponds to diffusive search. Although for any $D < \infty$ the cutoff formally disappears, this shows that the heavy tails can be strongly tempered by the damping factor and the curvature. Importantly, the heavy tails may be tempered in the directions of large curvatures while being preserved in the other directions, thus providing a flexible combination of random and directed search mechanisms.

We finally test our results using computer simulations in a simple example of a search in an unbounded

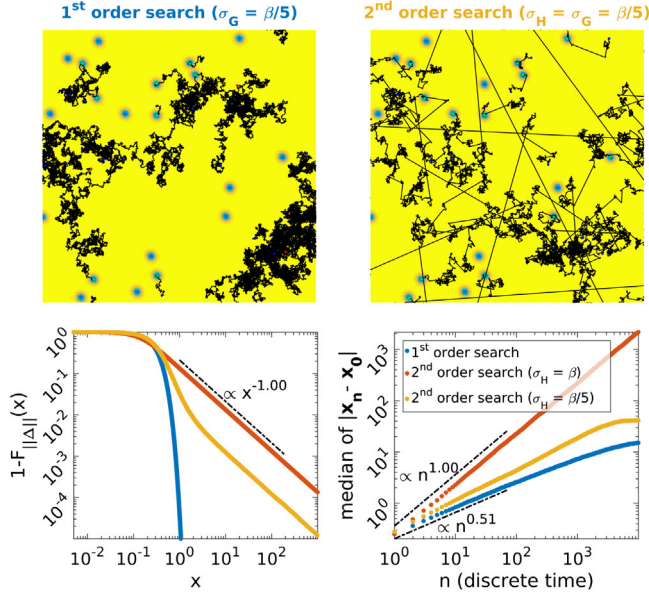


FIG. 1. An example of search processes in an unbounded two-dimensional space. The optimized function f is a sum of 20 Gaussians uniformly distributed within a 100×100 cell, which is periodically repeated across an infinite space. The targets are sparse, so that in most places f is flat and does not provide any information about the position of the targets due to measurement noise. The top two plots represent a cell of f (yellow corresponds to high values, blue to low values) and 20 exemplary trajectories of searches starting from randomly chosen positions within the cell (blue dots) and finishing at a target (green dots) or at some random position without finding the target (red dots) due to the time limitation (10^4 steps). The bottom left plot depicts the distributions of jump lengths averaged over time and an ensemble of 10^4 trajectories. The second-order search produces a power-law tail with an exponent $\alpha \approx 1$. The bottom right plot shows the scaling of a displacement with time. As expected, for short times the first-order search leads to a diffusive behavior which scales as $n^{1/2}$, whereas the second-order search with strong noise σ_H leads to a superdiffusive behavior which scales as n . For longer times, the median displacement saturates due to trapping at the targets.

two-dimensional space; see Fig. 1. First, the first-order search in (3) does not produce power-law tails, and its searching trajectory corresponds to that of normal diffusion except near a target. The median distance from the initial position scales as \sqrt{n} with time step n . Next, as predicted by our theory, the second-order search with a sufficiently large Hessian noise ($\sigma_H \approx f'' + \beta$) produces heavy tails of the jump length distribution. In this case, the median distance from the initial position scales linearly with time, which is a characteristic of the LF process with $\alpha = 1$. If the Hessian noise σ_H is a few times smaller than $f'' + \beta$, the behavior of the second-order method is in the middle between the above two extreme cases. In this case, the heavy tail of the step size distribution is present but somewhat tempered, in line with (11). As a consequence, the growth of the median distance from the initial position is initially $\sim \sqrt{n}$, similarly to normal diffusion, but slowly

builds up in time as $\sim n$ due to infrequent LF-like jumps. Note that, in the current simulation setup, the median distance saturates before the generalized central limit theorem predicts its linear growth, because the trajectories are trapped by the targets sooner. This indicates that the second-order method with an appropriate noise level (or the damping constant) can find a target faster than the first-order search or the *ad hoc* combination of directed search with power-law step sizes. The detailed analysis of the optimal choice of the damping factor will be given elsewhere, but, intuitively, it is beneficial to perform the first-order search in the direction of a convex surface and perform the LF search along the direction of a concave or plateau surface.

In summary, we analyze a stochastic version of Newton's optimization method. We argue that noise in the estimates of the Hessian leads to a heavy-tailed distribution of jumps, an indicator of LWs or LFs. We present conditions in $D = 1$ and $D \rightarrow \infty$ under which the appearance of the heavy tails is guaranteed, and we corroborate these findings with computer simulations in the biologically relevant case of $D = 2$.

