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A minimal model of intermittent search in dimension two

O Bénichou, C Loverdo, M Moreau and R Voituriez

Laboratoire de Physique Théorique de la Matière Condensée, UMR CNRS 7600, Université Pierre et Marie Curie, 4 Place Jussieu, 75252 Paris, France

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Abstract

We propose and analyse a model of bidimensional search processes, explicitly relying on the widely observed intermittent behaviour of foraging animals, which involves a searcher enjoying minimal orientational and temporal memory skills. We show analytically that, in the case of non-revisitable targets, intermittent strategies can minimize the search time, and therefore constitute real optimal strategies, as opposed to Lévy flights strategy which are optimal only in the particular case of revisitable targets. Two representative modes of target detection are presented, and they allow us to determine which characteristics of the optimal strategy are robust and do not depend on the specific characteristics of detection mechanisms. In particular, our study tends to show that the optimal duration of the ballistic phase is a universal feature of bidimensional intermittent search strategies. Last, by comparing the results of our minimal model to systematic search strategies, we show that if temporal and orientational memory skills speed up the search, they do not change the order of magnitude of the search time.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Many physical, chemical or biological processes are initiated by the encounter of a moving entity, the ‘searcher’, with a specific ‘target’ of unknown position. Striking examples include diffusion limited reactions [1], such as the association of a protein with its specific target site on DNA [2–4]. At larger scales, one could also mention the behaviour of animals searching for food, shelters or partners [5–12], or even human activities such as victim localization by rescuers [14]. These examples, involving processes of vital importance, underline the necessity for the searcher to minimize the search time and subsequently adopt the fastest strategy. This question of determining the trajectories which optimize the search efficiency, put forward in the early works [7–9], has recently motivated numerous studies in various fields [10, 11, 15–20].

Besides deterministic trajectories, relevant for instance in the case of organized human activities, and extensively studied in the context of systematic search [14], random trajectories have proved to play a crucial role in many search processes (involving for instance a searcher with fewer abilities). In particular, it has been shown that among the class of randomly reoriented ballistic trajectories, Lévy flights can optimize the encounter rate with random targets [9–11]. However, this result holds only when target detection obeys quite specific rules. Namely, Lévy strategies are optimal only in the particular case of non destructive search: in this model a target is found as soon as the searcher approaches closer than a given radius of detection, and is regenerated at the same location after a finite time [9, 11]. Obviously this prescription, if reasonable in some cases, should not be taken as a general rule. In the relevant case of destructive search, where each target definitely disappears after the first encounter, or in the case of a single target, one can show [9] that the trajectories optimizing the encounter rate with targets are simply linear ballistic motions, and therefore not of Lévy type. However, in the context of behavioural ecology, if destructive search is widely observed [5, 6], the purely ballistic strategy predicted by [9] in that case does not explain the generally observed reoriented animal trajectories [5].

As opposed to these Lévy strategies, where the searcher always moves at constant (and randomly oriented) velocity, it has been observed that numerous animal species, including lizards, fishes, and birds [6, 21], actually switch between two very distinct types of behaviour (and motion) while foraging. These intermittent search strategies combine phases of fast displacement, non-receptive to the targets, and slow reactive search phases, which only allow for target detection. If one thinks of an everyday-life situation, for instance the search for keys lost on a lawn, intermittent strategies are rather intuitive: one searches a small area carefully, then decides to explore an unvisited region and moves quickly to relocate and search again. However, the net efficiency of intermittent strategies cannot be elucidated on qualitative grounds only: if phases of fast displacement allow for the exploration of unvisited regions, they are also time consuming because they do not permit target detection.

A model of intermittent search in one dimension has been proposed in [12], and it proved to provide a satisfactory agreement with experimental data from behavioural ecology. As dimension two provides a much broader field of applications, in particular for both human and animal activities, we developed very recently [13] a model of bidimensional intermittent search. This model was designed to be minimal in the following sense: the searcher has no temporal memory, as the transition rates between phases are constant, and no orientational memory, as the direction of ballistic flights of the relocating phases is random. In the framework of this minimal model, we showed in [13] that bidimensional intermittent search strategies *do optimize* the search time for non-revisitable targets. Here, after briefly redefining the model, we provide a detailed derivation of the main results of [13]: in particular, we explicitly determine the optimal strategy by calculating the durations of each phases which minimize the search time for a target. We then put forward further features of this model and give new numerical simulations which confirm its validity. We also compare the efficiency of this intermittent searcher enjoying minimal memory skills with different strategies involving a more advanced searcher enjoying temporal or orientational memory. We show that quite unexpectedly memory effects are minor and do not change the order of magnitude of the search time. From a more technical point of view, we also obtain as a by-product the mean first passage time for a Pearson-type random walk, which belongs to a class of non-trivial problems which have been investigated for a long time [22–26]. Our approach relies on an approximate analytical solution based on a decoupling hypothesis, which is validated numerically over a wide range of parameters.

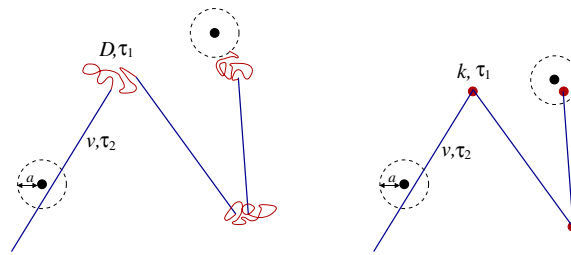


Figure 1. Two models of intermittent search: the searcher alternates slow reactive phases (regime 1) of mean duration τ_1 , and fast non-reactive ballistic phases (regime 2) of mean duration τ_2 . *Left*: the slow reactive phase is diffusive and detection is infinitely efficient. *Right*: the slow reactive phase is static and detection takes place with finite rate k .

2. Model

We start with the same model as already introduced in [13], which we briefly recall here for the sake of self-consistency. We are interested in a two-state searcher (see figure 1), whose position is labelled by \mathbf{r} . The searcher performs slow reactive phases (denoted 1), randomly interrupted by fast relocating ballistic flights of constant velocity v and random direction (phases 2). The duration of each phase i is assumed to be exponentially distributed with mean τ_i . As it has been observed that fast motion usually strongly degrades perception abilities [6, 21], we assume here that the searcher is able to detect a target only during reactive phases 1. Here we do not aim at modelling the detection phase accurately, which involves complex biological processes. However, we wish to propose essentially two basic modes of detection, which lead us to distinguish between two types of reactive phases 1. The first one, referred to in the following as the ‘dynamic mode’, corresponds to a diffusive modelling (with diffusion coefficient D) of the search phase as proposed in [12] in agreement with observations for vision [27], tactile sense or olfaction [5]. In this mode, detection is assumed to be infinitely fast: a target is found as soon as the searcher–target distance is smaller than a given reaction radius a . In contrast, in the second mode, denoted as the ‘static mode’, the searcher is immobile during the search phases, and the reaction occurs with a finite rate k . Note that this description is quite standard in reaction–diffusion systems [1] or operational searches [14]. Obviously a more realistic description is obtained by combining both modes and considering a diffusive searcher with diffusion coefficient D and finite reaction rate k . In order to reduce the number of parameters and to extract the main features of each mode, we first study them separately by taking successively the limits $k \rightarrow \infty$ and $D \rightarrow 0$ of this general case, which we eventually study numerically in this paper. More precisely, in the above-mentioned limiting cases, we address the following questions. What is the mean time it takes the searcher to find a target? Can this search time be minimized? And if so, for which values of the average durations τ_i of each phase? How does the mean search time compare with deterministic strategies?

