Active Brownian Particles with Energy Depots Modelling Animal Mobility

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Abstract

In the model of active motion studied here, Brownian particles have the ability to take up energy from the environment, to store it in an internal depot and to convert internal energy into kinetic energy. Considering also internal dissipation, we derive a simplified model of active biological motion.

For the take-up of energy two different examples are discussed: (i) a spatially homogeneous supply of energy, (ii) the supply of energy at spatially localized sources (food centers). The motion of the particles is described by a Langevin equation which includes an acceleration term resulting from the convertion of energy. Dependent on the energy sources, we found different forms of periodic motion (limit cycles), i.e. periodic motion between "nest" and "food". An analytic approximation allows the description of the stationary motion and the calculation of critical parameters for the take-up of energy. Finally, we derive an analytic expression for the efficiency ratio of energy conversion, which considers the take-up of energy, compared to (internal and external) dissipation.

Key words: active motion, internal energy depot, animal mobility

1 Introduction

The motion of Brownian particles resembles that of microscopic living creatures. Therefore, the British botanist ROBERT BROWN, who in 1827 discovered the erratic motion of small particles immersed in a liquid, considered them as living entities. After the turn of the century, EINSTEIN, SMOLUCHOWSKI, LANGEVIN and others have shown that the behaviour of Brownian particles can be explained by simple physical models. In this paper, we want to generalize the idea of Brownian particles to derive a simplified model of active biological motion. Therefore, we introduce active

Brownian particles which are Brownian particles with the ability to take up energy from the environment, to store it in an internal depot and to convert internal energy to perform different activities.

Previous versions of active Brownian particle models (Schimansky-Geier *et al.*, 1995, 1997, Schweitzer, 1997) consider specific activities, such as environmental changes and signal-response behavior. In these models, the active Brownian particles (or active walkers, within a discrete approximation) are able to generate a self-consistent field, which in turn influences their further movement and physical or chemical behavior. This non-linear feedback between the particles and the field generated by themselves results in an interactive structure formation process on the macroscopic level. Hence, these models have been used to simulate a broad variety of pattern formations in complex systems, ranging from physical to biological and social systems (Lam and Pochy, 1993, Lam, 1995, Schweitzer and Schimansky-Geier, 1994, 1996, Schimansky-Geier *et al.*, 1995, 1997, Schweitzer, 1997a,b, Stevens and Schweitzer, 1997, Schweitzer *et al.*, 1997, Helbing *et al.*, 1997).

The main objective of this work is to study the energetic aspects of active Brownian particles, rather than focus on environmental changes. This way, we continue investigations started by Steuernagel *et al.*. (1994). The new element considered in this paper, is the energy depot of the particles. We will start our investigations by adding to the dynamics of simple physical Brownian particles new mechanisms of energy take-up, storage and conversion of energy, and energy consuming motion. This way, the particles become more complex, which result in new dynamical features that may resemble active biological motion. Hence, the basic idea can be formulated as follows: how much of physics is needed to achieve a degree of complexity which gives us the impression of motion phenomena found in biological systems?

The motion of an organism can be active and passive (Alt, 1988, Alt and Hoffmann, 1990, Tranquillo and Alt, 1990). Passive motion can occur through Brownian motion if the organism is microscopically small (Fürth, 1920). Active motion, which is of interest for our investigations, has been intensively studied at many different levels of organization (Hall, 1977, Alt, 1980, Dunn and Brown, 1987, Calenbuhr and Deneubourg, 1991, Millonas, 1992, Schienbein and Gruler, 1993, Dickinson and Tranquillo, 1993, Gruler and Boisfleury-Chevance, 1994, Schweitzer and Schimansky-Geier, 1994, Steuernagel *et al.*, 1994). Active motion, as the name suggests, occurs under energy consumption and requires metabolic activity and a supply of fuel. Current models that describe biological motion ususally take for granted that energy is always present (Alt and Hoffmann, 1990). However, even simple mechanisms for active motion (tumbling, flagellar motion) (Brokaw, 1990) already require an input of energy, and so the maintenance of metabolic activity.

In this paper, we are particulary interested in the question how known types of Hamiltonian motion or Brownian motion could be extended by mechanisms of energy take-up, storage and conversion. These new elements should contribute to the development of a microscopic theory of active biological motion. The final goal of such a project could be a microscopic image of well known phenomenological models of biological motion, taking into account energy balances that are related to the mechanisms of energy pumping and energy dissipation.

