An Elementary Model for Directed Active Motion

O. STEUERNAGEL and W. EBELING

Institute für Physik, Humboldt-Universität zu Berlin, Invalidenstrasse 110,
D-10115 Berlin, Germany

and

V. CALENBUHR

CREA, École Polytechnique, 1 rue Descartes, F-75005 Paris, France

(Received 28 January 1994)

Abstract—A model of locally pumped Brownian particles is developed which shows some basic features of animal motion. Moving through the active region the particles are pumped with high valued energy and are accelerated. In particular, the dynamics shows limit cycles which resemble tracks. As generalizations stochastic motion and reservoirs carried by the particles are considered. A delay time between pumping with high-valued energy and acceleration is introduced.

1. BROWNIAN MOTION MODELS FOR THE ELEMENTARY MECHANISMS OF ANIMAL MOBILITY

To model animals exploring their vicinity, say to find food, various mechanisms have been suggested [1–9, 26]. We consider animal motion on the phenomenological level, describing the general phenomena without regard to specific biological features of the species. We do not care about creeping or swimming motion and alike. We rather consider the randomness or directedness of the trials. In this frame, motion of primitive organisms, like amoeba, is well described by the random zigzag of Brownian motion. The basic features of the model developed here are:

(i) the dynamics of the particles is given by a Langevin equation with space-dependent potential and friction [10–15];
(ii) the friction is on average positive but has areas with negative friction that model areas of food;
(iii) in generalized versions of the model a time delay between pumping and acceleration is introduced.

This mechanism is generating directed motion of the individuals, which are periodically visiting the pumping regions. Our major concern is with the recurrent—in our case cyclic—motion of individuals between some centre, the nest and these pumping/feeding sources in the environment [16]. Recurrent motion along preferred zones in physical space is reminiscent of biological streets. One may suspect that the formation of streets in this sense is inextricably connected to mechanisms of active motion.

Let us mention that the concept of negative friction-pumped active motion was developed in the theory of clocks, violin strings, organ pipes and alike and is responsible for self-sustained periodic motion [13, 17, 18].
The primary question that we want to address here is whether there are some underlying principles that can be found at many levels of biological organization in the context of street formation. Biological streets can be found at many different levels of biological organization. The insect reign is particularly rich in showing street-like structures as is exemplified by gregarious insects, e.g. caterpillars [8] and social insects, e.g. ants and termites [2, 16]. But also in mammals and, of course, in humans do we find the build-up and use of streets. In view of the numerous examples of street formation one would like to know whether there are some general properties that are common to all these phenomena. In particular, one would like to know about the necessary mechanisms in order to have street formation. A solution to this question at the level of social insects has been put forward [3, 4].

The formation of biological streets involves in many cases mechanisms like diffusion, chemotaxis and emission. In fact, a very small number of rules (or mechanisms) is sufficient to understand the formation of a chemical trail through a self-organization process: diffusion, chemotaxis, emission of an odorous substance that can be used as cue for chemotaxis and, at least one animal has to know the location of a reference point, say a nest [3, 5, 20–24].

The consumption of energy in these models is not taken care of explicitly. The model to be developed here contrasts with that very sharply, in that we are trying to make explicit precisely this point. Our model will reflect this on a simple, and yet general, footing. We shall start with a very simple mechanical model and will add more mechanisms in order to find out, which and how many mechanisms are necessary for target-directed food search from a purely physical point of view. The ultimate goal would be to have a mechanically inspired or based model that establishes a link to chemotaxis–diffusion models that are located at another level of description. The basic idea is that animals (or individuals in general) are modelled as simple particles. In the simplest case we describe individuals by particles, their random explorations by Brownian motion, the feeding resources by localized patches with negative friction and the environment by a potential landscape. In this study we try to be as independent from any biological implementation as possible. In the end we will then discuss our abstract model in comparison to models that are more realistic from the biological point of view.

Interactions or cooperations between the individuals could be introduced straightforwardly via interaction potentials or chemotactical agents, where the latter are certainly of great importance in biological street forming systems [2, 22].