3. Basic equations

We now present the basic equations combining the two active search modes introduced above in the case of a point-like target centred in a spherical domain of radius b with reflecting boundary. Note that this geometry mimics both relevant situations of a single target and of infinitely many regularly spaced non-revisitable targets. For this process, the mean first passage time (MFPT)

at a target satisfies the following backward equation [28]:

$$D\nabla_{\mathbf{r}}^2 t_1 + \frac{1}{2\pi\tau_1} \int_0^{2\pi} (t_2 - t_1) d\theta_{\mathbf{v}} - kI_a(\mathbf{r})t_1 = -1 \quad (1)$$

$$\mathbf{v} \cdot \nabla_{\mathbf{r}} t_2 - \frac{1}{\tau_2} (t_2 - t_1) = -1 \quad (2)$$

where t_1 stands for the MFPT starting from state 1 at position \mathbf{r} , and t_2 for the MFPT starting from state 2 at position \mathbf{r} with velocity \mathbf{v} . The function I_a is defined by $I_a(\mathbf{r}) = 1$ if $|\mathbf{r}| \leq a$ and $I_a(\mathbf{r}) = 0$ if $|\mathbf{r}| > a$. In the present form, these integro-differential equations (completed with boundary conditions explicitly given below) do not seem to allow for an exact resolution with standard methods. We propose in the following a decoupling approximation which turns out to be exact in the one-dimensional (1D) case.

3.1. Exact decoupling in one dimension

In one dimension, the velocity associated to the relocating phases assumes two opposite directions denoted $+$ and $-$. The analogue of equations (1), (2) in one dimension then reads

$$D \frac{d^2 t_1}{dx^2} + \frac{1}{2\tau_1} (t_{2+} + t_{2-} - 2t_1) - kI_a(x) = -1 \quad (3)$$

$$v \frac{dt_{2+}}{dx} + \frac{1}{\tau_2} (t_1 - t_{2+}) = -1 \quad (4)$$

$$-v \frac{dt_{2-}}{dx} + \frac{1}{\tau_2} (t_1 - t_{2-}) = -1. \quad (5)$$

This system of ordinary differential equations is most conveniently solved by introducing the auxiliary functions $s = (t_{2+} + t_{2-})/2$ and $d = (t_{2+} - t_{2-})/2$. Summing and subtracting equations (4) and (5) leads to

$$d = \frac{v}{\lambda_2} s'(x) \quad \text{and} \quad v d'(x) + \frac{1}{\tau_2} (t_1 - s) = -1. \quad (6)$$

The initial system of equations (3)–(5) is finally rewritten as

$$D t_1''(x) + \frac{1}{\tau_1} (s - t_1) - kI_a(x) = -1 \quad (7)$$

$$v^2 \tau_2 s''(x) + \frac{1}{\tau_2} (t_1 - s) = -1 \quad (8)$$

which can easily be solved by considering the two limiting modes of detection (dynamic or static).

3.2. Approximate decoupling in two dimensions

We propose here an approximate resolution of the integro-differential equations (1), (2), which closely parallels the 1D approach. We define the following auxiliary functions:

$$s(\mathbf{r}) = \frac{1}{2\pi} \int_0^{2\pi} t_2 d\theta_{\mathbf{v}}, \quad \mathbf{d}(\mathbf{r}) = \frac{1}{2\pi} \int_0^{2\pi} t_2 \mathbf{v} d\theta_{\mathbf{v}}. \quad (9)$$

Averaging equations (2) and (2) times \mathbf{v} over $\theta_{\mathbf{v}}$, one successively gets

$$\nabla \cdot \mathbf{d} - \frac{1}{\tau_2} (s(\mathbf{r}) - t_1) = -1 \mathbf{d} = \frac{\tau_2}{2\pi} \int_0^{2\pi} (\mathbf{v} \cdot \nabla t_2) \mathbf{v} d\theta_{\mathbf{v}}, \quad (10)$$

which gives in turn

$$\nabla \cdot \mathbf{d} = \frac{\tau_2}{2\pi} \sum_{i,j} \frac{\partial^2}{\partial x_i \partial x_j} \langle v_i v_j t_2 \rangle_{\theta_v} \quad (11)$$

where $\langle \cdot \rangle_{\theta_v}$ stands for the average over θ_v . We now make the following decoupling assumption,

$$\langle v_i v_j t_2 \rangle_{\theta_v} \simeq \langle v_i v_j \rangle_{\theta_v} \langle t_2 \rangle_{\theta_v} = \frac{v^2}{2} \delta_{ij} s(\mathbf{r}), \quad (12)$$

which leads, together with equation (10), to the diffusion-like equation:

$$\tilde{D} \nabla^2 s(\mathbf{r}) - \frac{1}{\tau_2} (s(\mathbf{r}) - t_1) = -1 \quad (13)$$

where $\tilde{D} = v^2 \tau_2 / 2$. Rewriting equation (1) as

$$D \nabla^2 t_1 + \frac{1}{\tau_1} (s(\mathbf{r}) - t_1) - k I_a(\mathbf{r}) t_1 = -1, \quad (14)$$

equations (13) and (14) provide a closed system for the variables s and t_1 , whose resolution is presented in the next sections. The key quantity of our study is the search time $\langle t \rangle$, defined as t_1 uniformly averaged over the initial position of the searcher

$$\langle t \rangle = \frac{2}{b^2} \int_0^b t_1 r \, dr. \quad (15)$$

This last averaging reflects the complete ignorance of the target position.

As we proceed to show by comparing our approximate analytical results to numerical simulations, the validity domain of assumption (12) is much broader than the ‘Brownian’ limit $v \rightarrow \infty$ and $\tau_2 \rightarrow 0$ with \tilde{D} fixed, in which t_2 is independent of the direction of \mathbf{v} . Indeed, it is also valid in the limit $v \tau_2 \gg b$, in which a ballistic phase includes many reorientations due to successive reflections on the boundary $r = b$. In addition, as shown previously, this assumption is exact in one dimension.

