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Intermittent search strategies revisited: effect of the jump length and biased motion

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Abstract

We study the kinetics of a search of a single fixed target by a large number of searchers performing an intermittent biased random walk in a homogeneous medium. Our searchers carry out their walks in one of two states between which they switch randomly. One of these states (search phase) is a nearest-neighbor walk characterized by the probability of stepping in a given direction (i.e. the walks in this state are not necessarily isotropic). The other (relocation phase) is characterized by the length of the jumps (i.e. when in this state a walker does not perform a nearest-neighbor walk). Within such a framework, we propose a model to describe the searchers' dynamics, generalizing results of our previous work. We have obtained, and numerically evaluated, analytic results for the mean number of distinct sites visited up to a maximum evolution time. We have studied the dependence of this quantity on both the transition probability between the states and the parameters that characterize each state. In addition to our theoretical approach, we have implemented Monte Carlo simulations, finding excellent agreement between the theoretical-numerical and simulations results.

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1. Introduction

The pursuit of optimal search strategies has motivated a great deal of recent work [1-3]. The determination of efficient search strategies has emerged as a crucial problem in behavioral ecology, inspiring extensive experimental and theoretical work [4-6]. It is also relevant in the broader domains of stochastic processes, applied mathematics and molecular biology as well as in social sciences and ecology [7-17].

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In addition to deterministic trajectories, random trajectories have been found to play a crucial role in many search processes (involving, for instance, searchers with less than perfect abilities). These random events can also be optimized so as to improve the success rate of a process. The optimizing strategies must themselves be adjusted to the underlying conditions of the search. For example, it has been shown that among the class of randomly reoriented trajectories, Lévy flights can optimize the encounter rate with random targets [13, 14]. However, Lévy strategies are optimal only in the particular case of non-destructive searches. In the case of destructive searches, where each target definitely disappears upon first encounter, or in the case of a single target, it is possible to show [10] that the trajectories optimizing the encounter rate with targets are simply linear ballistic motions, and therefore not of Lévy type. Also in contrast with the Lévy strategies, it has been observed that numerous animal species switch between two distinct types of behavior (and motion) while foraging [7, 10, 11]. In fact, many foragers, such as plankitovorous fish [18] and ground foraging birds and lizards [4-6], adopt intermittent searching behavior. These intermittent search strategies combine a relocation phase (in which the searcher may or may not capture the target), and a thorough search phase, which allows for easier target detection in the searched region. Such intermittent search strategies have been studied in the context of the *trapping problem* [7, 15-17], where the optimized observable is the mean first-passage time to detection of a target. They have also been studied in the context of the *target problem*, where the quantity that is optimized is usually the survival probability of the target [11].

In our previous work [9-11], we presented a theoretical model for the intermittent search kinetics of a hidden target. Here we revisit the target problem, in which we have a single static target and a set of diffusing searchers, and consider several types of foraging motion. Firstly, we consider the effect of the jump length on the proposed search process. Secondly, we study the influence of anisotropy of the displacements. We set up our scheme exploiting the *multi-state* random-walk formalism developed by Montroll and Weiss [19, 20].

The outline of this paper is as follows. In the next section, we present some results of the multi-state random-walk formalism as well as definitions of the functions to be used later. In section 3, we describe our model, focusing on the one-dimensional (1D) analytically solvable case and making the connection with the Monte Carlo simulations. In section 4, we present some results for the survival probability and related functions, while in the last section we draw some conclusions.

2. Some multi-state random-walk results

Here we recall a few basic results of the formalism developed by Weiss and Montroll [11, 19, 20] that are useful for our purposes. We assume that at time *t* a walker at site *s* on a 1D lattice can be in one of two internal states. The transition probabilities between the internal states are decaying exponential functions of time with the decay rate parameters γ_1 and γ_2 . In addition initially, that is, at time t = 0, the walker is at site s = 0, with probabilities p_i (i = 1, 2) of being in internal state *i*. The joint conditional probabilities $P_j(s, t|0, 0)$ of being at site *s* in the internal state *j* (j = 1, 2) given that the walker was initially at the origin satisfy

$$P_1(s,t|0,0) = g_1 P_{11}(s,t|0,0) + g_2 P_{12}(s,t|0,0),$$
(1)

$$P_2(s,t|0,0) = g_1 P_{21}(s,t|0,0) + g_2 P_{22}(s,t|0,0),$$
(2)

where $P_{ij}(s, t|0, 0)$ is the joint conditional probability of being at site *s* in the internal state *i* at time *t*, given that at t = 0 it was at s = 0 in the internal state *j*. The Weiss and Montroll