In this paper we start with a simple scenario of one particle bound by a cup-like potential, fed by a stripe with negative friction and step-by-step generalize to a population in a two-dimensional random landscape. Our results are partly quantitative, partly qualitative and related to questions in various fields such as solid-state theory or theory of stochastic processes, as will be outlined.

2. DETERMINISTIC MOTION ON A RANDOM FOOD PASTURE

2.1. The driving mechanism

In this section we investigate a specific mechanism that allows for cyclic motion of particles through an interplay of consumption and dissipation of kinetic energy. We show that this mechanism establishes cyclic motion on narrow tracks, which is stable in the way necessary for our purposes.

The general idea is easily sketched. We want to consider particles bound by a
potential—or spring—that perform specific, stable, cyclic motion. Motion in a potential alone is not very specific, and thus we eliminate all motion by an overall friction. This eventually leads all particles spiralling down into the potential valley, i.e. to the centre of the spring (or back to the nest). Now we assume spots where, quite artificially, but mathematically simple to model, negative friction (accelerating, enhancing ‘friction’) feeds energy to the particles passing through. The corresponding equation of motion for one particle reads:

$$m \ddot{x} + γ(\overrightarrow{x}) \dot{x} + \nabla \Phi(\overrightarrow{x}) = 0,$$

(1)

where the potential $\Phi(\overrightarrow{x}) = \Phi(|\overrightarrow{x}|)$ is to be cup-shaped and rotation symmetrical and $γ(\overrightarrow{x})$ may be of any complicated form, preferably uniformly positive with negative spots randomly interspersed. If the spots’ feeding effect is strong enough, cyclic motion through these is possible and will evade extinction by dissipation.

We find that each spot, quite independently of its shape, the kind of potential and the starting conditions of the motion, establishes one mode of stable cyclic motion. We discuss the corresponding sufficiency conditions and show that this mechanism also serves well to establish narrow tracks.

2.2. The driving mechanism in one dimension

As the closed form analysis can be performed only in the case of the harmonic potential with vanishing friction, we describe it first then generalize.

We want to start with the study of a harmonic potential in the low friction limit, and we want to see how cyclic motion can come about, so we need to understand the energy balance of the motion. As we do not want to bother about geometrical subtleties, we first analyse the 1D case and confirm its general validity later. The harmonic potential is not structurally necessary, but it is the only case that is analytically tractable, if reduced to vanishing friction. We want to understand the forms of motion governed by an equation like (1), and so investigate its simplified form:

$$m \ddot{x} + γ(x) \dot{x} + \partial_x \left( \frac{k}{2} x^2 \right) = 0,$$

(2)

where $γ(x) = γ_+ + γ_- (\Theta(x - a) - \Theta(x - b))$, $\Theta(x)$ is the step function, $γ_- < 0 < γ_+$ and $0 < a < b$. The condition $0 < a$ reflects that food shall not be located in the nest (potential valley), the motion in this case is trivial anyway, so we skip this case for the sake of brevity. After the transformations $x \rightarrow x \cdot a$, $t \rightarrow t \cdot m/γ_+$ and through the introduction of a friction-scaled frequency: $Ω = m/γ_+ \cdot ω := m/γ_+ \cdot \sqrt{k/m}$ equation (2) reads:

$$\ddot{x} + \left[ 1 + \frac{γ_-}{γ_+} \left( \Theta(x - 1) - \Theta(x - \frac{b}{a}) \right) \right] \dot{x} + Ω^2 x = 0.$$

(3)

There are three independent parameters, namely $Ω$ and the ratios $γ_-/γ_+$ and $b/a$ whose significance we seek to understand.