In Sect. 2, we introduce the idea of the internal energy depot and outline the basic dynamics of our model. In Sect. 3 we investigate the take-up and conversion of energy assuming a homogeneous energy supply. In Sect. 4 we derive some analytical approximations for the deterministic motion of active Brownian particles and find critical conditions for a continuous motion. In Sect. 5 we discuss the more complex case of spatially localized energy sources, and in Sect. 6, we conclude our investigations discussing the efficiency ratio of the energy conversion in the active Brownian particles.

2 Model of Active Brownian Dynamics

Let us now formulate the basic features of our model. We consider point-like objects moving in a two-dimensional space, their position given by the space vector $\underline{r}$. These moving particles are subject to friction, γ being the friction coefficient. Due to friction, the particles loose energy which is absorbed by the surrounding. Active particles, however, should be able to compensate this loss by an energy take-up at definite places on the plane. This denotes a difference to usual Brownian particles which gain energy only from thermal fluctuations. Moreover, active Brownian particles are able to store energy in *internal energy depots*, $e(t)$, which may be altered due to three different processes:

1. take-up of energy from the environment; where $q(t)$ is the flux of energy into the particle
2. internal dissipation, which is assumed to be proportional to the internal energy. Here the rate of energy loss, c, is assumed to be constant.
3. conversion of internal energy into motion, where $d(\underline{v})$ is the rate of conversion of internal to kinetic degrees of freedom. This means that the depot energy may be used to accelerate motion on the plane.

If we think of *biological objects*, the take-up of energy is similar to feeding which may occur at specific places, or food sources. The internal dissipation of stored energy, on the other hand, is then analogous to metabolic processes inside the organism. Further, it is considered that these biological object perform active motion, which also needs a supply of energy provided by the internal energy depot.

To be specific, it is assumed that the conversion rate of internal into kinetic energy depends on the velocity in a rather simple way:

$$d(\underline{v}) = d_2 v^2; \quad d_2 > 0 \tag{1}$$

The resulting balance equation for the energy depot is then given by:

$$\frac{d}{dt} e(t) = q(\underline{r}) - c\, e(t) - d_2 v^2(t)\, e(t) \tag{2}$$

We see that in general the depot is filled with a time lag. For the special case $d_2 \equiv 0$, i.e. only internal dissipation of energy and take-up of energy is considered, the explicit solution of eq.(2) is given by:

$$e(t) = e(0) + \int_0^t d\tau \exp[-c\tau]\; q(\underline{r}(\tau)) \tag{3}$$

The solution, eq. (3) shows that, in general, the content of the energy depot is a function of the historical path of the particle.

The total energy of the active Brownian particles at time t is defined as

$$E(t) = E_0(t) + e(t) \tag{4}$$

where $e(t)$ (eq. 2) is the depot energy and

$$E_0(t) = \frac{m}{2} v^2 + U(\underline{r}); \qquad \underline{v} = \dot{\underline{r}} \tag{5}$$

is the mechanical energy of the particles, consisting of a kinetic part, m being the mass of the object, and a potential energy $U(r)$. The mechanical energy, E_0, can be (i) increased by the conversion of depot energy into kinetic energy, (ii) decreased by the friction of the moving particle resulting in disspation of energy. Hence, the balance equation for the mechanical energy reads:

$$\frac{d}{dt} E_0(t) = \Big(d_2 e(t) - \gamma\Big)\, v^2 \tag{6}$$

With respect to eqs. (2, 6), the resulting change of the total energy is given by the balance equation

$$\frac{d}{dt} E(t) = q(\underline{r}) - c e(t) - \gamma v^2 \tag{7}$$

In general the friction coefficient of the active Brownian particles, γ, may be a complex function determined by different processes. We assume, that γ consists of two different parts:

$$\gamma = \gamma_0 + \gamma_1(\underline{r}) \tag{8}$$

γ_0 is the normal friction which has a positive sign, $\gamma_1(\underline{r})$ is an additional space–dependent friction, which can be also negative. This case, mentioned as *active friction* should be another source of acceleration of the objects, and has been studied in an earlier work (Steuernagel *et al.*, 1994).