Our model explains how a seemingly common behavior (LW with the fixed tail index $\alpha = 1$) can emerge from a generic and locally optimal search strategy in the presence of noise. This proposal is consistent with the role of evolution and adaptation under selection pressures in acquiring an advantageous search strategy. However, unlike some earlier proposals [22,35,83] that explore over the entire range of plastic α , our model gives only two possible rigid values for α : $\alpha = 1$ generally and $\alpha = 2$ in the limit of $(f'' + \beta)/\sigma_H \rightarrow \infty$. Moreover, our approach is distinct from the Lévy flight foraging hypothesis [22], because the possible evolutionary optimization is not carried within the family of random search strategies (e.g., over a range of α) but explicitly involves directed searches. Indeed, multiple specific mechanisms shaping directed search have been previously shown to produce LWs with an $\alpha = 1$, e.g., movements in narrow, confined environments [45], in bulk-mediated effective surface diffusion [45,84], and in patchy environments if foragers use information about patch quality [49]. Our proposal has two advantages over such findings: First, the second-order gradient-based optimization method is a well-established generic search strategy that works efficiently in many different environmental conditions. Second, by including taxis, our model suggests a specific continuous crossover between the random and directed search strategies as we further discuss below.

Our results suggest that some organisms may perform taxis according to Newton's (or some other second-order) optimization method, which should be possible to verify experimentally. The resulting random walks are inhomogeneous and anisotropic, with less jerky motion along directions with larger curvatures or weaker measurement noise. These are distinct features of our model that can be

taken advantage of in experiments aiming to assess whether foraging organisms employ second-order derivatives. The candidate organisms that use taxis and, in some conditions, perform LWs with $\alpha \approx 1$ include microglia [7], *Dictyostelium discoideum* [8,9], and *Drosophila* [11]. The strategy we introduce combines the characteristics of two algorithms that are known to be efficient in directed (second-order optimization) and random (LFs or LWs) search scenarios. This method should therefore perform well in a broad range of scenarios of stochastic optimization, which may be of interest for the machine learning community.

This work was supported by Brain/MINDS from Japan Agency for Medical Research and Development and RIKEN Brain Science Institute.