2.2.1. The minimal condition. We want to find the minimum condition for the existence of a stable limit cycle of the motion. In the low-friction limit $Ω^2$ dominates the equation, undamped oscillations and elliptical motion in phase space results and the energy change per cycle can be calculated explicitly. It amounts to the determination of the friction weighted areas $A_+$ and $A_-$ of the ellipse of motion in phase-space covered by $γ_-$ and $γ_+$. 

because:

\[
\Delta E_{\text{cycle}} = \int_{x=0}^{x=1} F \, dx = \int_{x=0}^{x=1} F_{\text{dissipative}} \, dx = \int_{x=0}^{x=1} \gamma(x) v(x) \, dx = -2 \int_{x=0}^{x=1} \gamma v \, dx
\]

\[
= -2 \left[ \int_{x=0}^{x=1} \gamma \, v \, dx + \int_{x=0}^{x=1} \gamma \, v \, dx + \int_{x=0}^{x=1} \gamma \, v \, dx \right] =: - (\gamma_+ A_+ + \gamma_- A_-).
\]

(4)

For illustration we have assumed $0 < a < b < x$; in general $A_-$ can even be zero if the motion is too weak to provide $\dot{x} > 0$. In the low friction limit $A_-(\dot{x})$ can be calculated directly:

\[
A_-(\dot{x}) = 0 \quad 0 \leq \dot{x} \leq a
\]

\[
A_-(\dot{x}) = 2 \int_{x=a}^{x=b} \frac{\dot{x}^2 \arccos \frac{a}{\dot{x}} - a \sqrt{\dot{x}^2 - a^2}}{2} \, dx
\]

\[
a \leq \dot{x} \leq b
\]

\[
A_-(\dot{x}) = 2 \int_{x=a}^{x=b} \frac{\dot{x}^2 \left( \arccos \frac{a}{\dot{x}} - \arccos \frac{b}{\dot{x}} \right) + b \sqrt{\dot{x}^2 - b^2} - a \sqrt{\dot{x}^2 - a^2}}{2} \, dx
\]

\[b \leq \dot{x}.\]  \hspace{1cm} (5)

A plot of $A_-(\dot{x})$ is easily understood qualitatively. Starting from $a$ on $A_-(\dot{x})$ grows about quadratically, like the ellipse itself. After $\dot{x}$ reaches $b$ this growth eventually goes down to linear growth as only the height of the strip in phase-space covered by $\gamma_-$ keeps growing.

To find the minimum condition for the existence of a stable limit cycle of the motion, the energy change per cycle necessarily has to be zero, so (4) becomes:

\[
\gamma_+ A_+ + \gamma_- A_- = 0 \Leftrightarrow \pi \omega \dot{x}^2 - \left(1 - \frac{\gamma_-}{\gamma_+} \right) A_- (\dot{x}) = 0.
\]

(6)

We are looking for the minimal ratio $\gamma_- / \gamma_+$ that is great enough to fulfill (6). This clearly means that the onset for this kind of behaviour must occur at $\dot{x}_\text{onset} > b$ as $A_-(\dot{x})$ just below $b$ grows stronger than $A_+ (\dot{x})$. The minimality does further imply that the parabola $\pi \omega \dot{x}^2$ and the properly weighed $A_-(\dot{x})$ curve touch tangentially but do not intersect, so the derivative of (6) shall be:

\[
\left[ \frac{\partial}{\partial \dot{x}} (\pi \omega \dot{x}^2 - \left(1 - \frac{\gamma_-}{\gamma_+} \right) A_- (\dot{x})) \right]_{\dot{x}=\text{onset}} \equiv 0.
\]

(7)

This allows us to get rid of $\dot{x}_\text{onset}$ and leads to the relation

\[
\left[ \frac{\gamma_-}{\gamma_+} \right]_{\text{onset}} = 1 - \pi \arccos \frac{a}{\sqrt{b^2 + a^2}} - \pi \arccos \frac{b}{\sqrt{b^2 + a^2}}.
\]

(8)

which in turn implies

\[
\dot{x}_\text{onset} = \sqrt{a^2 + b^2}.
\]

(9)

Astonishingly the question how to guarantee that two-dimensional motion is essentially confined to one dimension leads to just the same condition, as will be shown later!