Rewriting eq. (6) in a more explicit form, we get

$$m\dot{\underline{r}}\ddot{\underline{r}} + \dot{\underline{r}}\,\nabla U(\underline{r}) + \Big(\gamma_0 + \gamma_1(\underline{r})\Big)\, \dot{r}^2 = d_2 v^2 e(t) \tag{9}$$

Eq. (9) indicates that for $\dot{\underline{r}} = 0$, $d(v = 0) = 0$ yields for arbitrary values of $e(t)$, which is satisfied by the ansatz eq. (1).

We postulate now an equation of motion for the active Brownian particles which is consistent with eq. (9). This equation has the form of a LANGEVIN equation:

$$m\dot{\underline{v}} + \Big(\gamma_0 + \gamma_1(r)\Big)\, \underline{v} + \nabla U(\underline{r}) = d_2 e(t) \underline{v} + \sqrt{2D}\; \xi(t) \tag{10}$$

Stochastic differential equations, like the LANGEVIN equation, have long been used to describe the motion of biological objects (Alt, 1980, Schienbein and Gruler, 1993, Dickinson and Tranquillo, 1993). Compared to our previous investigations (Steuernagel *et al.*, 1994), the first term of the right-hand side of eq.(10) is the essential new element in this paper, reflecting the influence of the internal energy depot to the motion of Brownian particles.

The right-hand side of the LANGEVIN equation contains the driving forces for the motion. We assume that the acceleration of motion due to the conversion of internal into kinetic energy occurs in the direction of movement, expressed by the vector $\underline{e}_v = \underline{v}/v$. Further, as a second driving force we consider a stochastic force ξ with the strength D and white-noise fluctuations:

$$\langle \xi(t)\xi(t') \rangle = 2D\, \delta(t-t') \tag{11}$$

Following EINSTEIN, we assume an energy balance between the strength of the stochastic force, D, and the "normal" friction of the object, requiring the fluctuation-dissipation relation

$$D = \frac{\gamma_0 \theta}{m} \tag{12}$$

where $\theta = k_B T$ is a measure for the temperature. Assuming that the loss of energy resulting from the friction, and the gain of energy resulting from the stochastic force, are compensated in average, the balance equation for the mechanical energy, eq. (6), is modified for the stochastic case to:

$$\frac{d}{dt}\left(\frac{1}{2}m\dot{r}^2 + U(\underline{r})\right) = \Big(d_2 e(t) - \gamma_1\Big)\, \dot{r}^2 \tag{13}$$

A detailed discussion of the influence of noise on the motion of the object will be presented in a forthcoming paper.

3 Investigation of Energy Take-Up and Conversion

We notice first that the two terms in the energy balance, eq. (13), which describe the possible gain of kinetic energy, i.e. the conversion of internal energy and active friction, $(\gamma_1(\underline{r}) < 0)$, appear in a quite symmetric manner, describing a similar effect. So this description also covers the results presented previously (Steuernagel *et al.*, 1994). For further discussion in this paper, the case of active friction will be neclected. Then, the only source of energy for the moving particle is the take-up of energy from external sources, expressed by the function $q(\underline{r})$, which, in a biological context, could be considered as a "foraging function" in a figurative manner.

In order to investigate the dynamics of active motion, we first restrict ourselves to the deterministic case, $D = 0$ in eq. (10). That means the particle is not driven by a stochastic force, but it is initially in a non-stationary situation. In our investigations, the particle is assumed to have a certain initial velocity $v(t=0) \neq 0$ to start. Initially, the internal energy depot has no energy: $e(0) = 0$. During its motion, the particle takes up energy (q), but it also looses energy because of internal dissipation (c) and because of the friction (γ_0), which is not compensated, now.