4. Solution in the dynamic mode of detection

4.1. Calculation of the search time

We first present the solution of equations (13), (14) in the ‘dynamic mode’ ($k \rightarrow \infty$). We denote by t_i^{ext} (resp. t_i^{int}) the MFPT starting from state i and from a position exterior (resp. interior) to the target. Taking advantage of the spherical symmetry, we have for the exterior variables

$$D \frac{d^2 t_1^{\text{ext}}}{dr^2} + D \frac{1}{r} \frac{dt_1^{\text{ext}}}{dr} + \frac{1}{\tau_1} (s^{\text{ext}} - t_1^{\text{ext}}) = -1 \quad (16)$$

$$\tilde{D} \frac{d^2 s^{\text{ext}}}{dr^2} + \tilde{D} \frac{1}{r} \frac{ds^{\text{ext}}}{dr} + \frac{1}{\tau_2} (t_1^{\text{ext}} - s^{\text{ext}}) = -1. \quad (17)$$

As for the interior variables, $t_1^{\text{int}} = 0$ and

$$\tilde{D} \frac{d^2 s^{\text{int}}}{dr^2} + \tilde{D} \frac{1}{r} \frac{ds^{\text{int}}}{dr} - \frac{1}{\tau_2} s^{\text{int}} = -1. \quad (18)$$

The general solution of this linear system of ordinary differential equations reads

$$t_1^{\text{ext}}(r) = -\frac{1}{4} \frac{r^2(\tau_1 + \tau_2)}{D\tau_1 + \tilde{D}\tau_2} + A_1 + A_2 \ln(r) + A_3 I_0(\alpha r) + A_4 K_0(\alpha r) \quad \text{for } a < r < b \quad (19)$$

$$s^{\text{ext}}(r) = \frac{(D - \tilde{D})\tau_2\tau_1 - r^2(\tau_1 + \tau_2)/4}{D\tau_1 + \tilde{D}\tau_2} + A_1 + A_2 \ln(r) - \frac{D\tau_1}{\tilde{D}\tau_2} (A_3 I_0(\alpha r) + A_4 K_0(\alpha r)) \quad \text{for } a < r < b \quad (20)$$

$$s^{\text{int}}(r) = \tau_2 + A_5 I_0\left(r/\sqrt{\tilde{D}\tau_2}\right) + A_6 K_0\left(r/\sqrt{\tilde{D}\tau_2}\right) \quad \text{for } r < a \quad (21)$$

where I_i and K_i are modified Bessel functions, and $\alpha = (1/(D\tau_1) + 1/(\tilde{D}\tau_2))^{1/2}$. The resolution of equations (16)–(18) involves six unknowns A_i , which are determined by the following boundary conditions:

- $s^{\text{int}}(r)$ has to remain finite when $r \rightarrow 0$, which leads to $A_6 = 0$;
- the exterior boundary conditions are reflecting, which yields

$$\frac{dt_1^{\text{ext}}(b)}{dr} = 0 \quad \text{and} \quad \frac{ds^{\text{ext}}(b)}{dr} = 0; \quad (22)$$

- the continuity of t_1 , s and ds/dr at $r = a$ gives

$$t_1^{\text{ext}}(a) = t_1^{\text{int}}(a) = 0 \quad (23)$$

$$s^{\text{ext}}(a) = s^{\text{int}}(a) \quad (24)$$

$$\frac{ds^{\text{ext}}(a)}{dr} = \frac{ds^{\text{int}}(a)}{dr}. \quad (25)$$

Solving this linear system of six equations with six unknowns, and then averaging over the initial position of the searcher, we finally obtain for the search time (15)

$$\langle t \rangle = (\tau_1 + \tau_2) \frac{1 - a^2/b^2}{(\alpha^2 D\tau_1)^2} \left\{ \alpha \alpha (b^2/a^2 - 1) \frac{M}{2L_+} - \frac{L_-}{L_+} - \frac{\alpha^2 D\tau_1 (3 - 4 \ln(b/a)) b^4 - 4a^2 b^2 + a^4}{8\tilde{D}\tau_2 (b^2 - a^2)} \right\} \quad (26)$$

with

$$L_{\pm} = I_0\left(a/\sqrt{\tilde{D}\tau_2}\right) (I_1(b\alpha)K_1(a\alpha) - I_1(a\alpha)K_1(b\alpha)) \pm \alpha \sqrt{\tilde{D}\tau_2} I_1\left(a/\sqrt{\tilde{D}\tau_2}\right) (I_1(b\alpha)K_0(a\alpha) + I_0(a\alpha)K_1(b\alpha))$$

and

$$M = I_0\left(a/\sqrt{\tilde{D}\tau_2}\right) (I_1(b\alpha)K_0(a\alpha) + I_0(a\alpha)K_1(b\alpha)) - 4 \frac{a^2 \sqrt{\tilde{D}\tau_2}}{\alpha (b^2 - a^2)^2} I_1\left(a/\sqrt{\tilde{D}\tau_2}\right) (I_1(b\alpha)K_1(a\alpha) - I_1(a\alpha)K_1(b\alpha)).$$

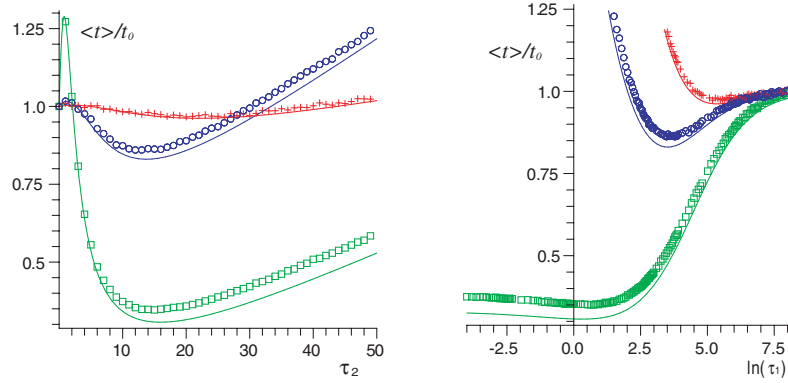


Figure 2. Simulations (points) versus analytical approximate (line) of the search time in the ‘dynamic mode’: the search time rescaled by the value in the absence of intermittence t_0 as a function of τ_2 (left) and $\ln \tau_1$ (right) (the logarithmic scale has been used due to the flatness of the minimum), for $D = 1, v = 1, b = 226$. *Left:* $a = 10, \tau_1 = 1.37$ (green boxes); $a = 1, \tau_1 = 33.6$ (blue circles); $a = 0.1, \tau_1 = 213$ (red crosses). *Right:* $a = 10, \tau_2 = 15.9$ (green boxes); $a = 1, \tau_2 = 13.7$ (blue circles); $a = 0.1, \tau_2 = 22$ (red crosses).