A plot of the onset relation (8) in relative coordinates shows a sensible result (Fig. 1).
The broader the enhancing region the smaller the strength of enhancement, bound by $-1$, as the enhancement must not be smaller than the dissipation. $b/a > 1$ simply reflects a stripe of finite width. If now one sets up a system which is sufficiently enhancing, that is, $\gamma_-$ lies below the plotted curve, this system is capable of stable cyclic motion:

2.2.2. Beyond minimality. In order to understand better the onset of stable limit cycles, let us have a look at a plot of $\Delta E_{\text{cycle}}(\hat{x})$ (Fig. 2).

The following plots (Fig. 3) show the values of $\hat{x}_{\text{unstable}}$ and $\hat{x}_{\text{stable}}$ for various parameter values, one clearly sees the boundary curve described by the onset condition that was plotted in Fig. 1.
2.2.3. Harmonic potential, any friction. As long as we stay away from the overdamped case $\gamma_+ \leq 2\sqrt{(k/m)}$ the considerations of the former section are fully valid but we cannot give explicit analytical relations for the onset and values of $\hat{x}_{\text{stable}}$ and the like. Still most plots look very much the same and really the last plots for the values of $\hat{x}_{\text{unstable}}$ and $\hat{x}_{\text{stable}}$ were found through numerical solution of the area condition (6) for non-vanishing friction. One finds that the behaviour is essentially the same as in the low-friction limit. Despite these correspondences we cannot give a simple, say topological, argument to prove this, but only could show this by numerically solving the transcendental equations involved.

2.2.4. Arbitrary cup-like potential. Again, if the potential is concave and $\gamma_+$ small enough to allow for oscillatory motion, we found very much the same behaviour. We investigated potentials such as $|x|$, $|x^{1.5}|$, $|x^3|$, $x^4$ and $x^6$. The plots (Fig. 4) deal with the $x^4$ case and
show all the same structurally well-understood features. Now we will give a concluding argument which might be a basis for a rigorous proof of our conjecture that the suggested driving mechanism can establish one mode of stable, cyclic motion per spot.

In our system the dissipated energy scales with the mean kinetrical energy:

\[- \int \gamma v \, dx = - \int_{r_{kz}} \gamma v^2 \, dt = - \gamma \cdot \langle v^2 \rangle.\]

According to the virial theorem of classical mechanics it thus is proportional to the average potential, if the potential has a monomial form \( \alpha \hat{x}^n \): \( \Delta E_{\text{cycle}} = \hat{x}^n \). Now, the enhancing region is bound so, if \( a < \hat{x} < b \), \( A_(\hat{x}) \) will grow about proportionally to \( \hat{x}^n \) and if \( b < \hat{x} \) this growth will, due to the boundeness, go down to an \( \hat{x}^{n-1} \) growth, as one dimension is
'frozen'. Thus, we end up with a sum of two functions. Due to monotony reasons this sum can have only two zeros, if any: the first corresponding to the unstable and the second to the stable limit cycle.

We have shown that our suggested driving mechanism can in principle lead to stable cyclic motion in 1D systems.

2.3. The driving mechanism in two dimensions

It is not clear that our investigation of the 1D case can be applied to the case of two dimensions. Fortunately, in 2D the motion of particles through food patches always shrinks down to 1D motion, which we now understand well. Without friction, motion in 2D in a concave, rotation-symmetrical potential is motion on more or less deformed ellipses that rotate—one could say precess—around the potential minimum. If one follows this precessing rotation, the ellipse-like curves have a steady length and width which, in the harmonic potential case, are the proper diameters of the elliptical motion in ordinary position space (not to be confused with the motion in phase-space we addressed before). We shall call the motion associated with the further extended end of the quasi ellipse the radial mode, designated by the index \( x \), the perpendicular one will be called transversal mode marked by \( y \).

We found that under the conditions we intend to describe, that is, motion under uniform positive friction with interspersed local spots of strongly enhancing patches of arbitrary shape, the 2D motion in position space eventually shrinks down to an effectively semistable, 1D, purely radial motion. The transversal motion fades away. This also implies that the precession rotation stops because purely radial motion does not show precession.