We still have to specify the spatial dependence of the two functions, the take-up of energy, $q(\underline{r})$, and the potential $U(\underline{r})$. In this section, we discuss the simple assumption that the take-up of energy is constant in time and space:

$$q(\underline{r}) = q_0 \tag{14}$$

This means that the particle can take-up energy everywhere during its motion. If we further assume a constant potential on the surface S,

$$U(\underline{r}) = const. \quad \text{for all } \underline{r} \in S \tag{15}$$

then the deterministic motion of the active particle can be described by the following set of equations:

$$\begin{aligned} \dot{\underline{r}} &= \underline{v} \\ \dot{\underline{v}} &= d_2 e(t)\underline{v} - \gamma_0 \underline{v} \\ \dot{e} &= q_0 - ce - d_2 v^2 e \end{aligned} \tag{16}$$

Let us first investigate the stationary solutions for the velocity, $\dot{\underline{v}} = 0$. With respect to the equation for the energy depot, $\dot{e}$, we can distinguish between two different cases:

(i) In the trivial case, we obtain the stationary solution $\underline{v} = 0$. Then, the equation for $e(t)$ and be easily integrated, and we find with $e(0) = 0$:

$$e(t) = \frac{q_0}{c}(1 - \exp(-ct)) \tag{17}$$

That means the value of the internal energy depot reaches asymototically a constant saturation value, q_0/c, while the particle is at rest.

(ii) The non-trivial case, $\dot{\underline{v}} = 0, \underline{v} \neq 0$, is only satisfied for a constant internal energy depot,

$$e(t) = e_0 = \frac{\gamma_0}{d_2}. \tag{18}$$

In this case, we find for the constant velocity, v_0:

$$v_0^2 = \frac{q_0}{\gamma_0} - \frac{c}{d_2} \tag{19}$$

These solutions are real only if the condition $q_0 d_2 > c\gamma_0$ is satisfied. Otherwise, the internal dissipation of energy exceeds the take-up of energy, and the particle comes to rest.

The possible stationary solutions can be shown in a bifuircation diagramm, Fig. 1, where the bifuraction point is determined by

$$d_2^{crit} = \frac{\gamma_0\, c}{q_0} \tag{20}$$

This relation defines a critical conversion rate, d_2^{crit}, dependent on the internal dissipation, c, the energy influx, q_0, and the friction coefficient, γ_0. Alternatively, also a critical friction coefficient, γ_0^{crit} can be defined by the same relation, as used in Fig. 2.

If the conversion rate of internal into kinetic energy, d_2, is less than a critical value, d_2^{crit}, the energy supply for the motion of the particle is not sufficient, and the particle comes to rest. Above the critical conversion rate, however, the particle can move with constant stationary velocities. Which direction is realized, depends on stochastic influences.

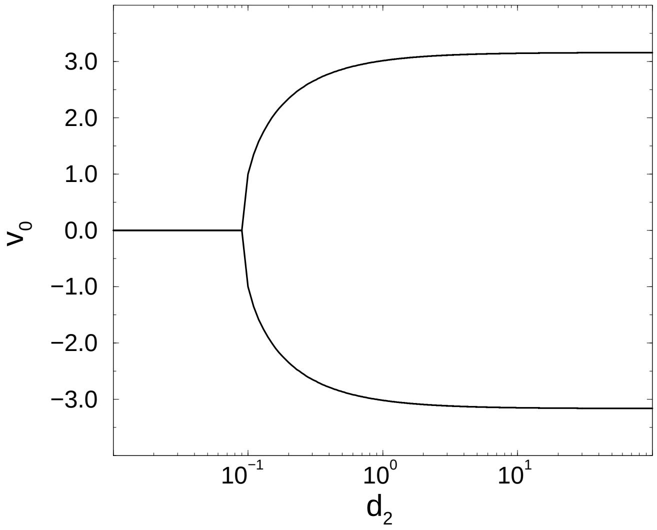

Figure 1: Bifurcation diagram for the stationary velocity, v_0, dependent on the conversion rate of internal into kinetic energy, d_2 (parameters: $q_0 = 1.0$; $c = 0.9$; $\gamma_0 = 0.1$).

In order to demonstrate how the stationary values for the internal energy depot and the velocity are reached, the set of equations (16) has been integrated using different values of γ_0.

The asymptotic values in Fig. 2 agree with the stationary solutions in eq. (17) and eq. (18). (19) respectively. For γ_0^{crit}, the critical slowing-down for the relaxation into the stationary state is also shown in Fig. 2.