*nalewkoz@gmail.com

†taro.toyoizumi@brain.riken.jp

- [1] M. F. Shlesinger, J. Klafter, and Y. M. Wong, *J. Stat. Phys.* **27**, 499 (1982).
- [2] M. F. Shlesinger and J. Klafter, in *On Growth and Form* (Springer, New York, 1986), pp. 279–283.
- [3] M. F. Shlesinger, B. J. West, and J. Klafter, *Phys. Rev. Lett.* **58**, 1100 (1987).
- [4] B. B. Mandelbrot, *The Fractal Geometry of Nature* (Freeman, New York, 1983).
- [5] R. Metzler and J. Klafter, *Phys. Rep.* **339**, 1 (2000).
- [6] T. H. Harris *et al.*, *Nature (London)* **486**, 545 (2012).
- [7] Y. Y. Grinberg, J. G. Milton, and R. P. Kraig, *PLoS One* **6**, e19294 (2011).
- [8] H. Takagi, M. J. Sato, T. Yanagida, and M. Ueda, *PLoS One* **3**, e2648 (2008).
- [9] A. M. Reynolds, *Physica (Amsterdam)* **A389**, 273 (2010).
- [10] G. Ariel, A. Rabani, S. Benisty, J. D. Partridge, R. M. Harshey, and A. Be’Er, *Nat. Commun.* **6**, 8396 (2015).
- [11] A. M. Reynolds and M. A. Frye, *PLoS One* **2**, e354 (2007).
- [12] A. M. Reynolds, A. D. Smith, R. Menzel, U. Greggers, D. R. Reynolds, and J. R. Riley, *Ecology* **88**, 1955 (2007).
- [13] S. Wolf, E. Nicholls, A. M. Reynolds, P. Wells, K. S. Lim, R. J. Paxton, and J. L. Osborne, *Sci. Rep.* **6**, 32612 (2016).
- [14] G. M. Viswanathan, V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley, *Nature (London)* **381**, 413 (1996).
- [15] N. E. Humphries, H. Weimerskirch, and D. W. Sims, *Methods Ecol. Evol.* **4**, 930 (2013).
- [16] D. W. Sims *et al.*, *Nature (London)* **451**, 1098 (2008).
- [17] D. Brockmann, L. Hufnagel, and T. Geisel, *Nature (London)* **439**, 462 (2006).
- [18] M. C. Gonzalez, C. A. Hidalgo, and A.-L. Barabasi, *Nature (London)* **453**, 779 (2008).
- [19] I. Rhee, M. Shin, S. Hong, K. Lee, S. J. Kim, and S. Chong, *IEEE/ACM Trans. Netw.* **19**, 630 (2011).
- [20] D. Brockmann and T. Geisel, *Neurocomputing: Variable Star Bulletin* **32–33**, 643 (2000).
- [21] M. E. Costa, F. Bonomo, and M. Sigman, *Front. Integr. Neurosci.* **3** (2009).
- [22] G. M. Viswanathan, S. V. Buldyrev, S. Havlin, M. G. E. Da Luz, E. P. Raposo, and H. E. Stanley, *Nature (London)* **401**, 911 (1999).
- [23] S. V. Buldyrev, S. Havlin, A. Y. Kazakov, M. G. E. da Luz, E. P. Raposo, H. E. Stanley, and G. M. Viswanathan, *Phys. Rev. E* **64**, 041108 (2001).
- [24] F. Bartumeus, J. Catalan, U. L. Fulco, M. L. Lyra, and G. M. Viswanathan, *Phys. Rev. Lett.* **88**, 097901 (2002).
- [25] E. P. Raposo, S. V. Buldyrev, M. G. E. da Luz, M. C. Santos, H. E. Stanley, and G. M. Viswanathan, *Phys. Rev. Lett.* **91**, 240601 (2003).
- [26] F. Bartumeus, M. G. E. da Luz, G. M. Viswanathan, and J. Catalan, *Ecology* **86**, 3078 (2005).
- [27] Z. Pasternak, F. Bartumeus, and F. W. Grasso, *J. Phys. A* **42**, 434010 (2009).
- [28] E. P. Raposo, F. Bartumeus, M. G. E. Da Luz, P. J. Ribeiro-Neto, T. A. Souza, and G. M. Viswanathan, *PLoS Comput. Biol.* **7**, e1002233 (2011).
- [29] V. V. Palyulin, A. V. Chechkin, and R. Metzler, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 2931 (2014).
- [30] N. E. Humphries and D. W. Sims, *J. Theor. Biol.* **358**, 179 (2014).
- [31] L. Kusmierz, S. N. Majumdar, S. Sabhapandit, and G. Schehr, *Phys. Rev. Lett.* **113**, 220602 (2014).
- [32] Ł. Kuśmierz and E. Gudowska-Nowak, *Phys. Rev. E* **92**, 052127 (2015).
- [33] A. M. Reynolds, *J. Phys. A* **42**, 434006 (2009).
- [34] F. Bartumeus, *Fractals* **15**, 151 (2007).
- [35] G. M. Viswanathan, E. P. Raposo, and M. G. E. Da Luz, *Phys. Life Rev.* **5**, 133 (2008).
- [36] D. D. Taub, K. Conlon, A. R. Lloyd, J. J. Oppenheim, and D. J. Kelvin, *Science* **260**, 355 (1993).
- [37] M. D. Gunn, K. Tangemann, C. Tam, J. G. Cyster, S. D. Rosen, and L. T. Williams, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 258 (1998).
- [38] J. Adler, *Science* **153**, 708 (1966).
- [39] H. C. Berg and D. A. Brown, in *Chemotaxis: Its Biology and Biochemistry* (Karger, Basel, 1974), pp. 55–78.
- [40] H. Szurmant and G. W. Ordal, *Microbiol. Mol. Biol. Rev.* **68**, 301 (2004).
- [41] Y. Zhu, A. Nern, S. L. Zipursky, and M. A. Frye, *Curr. Biol.* **19**, 613 (2009).
- [42] M. S. Miller and T. S. Keller, *J. Gravit. Physiol.* **6**, P99 (1999).
- [43] B. J. Duistermars, D. M. Chow, and M. A. Frye, *Curr. Biol.* **19**, 1301 (2009).
- [44] S. Wasserman, A. Salomon, and M. A. Frye, *Curr. Biol.* **23**, 301 (2013).
- [45] A. M. Reynolds, *Phys. Life Rev.* **14**, 59 (2015).
- [46] D. Boyer, O. Miramontes, G. Ramos-Fernandez, J. Mateos, and G. Cocho, *Physica (Amsterdam) A* **342**, 329 (2004).
- [47] M. C. Santos, D. Boyer, O. Miramontes, G. M. Viswanathan, E. P. Raposo, J. L. Mateos, and M. G. E. da Luz, *Phys. Rev. E* **75**, 061114 (2007).
- [48] A. M. Reynolds, *Phys. Rev. E* **78**, 011906 (2008).
- [49] A. M. Reynolds, *J. R. Soc. Interface* **9**, 1568 (2012).
- [50] A. M. Reynolds, *Proc. R. Soc. A* **470**, 20140408 (2014).
- [51] M. F. Shlesinger, *J. Chem. Phys.* **78**, 416 (1983).
- [52] A. M. Reynolds, *Sci. Rep.* **4**, 4409 (2014).