Table 1. Difference between simulations and analytical approximation (26) in the ‘dynamic mode’. $v = 1, D = 1$.

a	b			
	28.2	113	451	1800
10		0.113	0.0972	0.0812
1	0.0279	0.0348	0.0291	0.0348
0.1	0.0151	0.0171	0.0180	0.0167
0.01	0.0129	0.0126	0.00778	0.0147

4.2. Comparison with numerical simulations

In order to check the validity of the previous decoupling approximation, we performed numerical simulations of the search process. We used the algorithm developed in [29] to generate the diffusive phases. Expression (26) has proved to be in very good agreement with numerical simulations for a wide range of the parameters (see figure 2). More quantitatively, this agreement can be evaluated by computing the following quantity: $d = \left(\frac{1}{N} \sum_{i=1}^N \frac{(\langle t_i \rangle - f(\tau_{1,i}, \tau_{2,i}))^2}{\langle t_i \rangle^2} \right)^{\frac{1}{2}}$, with N the number of couples (τ_1, τ_2) for which we have calculated $\langle t \rangle$ in the simulation, and f the function (26). What we found (see table 1) is that the typical relative error between the approximate theory and the numerical simulations of the search time is less than 5%. More precisely, this error is small except when the condition $a \ll b$ is not fulfilled, and depends mainly on a (decreasing with a). Anyway, the analytical approximate captures very well the position of the minimum obtained from numerical simulations.

4.3. Optimization of the search time

Three lengths are involved in the problem: a, b and D/v . We investigate here the optimization of the search time in the three following cases: $a < b \ll D/v, a \ll D/v \ll b, D/v \ll a \ll b$.

4.3.1. $a < b \ll D/v$. In that case, intermittence is not favourable. Indeed, the typical time required to explore the whole domain of radius b is of order b^2/D for a diffusive motion, which is shorter than the corresponding time b/v for a ballistic motion. As a consequence, it is never useful to interrupt the diffusive phases by merely relocating ballistic phases.

4.3.2. $a \ll D/v \ll b$. In this second regime, one can use the following approximate formula for the search time:

$$\langle t \rangle = \frac{b^2}{4Dv^2\alpha^2} \frac{\tau_1 + \tau_2}{\tau_1\tau_2^2} \left\{ 4 \ln(b/a) - 3 - 2 \frac{(v\tau_2)^2}{D\tau_1} (\ln(\alpha a) + \gamma - \ln 2) \right\}, \quad (27)$$

γ being the Euler constant. An approximate criterion to determine if intermittence is useful can be obtained by expanding $\langle t \rangle$ in powers of $1/\tau_1$ when $\tau_1 \rightarrow \infty$ ($\tau_1 \rightarrow \infty$ corresponds to the absence of intermittence), and requiring that the coefficient of the term $1/\tau_1$ is negative for all values of τ_2 . Using this criterion, we find that intermittence is useful if

$$\sqrt{2} \exp(-7/4 + \gamma) vb/D - 4 \ln(b/a) + 3 > 0. \quad (28)$$

In this case, using equation (27), the optimization of the search time leads to

$$\tau_{1,\min} = \frac{b^2}{D} \frac{4 \ln w - 5 + c}{w^2(4 \ln w - 7 + c)}, \quad \tau_{2,\min} = \frac{b}{v} \frac{\sqrt{4 \ln w - 5 + c}}{w} \quad (29)$$

where w is the solution of the implicit equation $w = 2vbf(w)/D$ with

$$\frac{\sqrt{4 \ln w - 5 + c}}{f(w)} = -8(\ln w)^2 + (6 + 8 \ln(b/a)) \ln w - 10 \ln(b/a) + 11 - c(c/2 + 2 \ln(a/b) - 3/2) \quad (30)$$

and $c = 4(\gamma - \ln(2))$, γ being the Euler constant. A useful approximation for w is given by

$$w \simeq \frac{2vb}{D} f\left(\frac{vb}{2D \ln(b/a)}\right). \quad (31)$$

At the minimum, τ_1 and τ_2 satisfy the following scaling relation:

$$\frac{\tau_{1,\min}}{\tau_{2,\min}^2} = \frac{v^2}{D} \frac{1}{4 \ln w - 7}. \quad (32)$$

As $\ln w$ is a very slowly varying function, this optimal strategy corresponds to the case where the diffusion length is of the same order of magnitude as the ballistic length, as could have been expected.

On the other hand, the ratio of the minimum value of the search time over its value in absence of any intermittence is here given by

$$\frac{\langle t \rangle_{\min}}{t_0} \sim 2 \left\{ \frac{1}{4 \ln w - 5} + \frac{wD}{bv} \frac{4 \ln w - 7}{(4 \ln w - 5)^{3/2}} \right\} \left\{ \frac{4 \ln b/a - 3 + 2(4 \ln w) \ln(b/aw)}{4 \ln b/a - 3 + 4a^2/b^2 - a^4/b^4} \right\}. \quad (33)$$

If intermittence significantly speeds up the search in this regime (typically by a factor 2), it does not change the order of magnitude of the search time.

4.3.3. $D/v \ll a \ll b$. In the last regime $D/v \ll a \ll b$, the optimal strategy is obtained for

$$\tau_{1,\min} \sim \frac{D}{2v^2} \frac{\ln^2(b/a)}{2 \ln(b/a) - 1}, \quad \tau_{2,\min} \sim \frac{a}{v} (\ln(b/a) - 1/2)^{1/2}. \quad (34)$$

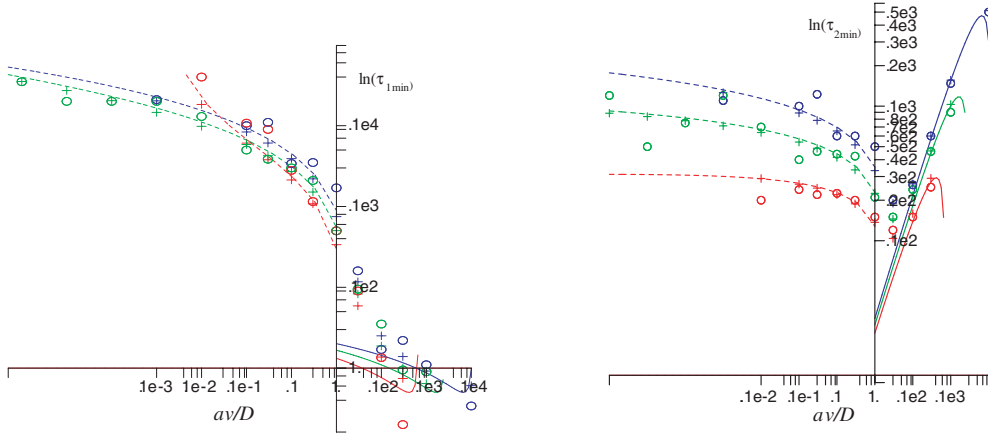


Figure 3. Values of τ_1 and τ_2 at the minimum of $\langle t \rangle$, obtained via the approximation in the case $a \ll D/v$ (29) (discontinuous line), via the approximation in the case $D/v \ll a$ (34) (continuous line), via the minimization of $\langle t \rangle$ (26) (crosses), and via the simulations (circles) (which are not very precise due to the flatness of the minimum), for $v = 1$, $D = 1$, $b = 113$ (red), $b = 451$ (light green), and $b = 1800$ (dark blue). *Left:* $\ln \tau_{1,\min}$ as a function of $\ln(av/D)$. *Right:* $\ln \tau_{2,\min}$ as a function of $\ln(av/D)$.