So far, we considered the case $U(\underline{r}) = 0$, which, in the deterministic case and for supercritical conditions, eq. (20), implies an unbound motion of the active Brownian particle which keeps its initial direction. In order to bound the particles motion to a certain area of the two-dimensional space (x_1, x_2), we have to specify the potential $U(x_1, x_2)$ with the condition $\lim_{x \to \infty} U(x) = \infty$. Let us start with the simplest case of a parabolic potential:

$$U(x_1, x_2) = \frac{1}{2} a(x_1^2 + x_2^2) \tag{21}$$

This potential originates a force directed to the minimum of the potential. In a biological context, it simply models a “home”, and the moving object always feels a driving force pointing to its “nest”.

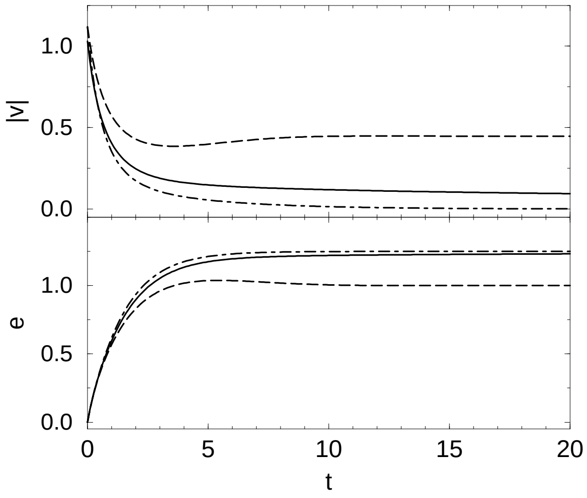

Figure 2: Absolute value of the velocity, $|\underline{v}|$, and internal depot energy, e, vs. time for three different values of the friction coefficient γ_0: 1.0 (dashed line), which is below the critical value, 1.25 (solid line), which is the critical value, 1.5 (dot-dashed line), which is above the critical value (parameters: $q_0 = 1.0$, $d_2 = 1.0$, $c = 0.8$, initial conditions: $\underline{r} = (1;0)$, $\underline{v} = (1;0.5)$).

With eq. (21) and $D = 0$, the LANGEVIN dynamics, eq. (10), for the movement of the active Brownian particle can be specified for the two-dimensional space. We get five coupled first-order differential equations:

$$\begin{aligned}
\dot{x_1} &= v_1 \\
\dot{x_2} &= v_2 \\
m\dot{v_1} &= d_2 e v_1 - \gamma_0 v_1 - \partial_1 U(x_1, x_2) \\
m\dot{v_2} &= d_2 e v_2 - \gamma_0 v_2 - \partial_2 U(x_1, x_2) \\
\mu \dot{e} &= q(x_1, x_2) - ce - d_2 e(v_1^2 + v_2^2) \qquad (22)
\end{aligned}$$

where the solution $v_1 = v_2 = 0$ is known to be a standard stationary point of the motion provided the particle does not feel any external force.

In eq. (22), we have introduced a formal parameter μ which may be used for an adiabatic switching of the depot variable $e(t)$. In the general case, $\mu = 1$, the depot is filled with a time lag, again. The limit $\mu \to 0$, however, describes a very fast adaptation of the depot, and we get as an adiabatic approximation

$$e(t) = \frac{q(x_1(t), x_2(t))}{c + d_2(v_1^2(t) + v_2^2(t))} \qquad (23)$$

In this approximation, the depot energy is simply proportional to the gain of energy from external sources, q, at the given location and decreases with the increase of the kinetic energy. In the following, we assume $q(\underline{r}) = q_0$, eq. (14), again.

Fig. 3 shows the movement of the particle in the potential U, eq. (21), as the result of an integration of eqs. (22) with $D = 0$ and $\mu = 1$. The figure clearly indicates that the deterministic motion, after an initial relaxation time with transient trajectories, tends towards a stationary motion on a limit cycle.

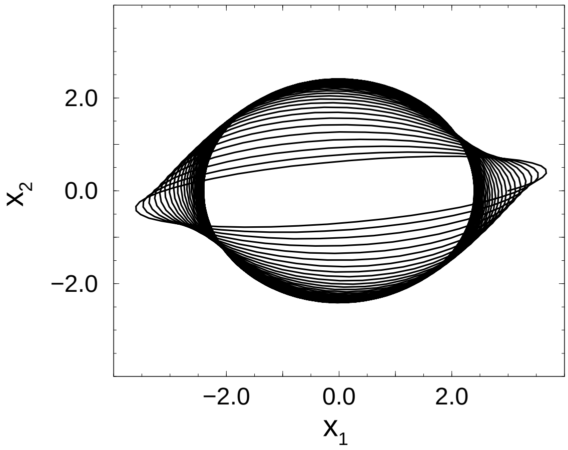

Figure 3: Trajectories in the x_1, x_2 space for the deterministic motion of the particle. Initial conditions: $x_1(0) = 3$, $x_2(0) = 0$, $v_1(0) = 3$, $v_2(0) = 1$, $e(0) = 0$ (parameters: $q_0 = 1.0$, $d_2 = 1.0$, $c = 0.9$, $\gamma_0 = 0.08$).