Figure 1. Schematic of the motion.

formalism leads to analytic closed expressions for $P_{ij}(s, t|0, 0)$ in Fourier–Laplace space. The relevant transformed results are

$$\hat{P}_{11}(k, u|0, 0) = \frac{u + \gamma_2 - \lambda_2(p_2(k) - 1)}{D(k, u)}$$
$$\hat{P}_{12}(k, u|0, 0) = \frac{\gamma_2}{D(k, u)}$$
$$\hat{P}_{21}(k, u|0, 0) = \frac{\gamma_1}{D(k, u)}$$
$$\hat{P}_{22}(k, u|0, 0) = \frac{u + \gamma_1 - \lambda_1(p_1(k) - 1)}{D(k, u)},$$

where

$$D(k, u) = (u + \gamma_2 - \lambda_2(p_2(k) - 1))(u + \gamma_1 - \lambda_1(p_1(k) - 1)) - \gamma_1\gamma_2,$$

 $p_i(k)$ is the lattice's structure factor for the state j, and λ_i is the diffusion parameter in state i.

3. The model

As was done in [9-11], we restrict ourselves to an infinite discrete chain, and we assume that the fixed target is located at the origin. We assume that the searcher has 'a general tendency' (i.e. a preferred direction of motion, not necessarily pointing toward the prey) that depends on its internal state. We include such a foraging behavior in our model as a biased walk.

In the following we assume that the searcher alternately displays two distinct search behaviors.

- A *search state* during which the searcher carries out a compact exploration of its local area. This local scanning is modeled as an ordinary nearest-neighbor random walk. Eventually the target is found if and when the searcher reaches the target location for the first time.
- A *relocation state* during which the searcher explores more distant regions of the lattice. The target is found during this phase only if the predator lands exactly on it.

At t = 0, we assume that a uniform distribution of searchers/predators begins the search process. The first searcher to find the target/prey catches it with unit probability (i.e. perfect trapping). Each predator performs the two types of motion on the lattice (see figure 1), that is, the random walk with jumps to nearest neighbors, with the rate parameter $\lambda_1 = \lambda$ (*search phase*), and a random walk but with jumps to the *N*th neighbors, with the same rate parameter, $\lambda_2 = \lambda$ (*relocation phase*).

We assume our random walks to be separable. In addition, in one dimension $p_1(k) = \cos(k) + i(1 - 2a)\sin(k)$ and $p_2(k) = \cos(Nk) + i(1 - 2\tilde{a})\sin(Nk)$. The coefficients *a* and \tilde{a} determine the jumping asymmetry along the lattice in each state.

In a homogeneous system, the survival probability $\phi(t)$ may be written as $\phi(t) = e^{-\rho S(t)}$, where S(t) is the mean number of distinct sites visited up to time t, and ρ is the initial

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occupation probability of each site (that is, the predators' density) [9, 19–21]. It was shown in [21] that when the target detection occurs in either of the two internal states,

$$S_{\text{Mar}}(u) = \frac{1}{u^2 P_{\text{Mar}}(s=0, u|0, 0)},$$
(3)

where $P_{\text{Mar}}(s, t|0, 0)$ is the marginal probability (conditioned on the initial site) of finding the predator at site *s* at time *t* regardless of the internal state,

$$P_{\text{Mar}}(s,t|0,0) = P_1(s,t|0,0) + P_2(s,t|0,0).$$
(4)

In the regime of rapid transitions between internal states (with $(\gamma_1 + \gamma_2) \gg \lambda$ and $u \ll (\gamma_1 + \gamma_2)$), $P_{\text{Mar}}(s, u|0, 0)$ may be expressed as [11]

$$P_{\text{Mar}}(s, u|0, 0) = \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{e^{iks} dk}{(1+u) - \left(\frac{\gamma_2}{\gamma_1 + \gamma_2}\right) p_1(k) - \left(1 - \frac{\gamma_2}{\gamma_1 + \gamma_2}\right) p_2(Nk)}.$$
(5)

With the abbreviations $\alpha = \frac{\gamma_1}{\gamma_1 + \gamma_2}$, $z = \frac{1}{u+1}$, b = 1 - 2a and $\tilde{b} = 1 - 2\tilde{a}$, we can write

$$P_{\text{Mar}}(s, u|0, 0) = \frac{z}{2\pi} \int_{-\pi}^{\pi} \frac{e^{iks} dk}{1 - z[(1 - \alpha)(\cos(k) + ib\sin(k)) + \alpha(\cos(Nk) + i\tilde{b}\sin(Nk))]}.$$
(6)

This expression is a slight generalization of equation (4.4) in [9] or of equation (15) in [11].