This optimal strategy corresponds to a scaling law

$$\frac{\tau_{1,\min}}{\tau_{2,\min}} \sim \frac{D}{a^2} \frac{1}{(2 - 1/\ln(b/a))^2} \tag{35}$$

which here does not depend on v .

The ratio of the minimum value of the search time over its value in the absence of intermittence is then given by

$$\frac{\langle t \rangle_{\min}}{t_0} \sim \frac{8D}{\sqrt{2}av} \left\{ \frac{1}{4\ln(b/a) - 3} \frac{I_0(2/\sqrt{2\ln(b/a)} - 1)}{I_1(2/\sqrt{2\ln(b/a)} - 1)} + \frac{1}{2\sqrt{2\ln(b/a)} - 1} \right\}. \tag{36}$$

Here, the optimal strategy leads to a qualitative change of the search time which can be rendered arbitrarily smaller than the search time in the absence of intermittence when $D/(av) \rightarrow 0$.

4.4. Remarks

We would like to comment on the previous results, and especially on the transitions between these regimes, which happen to be quite sharp.

First, the behaviour of $\tau_{1,\min}$ has remarkable features (see figure 3). This quantity sharply (but continuously) decreases when switching from regime $a \ll D/v$ to regime $a \gg D/v$, and quite surprisingly is not monotonic with b in the regime $a \ll D/v$.

Second, figure 3 clearly shows that $\tau_{2,\min}$ also displays a sharp (but continuous) change of monotonicity with respect to a between regimes $a \ll D/v$ and $a \gg D/v$.

Third, the efficiency of intermittent strategies is clearly illustrated in figure 4. In particular the search time can be rendered arbitrarily small in the regime $a \gg D/v$ by taking v large.

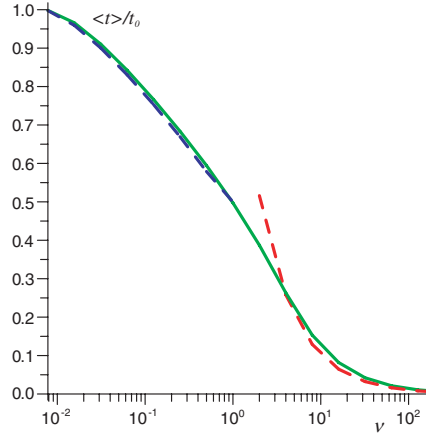


Figure 4. $\langle t \rangle_{\min}/t_0$ as a function of v in the dynamic case. The numerical minimization of $\langle t \rangle$ (26) (green continuous line), the approximation in the case $a \ll D/v$ (i.e. $v \ll D/a$) (32) (blue discontinuous line on the left), the approximation in the case $D/v \ll a$ (i.e. $D/a \ll v$) (34) (red discontinuous line on the right). $d1 = 1, a = 1, b = 11\,300$.

5. Solution in the static mode of detection

5.1. Calculation of the search time

In the ‘static mode’ ($D \rightarrow 0$), equation (14) becomes

$$s^{\text{ext}} = t_1^{\text{ext}} - \tau_1 \quad \text{for } r > a \quad \text{and} \quad s^{\text{int}} = t_1^{\text{int}}(1 + k\tau_1) - \tau_1 \quad \text{for } r < a. \quad (37)$$

Substituting these expressions in equation (13), we finally obtain

$$\tilde{D} \frac{d^2 t^{\text{ext}}}{dr^2} + \frac{\tilde{D}}{r} \frac{dt^{\text{ext}}}{dr} = -1 - \frac{\tau_1}{\tau_2} \quad \text{for } r > a \quad (38)$$

and

$$\tilde{D} \frac{d^2 t^{\text{int}}}{dr^2} + \frac{\tilde{D}}{r} \frac{dt^{\text{int}}}{dr} - k \frac{\tau_1}{\tau_2} = -1 - \frac{\tau_1}{\tau_2} \quad \text{for } r < a. \quad (39)$$

The solution of these equations reads

$$t_1^{\text{ext}}(r) = -\frac{r^2}{4\tilde{D}} \left(1 + \frac{\tau_1}{\tau_2}\right) + B_1 \ln r + B_2 \quad \text{for } r > a \quad (40)$$

$$t_1^{\text{int}}(r) = \frac{1}{k} \left(1 + \frac{\tau_1}{\tau_2}\right) + B_3 I_0 \left(r \sqrt{\frac{k\tau_1}{\tilde{D}\tau_2}}\right) + B_4 K_0 \left(r \sqrt{\frac{k\tau_1}{\tilde{D}\tau_2}}\right) \quad \text{for } r < a. \quad (41)$$

The resolution of equation (40) involves four unknowns, which are determined by the four following boundary conditions.

- First, $t^{\text{int}}(r)$ has to remain finite when $r \rightarrow 0$, which leads to $B_4 = 0$.
- Second, the exterior boundary conditions are reflecting, which yields

$$\frac{dt_1^{\text{ext}}(b)}{dr} = 0. \quad (42)$$

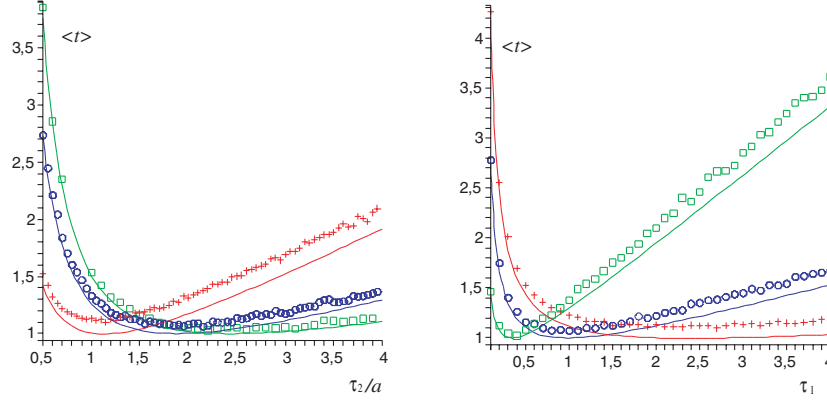


Figure 5. Simulations (points) and analytical approximate (lines) in the ‘static mode’. $k = 1, v = 1, b = 56$. $a = 10$ (red crosses) ($\tau_{1,\min} = 2.41, \tau_{2,\min} = 11.2$), $a = 1$ (blue circles) ($\tau_{1,\min} = 0.969, \tau_{2,\min} = 1.88$), $a = 0.1$ (green boxes) ($\tau_{1,\min} = 0.348, \tau_{2,\min} = 0.242$). *Left:* search time $\langle t \rangle$ as a function of τ_2/a , with $\tau_1 = \tau_{1,\min}$. *Right:* search time $\langle t \rangle$ as a function of τ_1 , with $\tau_2 = \tau_{2,\min}$.