- [53] D. W. Sims, A. M. Reynolds, N. E. Humphries, E. J. Southall, V. J. Wearmouth, B. Metcalfe, and R. J. Twitchett, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 11073 (2014).
- [54] A. Ott, J. P. Bouchaud, D. Langevin, and W. Urbach, *Phys. Rev. Lett.* **65**, 2201 (1990).
- [55] N. Srivastava, D. A. Clark, and A. D. T. Samuel, *J. Neurophysiol.* **102**, 1172 (2009).
- [56] L. C. M. Salvador, F. Bartumeus, S. A. Levin, and W. S. Ryu, *J. R. Soc. Interface* **11**, 20131092 (2014).
- [57] T. S. Biró and A. Jakovác, *Phys. Rev. Lett.* **94**, 132302 (2005).
- [58] I. Lubashevsky, R. Friedrich, and A. Heuer, *Phys. Rev. E* **79**, 011110 (2009).
- [59] A. M. Reynolds, P. Schultheiss, and K. Cheng, *Behav. Ecol. Sociobiol.* **67**, 1219 (2013).
- [60] E. Korobkova, T. Emonet, J. M. G. Vilar, T. S. Shimizu, and P. Cluzel, *Nature (London)* **428**, 574 (2004).
- [61] Y. Tu and G. Grinstein, *Phys. Rev. Lett.* **94**, 208101 (2005).
- [62] A. L. Barabási, *Nature (London)* **435**, 207 (2005).
- [63] F. Matthäus, M. Jagodič, and J. Dobnikar, *Biophys. J.* **97**, 946 (2009).
- [64] F. Matthäus, M. S. Mommer, T. Curk, and J. Dobnikar, *PLoS One* **6**, e18623 (2011).
- [65] A. M. Reynolds, *Physica A (Amsterdam)* **390**, 245 (2011).
- [66] G. G. Katul, A. Porporato, R. Nathan, M. Siqueira, M. B. Soons, D. Poggi, H. S. Horn, and S. A. Levin, *Am. Nat.* **166**, 368 (2005).
- [67] M. W. Shaw, T. D. Harwood, M. J. Wilkinson, and L. Elliott, *Proc. R. Soc. B* **273**, 1705 (2006).
- [68] A. M. Reynolds, *Am. Nat.* **181**, 555 (2013).
- [69] S. Petrovskii, A. Mashanova, and V. A. Jansen, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 8704 (2011).
- [70] S. G. Nurzaman, Y. Matsumoto, Y. Nakamura, S. Koizumi, and H. Ishiguro, in *Proceedings of the IEEE International Conference on Robotics and Biomimetics, 2008, ROBIO 2008* (IEEE, New York, 2009), pp. 806–811.
- [71] V. Ziburdaev, S. Denisov, and J. Klafter, *Rev. Mod. Phys.* **87**, 483 (2015).
- [72] E. P. Wigner, *Ann. Math.* **67**, 325 (1958).
- [73] D. Voiculescu, *Inventiones Mathematicae* **104**, 201 (1991).
- [74] J. H. Schenker and H. Schulz-Baldes, *arXiv:math-ph/0505003*.
- [75] L. Erdős, *Russ. Math. Surv.* **66**, 507 (2011).
- [76] G. Samorodnitsky and M. S. Taqqu, *Stable Non-Gaussian Random Processes: Stochastic Models with Infinite Variance* (CRC Press, Boca Raton, FL, 1994), Vol. 1.
- [77] J. P. Nolan, Modeling financial data with stable distributions, in *Handbook of Heavy Tailed Distributions in Finance*, edited by S. T. Rachev (Elsevier-North Holland, Amsterdam, 2005).
- [78] M. Teuerle and A. Jurlewicz, *Acta Phys. Pol. B* **40**, 1333 (2009).
- [79] M. Teuerle, P. Żebrowski, and M. Magdziarz, *J. Phys. A* **45**, 385002 (2012).
- [80] K. Szczepaniec and B. Dybiec, *Phys. Rev. E* **90**, 032128 (2014).
- [81] K. Szczepaniec and B. Dybiec, *J. Stat. Mech.* (2015) P06031.
- [82] B. Dybiec and K. Szczepaniec, *Eur. Phys. J. B* **88**, 184 (2015).
- [83] M. E. Wosniack, M. C. Santos, E. P. Raposo, G. M. Viswanathan, and M. G. da Luz, *PLoS Comput. Biol.* **13**, e1005774 (2017).
- [84] O. V. Bychuk and B. OShaughnessy, *J. Chem. Phys.* **101**, 772 (1994).