The corresponding change of the internal energy depot of the object is presented in Fig. 4.

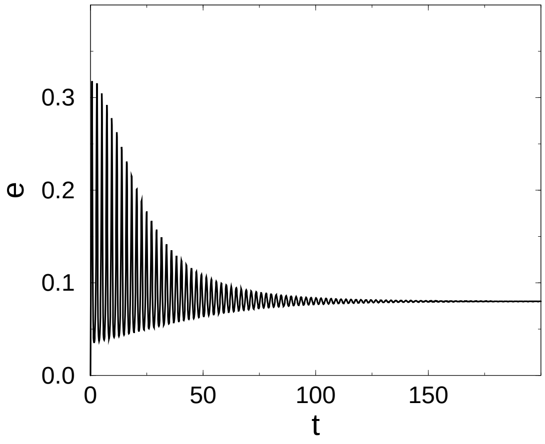

Figure 4: Evolution of the internal energy depot for the motion shown in Fig. 3.

We see that the stationary motion of the object on a limit cycle corresponds to a saturation value of the internal energy depot, obtained after the period of relaxation. An analytic approximation for the stationary level of the internal energy will be given in the next section.

4 Approximative Analytical Solutions for the Deterministic Limit Cycle Motion

As shown in the previous section, the deterministic motion of the active particles depends on the internal energy depot, e, which itself is determined by the take-up (q) and the loss (c) of energy, and the conversion rate (d). For the analytical approximations, we restrict ourselves to the previous case of the 2-dimensional motion, eq. (22), with $D = 0$, $\mu = 0$, $q(x_1, x_2) = q_0$ (eq. 14) and a parabolic potential U (eq. 21).

Near the origin of the potential, the energy of the internal depot (eq. 23) can be approximated by the constant

$$e = \frac{q_0}{c}, \quad \text{if} \quad (v_1^2 + v_2^2) \ll c/d_2 \tag{24}$$

Inserting eq. (24), into the equation of motion, eq. (22), we find:

$$\ddot{x}_i + 2\alpha \dot{x}_i + \omega_0^2\, x_i = 0 \quad \text{with} \quad \alpha = \frac{\gamma_0}{2m} - \frac{d_2 q_0}{2m\, c} \;\; ; \;\; \omega_0^2 = \frac{a}{m} \quad (i = 1, 2) \tag{25}$$

For $\alpha^2 < \omega_0^2$, the phase-space trajectories resulting from eq. (25) are described by the spiral solution

$$\{x_i, v_i\} = e^{\alpha t}\{A_1 \cos(\omega t) + A_2 \sin(\omega t)\} \;\; ; \quad \omega = \sqrt{\omega_0^2 - \alpha^2} \quad (i = 1, 2) \tag{26}$$

where A_1, A_2 are specified by the intial conditions. Eq. (26) means that the projection of the motion of the particle on any pair of the axes $\{x_1\ x_2\ v_1\ v_2\}$ corresponds to expanding or shrinking ellipses. Fig. 5 presents the case of a subcritical motion of the particle, i.e. the take-up of energy or the conversion of internal energy into kinetic energy is not large enough to continue moving, and the active particle finally “dies” in the minimum of the potential.