Again we first investigate this question in the harmonic potential case in the low friction limit and generalize afterwards.

2.3.1. The fading transversal mode for the harmonic potential, low friction limit. The ellipse of motion, parameterized by the angle of revolution \( \phi = \omega t \), reads:

\[
\begin{align*}
x_0(t) &= \xi_x \cos \phi \\
x_\perp(t) &= \xi_\perp \sin \phi.
\end{align*}
\]

This ellipse will cross a food patch of arbitrary form at a radial distance from \( a \) to \( b \).

What are the conditions for the transversal mode dying away and the radial mode remaining? Clearly this will be the case if the relative amount of energy pumped into the radial mode is greater than the relative amount of energy pumped into the transversal mode. Especially in the case of a stable limit cycle of the former this implies exponential decay of the latter. So we intend to understand under which conditions we will find:

\[
\frac{\Delta E_\perp}{E_{\text{kinetic}}} < \frac{\Delta E_\parallel}{E_{\text{kinetic}}},
\]

This means we have to integrate over one revolution to determine the \( \Delta E \)s. If one translates the intersections with the patch into the corresponding angles of revolution

\[
\phi_a = \arccos \left( \frac{a}{\xi_x} \right) \quad \text{and} \quad \phi_b = \arccos \left( \frac{b}{\xi_x} \right),
\]

the condition (11) can, through some lengthy calculation, be transformed into the following inequality:

\[
\sin(\phi_a) < \sin(\phi_b).
\]
With the help of (12) this inequality is equivalent to

$$a^2 + b^2 < \hat{x}_1^2$$

(14)

which has to be fulfilled in any case according to the onset condition (8). Thus we find that the necessary condition for the existence of a stable limit cycle (8) does automatically imply the decay of the transversal mode!

2.3.2. Cup-like potential, any friction. Assuming the non-overdamped case again, everything that was said in the last section seems to apply equally well to any cup-like potential with any value of friction provided \( \gamma_0 \) is strong enough. Unfortunately, we cannot substantiate this claim much further as we cannot tackle the problem analytically. At least extensive numerical integrations of the trajectories were being done in a variety of cases. We modified the potential and changed the three parameters mentioned with equation (3). We do not claim to have checked out every possible configuration, but in the many investigated cases we uniquely found the behaviour sketched before: If the spots are strongly feeding and consequently allow for cyclic motion, this is energetically stable and transversally contracting.

The motion described is energetically stable in its radial mode, and the transversal mode dies out. This does not mean, however, that the radial mode’s direction is stable. It rather is semistable in that it can be shifted without resistance. There is no attractive force that holds the cyclic motion in a patch. Minimal noise applied to the motion will thus not alter the form significantly but will eventually drive it out of the feeding region.

If a cyclic motion runs through a patch there is only one such stable motion as we have made plausible at the end of subsection 2.2. Of course, by a special alignment of patches one could set up several stable cycles pointing in the same direction.

2.4. Deterministic motion in a random environment

A straightforward generalization of the previous considerations is a setup with many randomly distributed patches of arbitrary form in the potential valley. By the onset condition (8) we know the further off the centre the stronger the enhancing power of the particular patch to allow for the sought stable cyclic motion. Conversely, this argument expresses the fact that all closely situated or strongly feeding patches can establish a cycle, i.e., are worth to be visited by the individuals. If one also modifies the potential landscape to a Gaussian random landscape, or something similar that reflects a more irregular environment, a new type of motion can come about. Provided the patches are strong enough or the depressions of the landscape not too low, particles can be ejected from one valley into the next, and thus cover large distances. This is, however, sensitive to a particle’s initial position. A slight variation can cause a formerly ‘successful’ particle not to traverse pastures that are impropitiously aligned. Thus the particle will not travel a long way. So this scenario makes sense only if we assume a fluctuating, Brownian force acting on the particles in order equip these with ‘fuzzy’ behaviour, because otherwise the sensitive dependence on the initial conditions of each particles motion distorts the picture. Thus we arrive at a picture comparable to solid-state considerations of random potentials, and we expect similar effects to occur [12]. The bound states are those stuck in a valley, and free states in our case are the others that manage to pass into a neighbouring valley and so forth. In the stochastic case the equation of motion for one particle (1) becomes

$$m \ddot{x} + \gamma(\xi) \dot{x} + \nabla \Phi(\xi) = \sqrt{2 \xi(t)} \nabla \Phi(\xi(t)),$$