- Last, we express the continuity of t_1 and dt_1/dr at $r = a$:

$$t_1^{\text{ext}}(a) = t_1^{\text{int}}(a) \tag{43}$$

$$\frac{dt_1^{\text{ext}}(a)}{dr} = \frac{dt_1^{\text{int}}(a)}{dr}. \tag{44}$$

Solving this linear system of four equations with four unknowns, and then averaging over the initial position of the searcher, we finally obtain for the search time

$$\langle t \rangle = \frac{\tau_1 + \tau_2}{2k\tau_1 y^2} \left\{ \frac{1}{x} (1 + k\tau_1)(y^2 - x^2)^2 \frac{I_0(x)}{I_1(x)} + \frac{1}{4} [8y^2 + (1 + k\tau_1)(4y^4 \ln(y/x) + (y^2 - x^2)(x^2 - 3y^2 + 8))] \right\} \tag{45}$$

where

$$x = \sqrt{\frac{2k\tau_1}{1 + k\tau_1} \frac{a}{v\tau_2}} \quad \text{and} \quad y = \sqrt{\frac{2k\tau_1}{1 + k\tau_1} \frac{b}{v\tau_2}}. \tag{46}$$

5.2. Comparison with numerical simulations

Here again, this expression (45) is in very good agreement with numerical simulations for a wide range of parameters (see figure 5 and table 2). The agreement is quantitatively supported by calculating $d = \left(\frac{1}{N} \sum_{i=1}^N \frac{(\langle t_i \rangle - f(\tau_{1,i}, \tau_{2,i}))^2}{\langle t_i \rangle^2} \right)^{\frac{1}{2}}$, where N is the number of couples (τ_1, τ_2) for which we have calculated $\langle t \rangle$ in the simulation and f is the function given by equation (45). The error is about 5–8%, and does not seem to depend on a as in the ‘dynamic’ mode, but rather on a/b . Once again, the minimum obtained from the simulations is very well described by the analytical approximate.

5.3. Optimization of the search time

In this case, intermittence is trivially necessary to find the target: indeed, if the searcher does not move, the MFPT is infinite. Once again, we have three characteristic lengths a, b and v/k .

Table 2. Difference between simulations and analytical approximation (45) in the static case. $k = 1, v = 1$.

a	b				
	113	28.2	7.05	1.69	0.564
10	0.0666	0.0821			
1	0.0496	0.0574	0.0724		
0.1			0.0517	0.0630	0.0754

In the regime $b \gg a$, the optimization of the search time (45) leads to

$$\tau_{1,\min} = \left(\frac{a}{vk}\right)^{1/2} \left(\frac{2 \ln(b/a) - 1}{8}\right)^{1/4}, \quad (47)$$

$$\tau_{2,\min} = \frac{a}{v} (\ln(b/a) - 1/2)^{1/2}, \quad (48)$$

which corresponds to the scaling law $\tau_{2,\min} = 2k\tau_{1,\min}^2$. Note that this relation does not depend on v , and that these results hold for any v/k .

On the other hand, a very good approximation for the minimum search time is given by the following truncated $1/v$ expansion:

$$\begin{aligned} \langle t \rangle_{\min} = & \frac{b^2}{a^2k} - \frac{2^{1/4}}{\sqrt{vka^3}} \frac{(a^2 - 4b^2) \ln(b/a) + 2b^2 - a^2}{(2 \ln(b/a) - 1)^{3/4}} - \frac{\sqrt{2}}{48ab^2v} \\ & \times \{(96a^2 - 192b^4) \ln^2(b/a) + (192b^4 - 144a^2b^2) \ln(b/a) + 46a^2b^2 \\ & - 47b^4 + a^4\} (2 \ln(b/a) - 1)^{-3/2}. \end{aligned} \quad (49)$$

6. Comparison of both modes of detection

First, it should be pointed out that the dynamic mode of detection is always more efficient than the static mode of detection, as the reaction rate is infinitely fast in the dynamic mode.

Second, the following remarkable characteristics of intermittent search processes can be extracted from the main results (34) and (47), (48) obtained in the two modes of search. (i) In both cases the search time $\langle t \rangle$ presents a global minimum for finite values of the τ_i , which means that intermittence is an optimal strategy. (ii) A very striking and non-intuitive feature is that both modes of search lead to the *same optimal value* of $\tau_{2,\min}$ (when $D/v \ll a \ll b$). As this optimal time does not depend on the specific characteristics D and k of the search mode, it seems to constitute a general property of intermittent search strategies. To investigate the validity of this assertion further, we have numerically simulated a search process combining the two previous detection mechanisms. Once again we obtain a global minimum, and the value of $\tau_{2,\min}$ is very close to the common value $\frac{a}{v} (\ln(b/a) - 1/2)^{1/2}$, as soon as $D/v \ll a \ll b$ (see figure 6).

7. Comparison with systematic search strategies

Up to now, the model under study involved a searcher with minimum memory skills. First, due to the exponential distribution of the waiting times in each of the two phases, the searcher has no temporal memory. Second, as the direction of the velocity in the relocating phases is uniformly distributed, the searcher has no orientational memory. In that sense, the model presented here is 'minimal'.

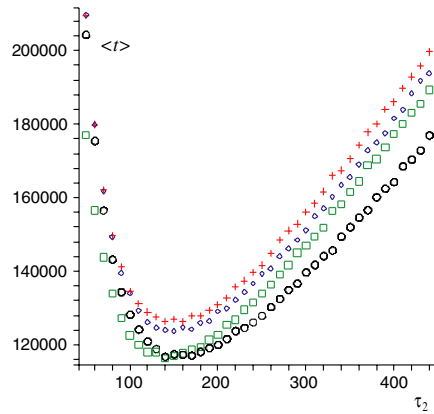


Figure 6. The robustness of the law for $\tau_{2,\min}$. The search time $\langle t \rangle$ as a function of τ_2 , with $\tau_1 = \tau_{1,\min}$, for different descriptions of the search phase: ‘dynamic mode’ ($D = 1, k = \infty, \tau_1 = 9.19$) (black circles), ‘static mode’ ($D = 0, k = 1, \tau_1 = 8.8$) (red crosses), intermediate mode ($D = 1, k = 100, \tau_1 = 0.165$) (green squares), another intermediate mode ($D = 1, k = 1, \tau_1 = 10$) (blue diamonds). For all the simulations, $a = 100, b = 1800, v = 1$.