For larger amplitudes the condition, eq. (24), gets violated and we have to solve the equations of motions resulting from eq. (22) with $D \equiv 0$, $\mu \equiv 0$ (eq. 23) and eq. (21):

$$m\ddot{x}_i = \frac{d_2 q_0 \dot{x}_i}{c + d_2(v_1^2 + v_2^2)} - a x_i - \gamma_0 \dot{x}_i \qquad (i = 1, 2) \tag{27}$$

The solution of this equation is unknown but, with a little trick (Feistel and Ebeling, 1989), we can find an approximative solution. Counting on the fact that, at least in the harmonic case, the average of the potential energy is equal or rather close to the average of the kinetic energy:

$$\left\langle \frac{m}{2}\left(v_1^2 + v_2^2\right)\right\rangle \cong \left\langle \frac{a}{2}\left(x_1^2 + x_2^2\right)\right\rangle \tag{28}$$

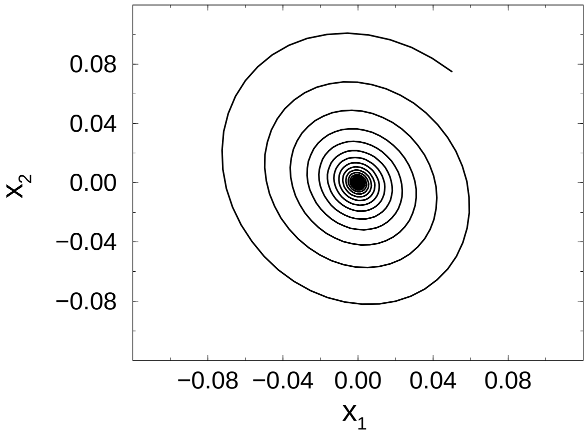

Figure 5: Trajectories in the x_1, x_2 space for the subcritical motion of the object $(q_0 d_2 < \gamma_0 c)$ (parameters: $q_0 = 0.1$, $d_2 = 0.1$, $c = 0.1$, $\gamma_0 = 0.2$)

we can modify the function $d(\underline{v})$ as follows:

$$d_2\,(v_1^2 + v_2^2) = d_2\,\left\{\frac{1}{2}\left(v_1^2 + v_2^2\right) + \frac{a}{2m}\left(x_1^2 + x_2^2\right)\right\} \tag{29}$$

Specifying the mechanical energy of the object, eq. (5):

$$E_0 = \frac{m}{2}\left(v_1^2 + v_2^2\right) + \frac{a}{2}\left(x_1^2 + x_2^2\right) \tag{30}$$

we get from eq.(27) for the change of the mechanical energy:

$$\frac{dE_0}{dt} = \left[\frac{d_2 q_0}{c + d_2 E_0/m} - \gamma_0\right]\left(\frac{\partial E_0}{\partial v_i}\right)^2 \frac{1}{m^2} \tag{31}$$

Eq. (31) indicates that stable orbits with constant mechanical energy exist in the stationary limit:

$$E_0 = m\frac{d_2 q_0 - \gamma_0 c}{d_2 \gamma_0} \tag{32}$$

if the constraint $d_2 q_0 > \gamma_0 c$ applies. For the adiabatic approximation considered, eq. (32) provides a relation between the energy dissipation due to friction (γ_0) and the different parameters that determine the level of the internal energy depot: take-up of energy (q_0), internal dissipation (c), and conversion of internal to kinetic energy (d_2).

We note that the critical condition obtained from eq. (32) agree with the result, eq. (20), derived in the previous section for the potential $U \equiv 0$. It can be also shown for the supercritical case that the stationary velocity for the motion in the potential $U(x_1, x_2)$, eq. (21), agrees with the previous result of eq. (19). By taking advantage of the eqs. (30), (28), the stationary velocity can be derived from eq. (32):

$$v_{stat}^2 = (v_1^2 + v_2^2) = \frac{d_2 q_0 - \gamma_0 c}{d_2 \gamma_0} \tag{33}$$

Inserting this expression into eq. (23), the stationary value of the internal energy depot can be estimated as:

$$e = \frac{\gamma_0}{d_2}, \quad \text{if} \quad (v_1^2 + v_2^2) = v_{stat}^2 \tag{34}$$

which agrees with eq. (18) and with the result of the computer simulations, shown in Fig. 4.

Accordingly, the stationary limit predicts that beyond a critical value of the energy take-up

$$q_0 > q_0^{crit} = \frac{\gamma_0 c}{d_2} \tag{35}$$

limit cycles for the motion of the object exist which are closed trajectories on the ellipsoid

$$\frac{m}{2}\left(v_1^2 + v_2^2\right) + \frac{a}{2}\left(x_1^2 + x_2^2\right) = m\left(\frac{q_0}{\gamma_0} - \frac{c}{d_2}\right) \tag{36}$$

In the four-dimensional phase space, the ellipsoid defines the hyper plane of constant energy, which holds all limit cycles. A projection of the limit cycle to the configuration space results in a circle. However, in the case of spatially localized supply of energy, discussed in the next section, the limit cycle may degenerate, and the above description has to be modified.