3.1. The effect of the jump length in the search process

Here we consider the effect of the length of the jumps on the search process, postponing the discussion of the anisitropy of the displacement to the next subsection. We therefore take $b = \tilde{b} = 0$, and hence

$$P_{\text{Mar}}(s, u|0, 0) = \frac{z}{\pi} \int_0^{\pi} \frac{\cos(ks) \, dk}{1 - z[(1 - \alpha)\cos(k) + \alpha\cos(Nk)]}.$$
(7)

Let k_i be the roots of $1 - z[(1 - \alpha)\cos(k) + \alpha\cos(Nk)] = 0$. Using the identity

$$2\cos(Nk) = (2\cos(k))^{N} - N(2\cos(k))^{N-2} + \frac{N}{2}\binom{N-3}{1}(2\cos(k))^{N-4} - \cdots.$$
(8)

Equation (7) can be written as

$$P_{\text{Mar}}(s, u|0, 0) = \frac{1}{2^{N-1}\alpha} \sum_{i=1}^{N} A_i \int_0^{\pi} \frac{\cos(ks)}{(\cos(k) - \cos(k_i))} \, \mathrm{d}k,\tag{9}$$

where the coefficients A_i are functions of the k_i .

The evaluation of the integral up to N = 4, although tedious, is straightforward and can be done analytically. The results following the numerical Laplace inversion are shown in section 4. Results for N > 4 are also shown, but these are obtained from Monte Carlo simulations.

3.2. Drift-controlled random walks

We now consider a certain degree of anisotropy in the displacement of the random walk. In order to simplify the analysis, we only consider jumps to next nearest neighbors (N = 2) in the relocation phase. The general case of arbitrary values of *b* and \tilde{b} is treated in the appendix.



Figure 2. Total mean number of distinct sites visited up to time t = 100. The lines represent theoretical–numerical calculations, and the symbols represent the Monte Carlo simulations. The circles correspond to walks in which the relocation state takes the walker to next-nearest neighbors, while the squares are for walks to third neighbors and crosses to fourth neighbors in this phase.

Here, if we have the same anisotropy in both states $(b = \tilde{b})$, then for $b \ll 1$ $(a \simeq \frac{1}{2})$ we can carry out a perturbative analysis of equation (6) in terms of b,

$$P_{\text{Mar}}(s, u|0, 0) = \frac{1}{\pi} \int_0^{\pi} \cos(ks) P_{\text{Mar}}(k, u|0, 0) \Big|_{b=0} dk + \frac{b^2}{\pi} \int_0^{\pi} \cos(ks) \frac{\partial^2 P_{\text{Mar}}(k, u|0, 0)}{\partial b^2} \Big|_{b=0} dk + \cdots$$
(10)

When b = 0 the odd coefficients vanish from the integrand. The results, after performing the numerical Laplace inversion, are shown in the next section.

4. Results

In order to test our theoretical results we present comparisons with Monte Carlo simulations. To evaluate the theoretical expressions we have used a numerical procedure to perform the inverse Laplace transform [22]. For the initial condition, we have chosen $g_1 = g_2 = 1/2$, and the total evolution time was set equal to t = 100. Regarding the Monte Carlo simulations, the process is such that at each click of the clock the searcher decides whether to jump into the search state or the relocation state with transition probability α or $1 - \alpha$, respectively. We have averaged this walk over 10^5 realizations.