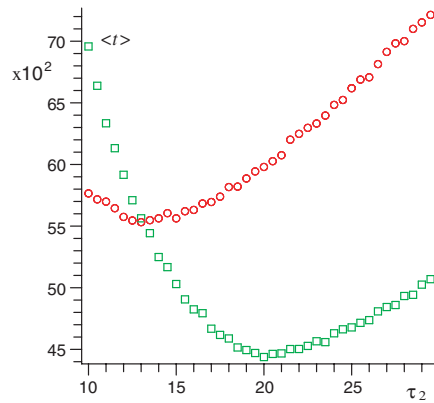


Figure 7. Comparison between the search without temporal memory (red circles) and the search with temporal memory (green squares). $\langle t \rangle$ as a function of τ_2 . ‘Static mode’: $k = 1, v = 1, L = 200, a = 10, \tau_1 = 2, 6$.

In this section, we address the question of determining the influence of this lack of memory skills on the search efficiency, limiting ourselves to the static detection mechanism.

7.1. Effect of temporal memory

We first investigate numerically the influence of the temporal memory by considering the extreme case of a complete temporal memory, corresponding to a searcher spending deterministic times in each of the two phases. In other words, the transitions between states only occur at times $\tau_1, \tau_1 + \tau_2, 2\tau_1 + \tau_2, \dots$. The numerical simulations reveal that the search time still presents a global minimum as a function of the two variables τ_1 and τ_2 , but for different values of τ_1 and τ_2 (see figure 7). On the other hand, the minimum value of the search time obtained for this deterministic model is always less than the analogue quantity in the case of exponentially distributed times, but of the same order of magnitude. More precisely, the gain

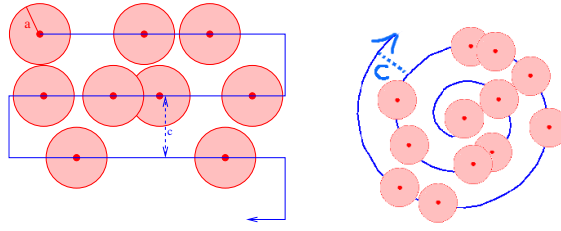


Figure 8. Systematic explorations of space. *Left:* lawn mower, *right:* spiral.

is less than 40% in the range of parameters we studied, and decreases when b/a increases. As a consequence, having temporal memory does not considerably change the search time. A similar but 1D situation was studied (analytically and numerically) in [30], providing the same general conclusion.

7.2. Effect of orientational memory

As for the question of evaluating the influence of orientational memory, we have numerically considered two types of systematic explorations of space. The first one corresponds to the so-called ‘lawn mower’ strategy (cf figure 8 left) and the second one to a regular spiral (cf figure 8 right).

The search time in the ‘lawn mower’ strategy can be roughly estimated by using a 1D model. Indeed, the trajectory in a square of side $2b$ can be ‘unfolded’ into a straight line of length L such that $(2b)^2 = 2aL$, wherein lies a target of linear size $2a$. This effective 1D model is then very close to the one exposed in section 3.1, except that now there is a single ballistic state of velocity $+v$. The equations for the MFPT are in this case (keeping the notations of previous sections)

$$\frac{1}{\tau_1} (t_2 - t_1) - kI_{[0,2a]}(x) = -1 \quad (50)$$

$$v \frac{dt_2}{dx} + \frac{1}{\tau_2} (t_1 - t_2) = -1. \quad (51)$$

This system holds for $0 \leq x \leq L$, and is completed by periodic boundary conditions for the functions t_1, t_2 . $I_{[0,2a]}(x) = 1$ for $0 \leq x \leq 2a$ and $I_{[0,2a]}(x) = 0$ for $2a < x < L$. The detection time (t) can be calculated straightforwardly from this approximate 1D model which, in the large domain limit, leads to the very simple form of the search time:

$$\langle t \rangle_{\text{lawn mower}} \approx \frac{\tau_1 + \tau_2}{\tau_2} \frac{b^2}{va} \coth \left(\frac{ak\tau_1}{v\tau_2(1 + k\tau_1)} \right). \quad (52)$$

The ‘spiral’ strategy gives similar values of the search time in the limit $a \ll b$, as shown by numerical simulations.

These systematic strategies prove to be always more efficient than our minimal model, but the relative gain, increasing with b/a , is typically of order 1 (see figure 9). As previously, memory skills do not significantly improve the search efficiency.

8. MFPT for a Pearson-type random walk

Finally we remark that this model provides as a by-product an approximation for the MFPT for a Pearson-type random walk in the spherical geometry previously defined: the searcher performs ballistic flights reoriented at exponentially distributed times, and, as opposed to