(15)

only in very special cases can analytical results be derived, as we will show later. Still,
general consideration are at hand. If $\gamma(\vec{x}) = \gamma_0$ is a positive constant, the Einstein relation
\[ \epsilon = \frac{\gamma k_0 T}{m} \] (16)
holds, and therefore a general solution for the equilibrium probability density associated with (15) is known:
\[ P_{eq}(\vec{x}, \vec{v}) = C \exp\left[-\Phi(\vec{x})/kT\right] \exp(-m\vec{v}^2/2kT). \] (17)
Through our modification of $\gamma(\vec{x})$ no Einstein relation holds, and so we expect deviations from the Maxwell-Boltzmann distribution (17). Yet we can give an argument concerning average long-time behaviour. In the above equation (15) $\sqrt{2\epsilon} \xi(t)$ account for the energy pumped into the particles motion which by the term $\gamma(\vec{x})\vec{v}$ is dissipated or even further enhanced, depending on the sign of $\gamma$. Therefore $\gamma$ has to be positive on average to prevent the system from ‘boiling’. To be more precise we can transform the virial argument of the conclusion in subsection 2.2 into this new context. On average the energy pumped in is dissipated, so for long times $\tau$ we have in stationary states
\[ \lim_{\tau \to \infty} \frac{1}{\tau} \int_0^\tau d\tau \gamma(\vec{x})\vec{v}^2 = \frac{f}{2} m \epsilon \] (18)
from the integration of equation (15), $f$ is the dimension of the state-space, here: $f = 2$, $\gamma(\vec{x})$ has to be compatible with this.

3. GENERALIZATIONS

3.1. The stochastic case

Realistic motion of many animals is strongly influenced by stochastic effects. This leads to Brownian-motion-like trajectories. Therefore, in order to be more realistic, the search for food should be modelled as a stochastic motion of the considered particle. Thus the direction of motion changes from time to time. The simplest approach in describing such a stochastic search is to add a fluctuating force in the equation of motion. We will assume stochastic alternations of the momentum with short-time correlations yielding a Langevin equation:
\[ \vec{v}' = -\gamma(\vec{x})\vec{v}' - \frac{\partial \Phi}{\partial \vec{x}} + \sqrt{2\epsilon} \xi(t) \]
with:
\[ \langle \xi \rangle = 0, \quad \langle \xi(t) \xi(t') \rangle = \delta(t - t'). \] (19)
(19) represents a stochastically forced, dissipative, nonlinear oscillator [18] which was investigated for several $\gamma(x)$ with one spatial dimension in the past [10, 14, 15, 18, 25]. Nevertheless, exact analytical expressions for the corresponding stationary probability distribution are known, only if $\gamma$ is a function of the Hamiltonian $H$. In our case, averaging over one period may be employed [10, 14]. In the 1D case the Fokker–Planck equation for the probability density $P(x, v, t)$ corresponding to the Langevin equation (19) and the considered friction is
\[ \frac{\partial P(x, v, t)}{\partial t} + v \frac{\partial P}{\partial x} - \frac{\partial \Phi}{\partial x} \frac{\partial P}{\partial v} = \frac{\partial}{\partial v} \left[ \gamma(x)P(x, v, t) + \epsilon \frac{\partial P}{\partial v} \right]. \] (20)
In the much more interesting 2D case in general situations we have to consider motion of an ensemble of Brownian particles in a plane under the action of a conservative force derived from a random potential $\Phi(x_1, x_2)$ subject to randomly distributed friction $\gamma(x_1, x_2)$. Naturally the friction function has to fulfill the following requirements:

(i) The overall friction is positive.
(ii) The friction distribution exhibits negative islands $\gamma(x_1, x_2) < 0$.