4.1. The Jump length in the search process

In figure 2 we show S(t), the mean number of distinct sites visited, for different jump lengths in the relocation state as a function of α . From the figure we can see that there is excellent agreement between the theoretical–numerical results and the Monte Carlo simulations. From this figure it is also apparent that the maximum mean number of distinct sites visited varies with the jump length. This behavior is described in figure 3, where we show the maximum



Figure 3. First panel: transition probability that leads to a maximum in the mean number of distinct sites visited, as a function of the jump length. Second panel: maximum mean number of distinct sites visited as a function of the jump length in the relocation state, that is, the mean number of distinct sites visited at the values of α corresponding to the maxima in figure 2. All data are obtained from Monte Carlo simulations.

mean number of distinct sites visited as a function of the jump length in the relocation state. The figure shows a curve increasing toward a plateau value which arises when the jump length increases so that the possibility of jumping to the sites already visited during relocation is low.

4.2. Drift-controlled random walk

The walk with a small bias, that is, a small departure from the case analyzed in [11], is shown in figure 4. This figure shows that a small bias produces small departures from the unbiased response. There is excellent agreement between the numerical–analytical results and the Monte Carlo simulations.

In figure 5(*a*), we show the phase diagram that summarizes the behavior of the system with a bias up to a fixed evolution time t = 100. The diagram is plotted as a function of α , the parameter that regulates the intermittency, and of the bias difference $(a - \tilde{a})$. The mean number of distinct sites visited is shown in gray scale, with darker regions representing larger



Figure 4. The mean number of distinct sites visited for a small bias at time t = 100. The lines represent numerical calculations, the symbols represent Monte Carlo simulations: the circles correspond to the case of no bias, while the black squares are for a = 0.55.

values of $S(\alpha, a - \tilde{a}; t = 100)$. In this figure we only show the positive values of $(a - \tilde{a}); - (a - \tilde{a})$ generates the same diagram.

In order to emphasize the effects of the bias, in figure 5(b) and (c) we show cuts of $S(\alpha, a - \tilde{a}; t = 100)$. Each section (I–VI) of the phase diagram is represented by a curve. In particular, we exhibit the case where there is a strong bias in each state and we compare different biases in the relocation state. These curves show a rich dynamical phenomenology. When the bias in the relocation state is the opposite to that of the search state, the curves show a local maximum and a local minimum (curves I and II in figure 5(b). This is a novel result because up to now the nonmonotonic responses obtained from similar systems had shown only a maximum. As the bias during the relocation state is decreased (see, for example, the case $\tilde{a} = 0.45$), the maximum disappears and a small plateau of the constant S(t) appears (curve III). When the bias in the relocation state increases toward the direction of that of the search state, the curves decrease monotonically (curves IV and V in figure 5(c)). However, when the values of both biases are in the same or almost the same direction, the maximum reappears (curve VI). We note the excellent agreement between the analytical–numerical results and the Monte Carlo simulations.

The minimum obtained in figure 5(a) can be understood in the following way.

- The walker in the two states of motion has a general tendency (bias) that points in opposite directions, i.e. the tendency in one state is against the one in the other state.
- The cases $\alpha \sim 0$, $\alpha \sim 1$ (single state movement) are straightforward to analyze. These correspond to the searcher being in the search mode or in the relocation mode almost all of the time, respectively, and, since both are biased, we have $S_{\alpha \sim 0}(t) \sim |1 2a| t$ or $S_{\alpha \sim 1}(t) \sim |1 2\tilde{a}| t$, as seen in figure 5(b) [19].
- For the behavior near the minimum ($\alpha < 0.5$) the walker remains most, but not all, of its time in the search state. In this state (jumps to nearest neighbors), the exploration is compact; every site is visited, so each transition in the relocation state is likely to end at a site that has already been visited in the search phase, contributing in this way to a minimum in the mean number of distinct sites visited.



Figure 5. (*a*) A phase diagram of the system with a bias for a fixed time t = 100 as a function of α (the parameter that regulates the intermittency) and the bias difference $(a - \tilde{a})$. In this figure, darker gray means a larger value of the distinct number of sites visited, $S(\alpha, a - \tilde{a}; t = 100)$. Also shown are the numerical calculations (lines) and Monte Carlo simulations (symbols) for the mean number of distinct sites visited up to time t = 100, for a quasi-ballistic movement in the search phase (a = 0.9); (*b*) biased movement to the right in the relocation phase, with circles for $\tilde{a} = 0.1$ (I), squares for $\tilde{a} = 0.3$ (II), and crosses for $\tilde{a} = 0.45$ (III); (*c*) biased movement to the left, with crosses for $\tilde{a} = 0.6$ (IV), squares for $\tilde{a} = 0.7$ (V) and circles for $\tilde{a} = 0.9$ (VI).