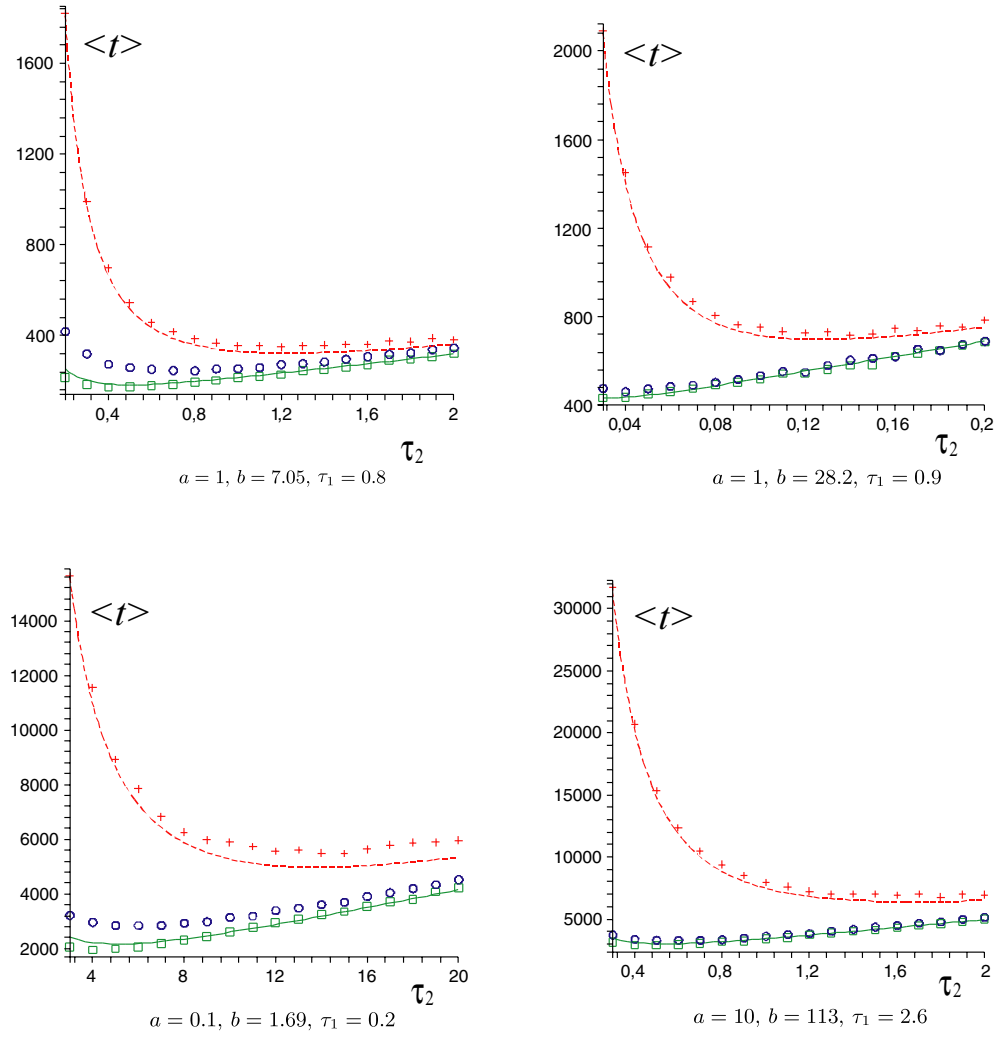


Figure 9. Comparison between the model without memory (simulations (red crosses) and analytical approximate (45) (red discontinuous line)) with the ‘lawn mower’ systematic strategy (simulations (green squares) and analytical approximate (green line)) and the spiral systematic strategy (blue circles). The search time $\langle t \rangle$ as a function of τ_2 . $k = 1$ (static mode), $v = 1$.

standard Pearson walks, the target can be found only when the distance between the target and a reorientation point is less than a . This quantity, obtained here straightforwardly by taking $k \rightarrow \infty$ and $\tau_1 \rightarrow 0$ in equation (45), is written as

$$\langle t \rangle = \frac{(b^2 - a^2)^2}{\sqrt{2}vab^2} \frac{I_0(a\sqrt{2}/v\tau_2)}{I_1(a\sqrt{2}/v\tau_2)} + \frac{1}{v^2\tau_2b^2} \left(b^4 \ln(b/a) + \frac{1}{4}(b^2 - a^2)(a^2 - 3b^2 + 4v^2\tau_2^2) \right). \tag{53}$$

This approximation of the search time is in good agreement with numerical simulations (see figure 10). To our knowledge, a similar result for standard Pearson walks is still missing. Note that in the limit $v \rightarrow \infty, \tau_2 \rightarrow 0$ with $\tilde{D} = v^2\tau_2/2$ fixed, the approximate expression (53)

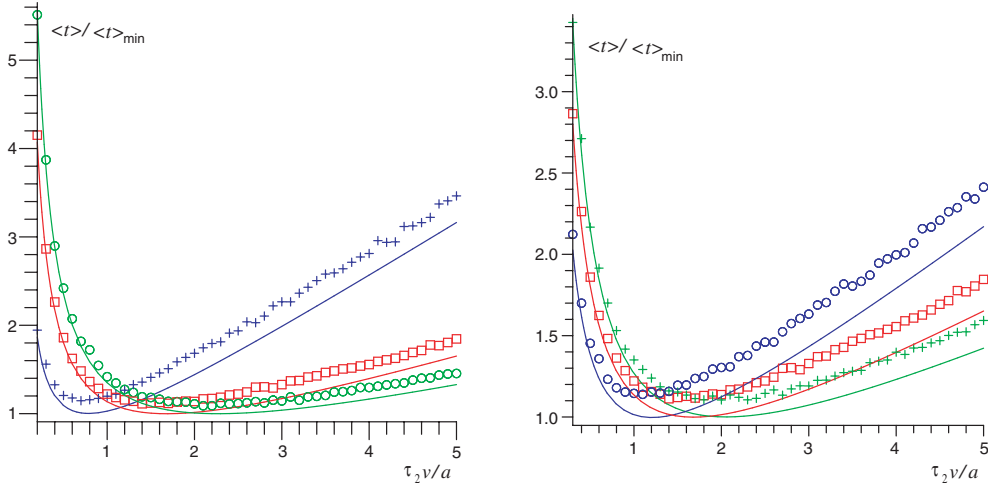


Figure 10. Simulations (points) versus analytical approximate (line) of the search time for a Pearson like random walk: the search time rescaled by the value at its minimum as a function of $\tau_2 v / a$. $v = 1$. *Left:* $b = 28.2$, $a = 10$ (blue crosses), $a = 1$ (red boxes), $a = 0.1$ (green circles). *Right:* $a = 1$, $b = 7.05$ (blue circles), $b = 28.2$ (red boxes), $b = 113$ (green crosses).

gives

$$\frac{1}{8b^2 \tilde{D}} (b^4 (4 \ln(b/a) - 3) + 4a^2 b^2 - a^4) \quad (54)$$

which is the well known exact expression for the MFPT of a Brownian particle between concentric spheres [28], with a starting point uniformly distributed in the whole sphere of radius b . Moreover, for $b \gg a$, the search time (53) is minimized again for the same value (34) and (48) of τ_2 , in agreement with the limit $k \rightarrow \infty$ of equations (47), (48).

9. Conclusion

We have studied a two-state model which permits us to optimize the encounter rate with immobile and non-revisitable targets. This model deeply relies on intermittent search strategies, widely observed in nature at different scales, as in the case of a protein searching for its specific site on a DNA molecule, or in the case of animals searching for food. These intermittent strategies, combining local scanning phases and mere relocating phases, are relevant as soon as motion and searching activities cannot be performed simultaneously, as is generally the case when targets are hidden and not directly accessible. Invoking a decoupling approximation successfully validated by numerical simulations, we have shown analytically that the search time has a global minimum as a function of the times spent in each phase. In other words, a searcher for randomly hidden targets has a unique optimal way of sharing its time between local scanning phases and mere relocating phases, which means that intermittent strategies are real optimal search strategies. This has to be opposed to Lévy strategies, which are optimal only in the very specific case of revisitable targets. In addition, we have shown that the optimal duration of the relocating phases is essentially independent of the detail of the detection mechanism involved during local scanning phases. As a consequence, it appears to be a universal feature of intermittent search strategies. Last, in this model, the searcher enjoys minimal memory skills, in the sense that it has no temporal memory (the transition rates between phases are

time independent), and no orientational memory (the direction of ballistic flights of relocating phases is random). Quite unexpectedly, it turns out that more systematic strategies, involving searchers with either temporal memory or orientational memory, do not change the order of magnitude of the search time.

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