The Fokker–Planck equation for this 2D case is

$$\frac{\partial P(x_1, x_2, t)}{\partial t} + \left( \frac{\partial}{\partial x_1} v_1 P + \frac{\partial}{\partial x_2} v_2 P \right) - \left( \frac{\partial \Phi}{\partial x_1} \frac{\partial P}{\partial v_1} + \frac{\partial \Phi}{\partial x_2} \frac{\partial P}{\partial v_2} \right)$$

$$= \frac{\partial}{\partial v_1} \left[ \gamma(x_1, x_2) P(x_1, x_2) + \epsilon \frac{\partial P}{\partial v_1} \right] + \frac{\partial}{\partial v_2} \left[ \gamma(x_1, x_2) P(x_1, x_2) + \epsilon \frac{\partial P}{\partial v_2} \right]. \quad (21)$$

Here we have assumed for simplicity that the noise $\epsilon$ is independent of the variables. In the general 2D case the Fokker–Planck equation cannot be solved explicitly. Therefore one has to perform simulations which typically show that the equilibrium velocity distribution $P_{eq}$ has strong deviations from the Maxwell distribution, as due to pumping the fraction of particlals faster than average is significantly enhanced.

The condition that in the stationary state there is a balance between gain and loss of energy leads to

$$\int dx_1 dx_2 dv_1 dv_2 \gamma(x_1, x_2) (v_1^2 + v_2^2) P_{eq}(x_1, x_2, v_1, v_2) = m \epsilon. \quad (22)$$

This is a generalization of Einstein’s relation discussed above for a 2D active Brownian particle.

3.2. Delayed friction

A major drawback of the proposed model is the absence of any kind of reservoir of the acting particles, which thus only carry their actual kinetic and potential energy and are consequently in perpetual danger of getting trapped in regions without food, and are accelerated to high velocities inside the feeding regions. A simple improvement of our model somewhat cures these defects. We suggest to modify the action of the friction onto the particle by some kind of delayed friction, which depends on the particles’ recent history. We think of a modified equation of motion with the substitution:

$$\gamma(\vec{x}) \vec{x} \rightarrow \Gamma(t) \vec{x}$$

where

$$\Gamma(t) = \int_{-\infty}^{t} d\tau K(\vec{x}(\tau), t - \tau). \quad (23)$$

A specific example is the form

$$\Gamma(t) = \int_{-\infty}^{t} \frac{d\tau}{t_0} \gamma(\vec{x}(\tau)) \exp\left[-(t - \tau)/t_0\right] \quad (24)$$

where $t_0$ is a memory time that determines for how long the friction encountered in the past influences the present motion of the particle. In the limit $t_0 \to 0$, $\Gamma(t)$ again is the old $\gamma(x(t))$, while a properly adjusted choice of $t_0 > 0$ delays the acceleration somewhat, and thus accounts for the simple reservoir we intend to include. This leads to new equations of
motion, and (1) becomes the coupled system:

\[ m \ddot{x} + \Gamma(t) \dot{x} + \nabla \Phi(x) = 0, \]
\[ \dot{\Gamma}(t) = \frac{1}{t_0} (\gamma(x(t))) - \Gamma(t). \]  

(25)

This introduction of the relaxation time \( t_0 \) into the dynamic equations leads to a delay of the acceleration processes. The model with delayed friction has the property that the acceleration occurs only some time \( t_0 \) after passing through the food. In this way, with an appropriate choice of \( t_0 \), the simulations show a much more realistic behaviour. This depicts to some extent the motion of insects that run fast between and slowly in food spots.