One might ask why a minimum is not reached for values of $\alpha > 0.5$. For these values of α , the walker remains most of its time in the relocation state (jumps to further neighbors). In this state, the pattern of visited sites may be thought of as a 'strainer'. This could be interpreted as a defective way of covering territory. However, as transitions to the search state are allowed, the excursions in this mode are likely to fill the gaps left by the walker on its journey during the relocation phase. Thus, transitions in this regime ($\alpha > 0.5$) contribute positively, increasing the mean number of distinct sites visited.

5. Conclusions

We have presented a simple model for the search kinetics of a target hidden at the origin of a chain by a set of searchers performing intermittent motion. The model is based only on random walks, and complements previous related results given in [9-11]. Here we have considered both the influence of anisotropy in the displacement of the searcher and the effect of the jump length on the proposed search process.

The intermittency has been characterized by the probability density functions for jumps between internal states. For simplicity, we have restricted the analysis of intermittency to time exponential functions with the parameters γ_1 and γ_2 . However, the present framework is not restricted to these choices.

The present generalization of the work in [11] allowed us to obtain a rich system dynamics for the mean number of distinct sites visited, passing from a single minimum, through monotonic behavior, to situations with both a local maximum and a local minimum, and finally to a single maximum. All of these results are predicted by the theory and supported by the Monte Carlo simulations, with excellent agreement between the two.

The present model of intermittent search can be generalized in several directions: higher dimensions, finite size domain systems, continuous systems, imperfect detection, dynamical behavior of the target, non-Markovian transitions between internal states, etc. All of these aspects will be the subjects of future work.

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Appendix. Drift-controlled random walk

Here we describe some essential details for section 3.2. In order to simplify the analysis we consider jumps to next nearest neighbors (N = 2) in the relocation state. We start with equation (6), and adopt the notation $P_{\text{Mar}}(s, u|0, 0) \equiv P_{\text{Mar}}(s, u)$. Defining $v = \exp(ik)$ and using the known relations $\cos(Nk) = \frac{\exp(iNk) + \exp(-iNk)}{2}$, $\sin(Nk) = \frac{\exp(iNk) - \exp(-iNk)}{2i}$, equation (6) can be transformed into an integral along the unit circle in the complex plane,

$$P_{\text{Mar}}(s,u) = \frac{1}{2\pi i} \oint_{|v|=1} \frac{\nu^{s+1} \, d\nu}{\frac{-\alpha(1+\tilde{b})}{2} \left[\nu^4 + \frac{(1-\alpha)(1+b)}{\alpha(1+\tilde{b})} \nu^3 - \frac{2}{z\alpha(1+\tilde{b})} \nu^2 + \frac{(1-\alpha)(1-b)}{\alpha(1+\tilde{b})} \nu + \frac{(1-b)}{(1+\tilde{b})} \right]}.$$
 (A.1)

The roots of the denominator in equation (A.1) can be found using standard procedures [23]. Calling the *l*-root v_l , we write the last integral as

$$P_{\text{Mar}}(s,u) = -\frac{2}{\alpha(1+\tilde{b})} \frac{1}{2\pi i} \oint_{|\nu|=1} \prod_{l} \frac{\nu^{s+1}}{\nu - \nu_{l}} \, \mathrm{d}\nu = -\frac{2}{\alpha(1+\tilde{b})} \sum_{l} \frac{A_{l}}{2\pi i} \oint_{|\nu|=1} \frac{\nu^{s+1}}{\nu - \nu_{l}} \, \mathrm{d}\nu.$$
(A.2)

The last equality follows upon expanding the product into partial fractions. The coefficients A_l are expressed in terms of the v_l , e.g., $A_1 = [(v_1 - v_2)(v_1 - v_3)(v_1 - v_4)]^{-1}$, $A_2 = [(v_2 - v_1)(v_2 - v_3)(v_2 - v_4)]^{-1}$ and so on. Considering the roots that lie inside the unit circle, equation (A.2) is ready to be evaluated using Cauchy's residue theorem.

While we are able to obtain analytical results in Laplace space, their size and complexity makes the analysis a difficult task. The inversion of the Laplace transform of these results is beyond our capabilities and so we have used a numerical procedure instead [22].

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