4. DISCUSSION

The model has an interest at the physical as well as at the biological level. From the biological point of view, the most interesting aspect is the development of the repetitive radial motion in the 2D case. This behaviour is reminiscent of directed motion or even motion on trial-like structures in biology. The invention of directed motion in biological evolution is the first step towards overcoming the difficulties encountered in systems where food retrieval is entirely based on diffusion mechanisms. There is an abundant literature on 'biological diffusion' [20]. Most of these models, as well as those where directed motion (e.g. chemotaxis) is included, are usually based on mean-field equations [19, 24]. (There are also types of directed motion other than chemotaxis-diffusion. This last one, however, is the most often found at a microscopic level.) In general, it is taken for granted that there are energy-consuming mechanisms that lead to directed or active motion, and they are not explicitly formulated in the models.

Two questions arise immediately. First, is this a more mechanistic but also less realistic approach discussed here in agreement with other models that consider a higher levels of organization? Second, what would be the necessary modifications in order to formulate a more realistic model and to approach the mean-field models on the other hand?

Our approach here is an attempt at starting to build a model from first principles and try to meet the mean-field models by adding more realistic mechanisms. Although the mechanisms are implemented in quite different ways in the two approaches, there is one aspect that becomes more transparent here: the particle that 'explores' its environment is in a delicate energetic balance as it retrieves and dissipates energy. One sees nicely how the range of activity of the particle depends on its energy budget. Of course, our model is not very realistic from the biological point of view. Nevertheless, the particles can continuously move back and forth between energy sources and energy sinks, which can be seen as a mechanical model for foraging.

At the present stage it would be quite artificial to compare a chemotaxis-diffusion model with the model developed and described here. Such a discussion should be postponed until a more complete model is available. Nevertheless, our basic question—namely, what are the minimal rules necessary to have street formation?—is partly answered by our model. Whether these rules, namely an environmental potential with energy sources and sinks, are comparable to those that are found in mean-field type models is another question. The formulation of our model using environmental potentials entails a strong spatial dependence of the particles. This dependence goes so far that one can consider the energy minima of the potentials (the nest) as some reference points. This confirms—by the token of a totally different argument—what was found at the level of mean-field emission–chemotaxis–diffusion systems; namely, that at least one individual has to know where the nest is located.
What are the modifications that one would like to implement in order to amend the performance of the particles and to render the model more realistic. A first modification has already been introduced in section 3.2. The discussion of the impact of the introduction of a reservoir will be discussed elsewhere. The next step then would be to allow for various types of interactions between many particles exploring a given area. By having the particles modify their environment as a function of the particles’ or the environment’s state one would come already very close to emission–chemotaxis–diffusion type of model.

There is an important note that we wish to add. We do not consider our model to be an alternative to models of the origin of life. A mechanical particle would be too naive a view of that. Moreover, we may be misunderstood in that people may find it appealing to consider our model as a metaphor for some sort of spring/life analogy. However, the behaviour that is described in this paper is reminiscent of what one could call an energy pump. And it may be possible to find other analogies than the buildup of a trail.

A highly contentious issue in biology still is the question where purposefulness—as is apparent to the observer of a biological system—comes in. One would like to find answers that are not teleologically contaminated. Models like the one presented here may help to locate the point or the region where the behaviour of a mechanical particle becomes ‘purposeful’ for the particle.

As was already said above, one of the major drawbacks of our model is that the particles get trapped when there is no food. In a more realistic model—which would help to come closer to the mean-field models—one would want to have particles that are not entirely dependent on the energy balance between potential and kinetic energy. In order to fulfill this one could endow the particles with an energy reservoir, such that they could take in high-valued energy at some particularly points and use this energy reservoir to maintain some of their activities. This would also enable the particles to leave the nest independently. In this case, however, the system would no longer be tractable analytically. Our idea to employ delayed friction is a first step in this direction. The next step then would be to allow for various types of interactions between many particles exploring a given area. By having the particles modify their environment as a function of the particles’ or the environment’s state, one would come already very close to emission–chemotaxis–diffusion type of model.

Acknowledgements—VC gratefully acknowledges financial support from the Fritz Thyssen Stiftung. This work was supported by DFG via the SFB 230. We thank L. Schimansky–Geier and F. Schweitzer for discussions.

REFERENCES