Of course, the adiabatic appproximation does not apply during the initial period of motion, however, in the asymptotic limit our approximation remains valid. This is also shown in Fig. 6, which is a numerical solution of the equation of motion (eq. 27) and thus allows an estimation of the time lag before the stationary regime of motion is reached. For Fig. 6, we have also numerically tested the validity of eq. (36) which applies for the stationary motion.

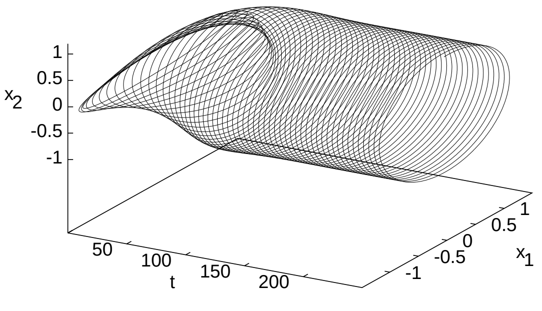

Figure 6: Trajectories in the x_1, x_2 space for the deterministic motion of the particle (parameters: $q_0 = 0.5$, $\gamma_0 = 0.2$, $c = 0.01$, $d_2 = 0.9$, $a^2 = 2$, initial conditions: $x_1(0) = 1$, $x_2(0) = 0$, $v_1(0) = 1$, $v_2(0) = 0.33$)

5 Localized Energy Sources

In real life, animal motion occurs in complicated landscapes which typically contain localized "nests", "foraging places" and "obstacles". This may lead to a rather complex motion of the biological creatures. In the following we will study a simple case where the gain of energy is restricted to certain locations, or "foraging places". The consideration of additional "obstacles" is discussed in a subsequent paper (Schweitzer *et al.*, 1997b).

If the the energy sources are localized in space, the active Brownian particles in our model are not able to take-up energy everywhere, but only in a restricted area. This is reflected in a space dependence of the energy influx (or foraging function) $q(\underline{r})$, which is zero everywhere except at specific locations. In order to investigate this case let us study a food source modeled as a circle:

$$q(x_1, x_2) = \begin{cases} q_0 & \text{if } [(x_1 - a)^2 + (x_2 - b)^2] \leq R^2 \\ 0 & \text{elsewhere} \end{cases} \tag{37}$$

Now, the moving particle is only able to increase its energy depot inside the circle. It is noteworthy, that the active particle is *not* attracted by the food source due to long-range attraction forces. Therefore, in a deterministic motion, the initial conditions completely determine whether the particle is able to hit the circle or not. In order to give the particle a possibility to hit the food circle by chance, we have to consider its movement as a stochastic motion. But for the assumed balance between friction and noise, eq. (12), the only source of energy for the moving object is still the take-up of energy from external sources.

Fig. 7 represents the stochastic motion of a particle which can "feed" inside a certain area, but also feels a certain force driving it back to its "nest". The take-up of energy inside the food circle determines how far the active Brownian particle can reach out from the nest again. After an initial period of stabilization, we see an oscillatory movement between the "food" and the "nest" for a certain period of time.

Fig. 8 presents more details of the motion of the active Brownian particle. Considering the time-dependent change of the internal energy depot and the space coordinates, we can distinguish between two stages: In a first stage, the particle has not found the "feeding place", thus its energy depot is empty while the space coordinates fluctuate around the coordinates of the "nest". The second stage starts when the particle by chance, due to stochastic influences, reaches the localized energy source. Then the internal depot is soon filled up, which in turn allows the particle to reach out further, shown in the larger fluctuations of the space coordinates. This accelerated movement, however, leads the active particle away from the energy source, and soon the internal depot is exhausted again, until the particle returns to the energy source. Fig. 8 shows the corresponding oscillations in the energy depot. Due to stochastic influences, the oscillatory regime can break down. But a new cycle can be initiated if the particle hits the energy source by chance, again.

Interestingly, every cycle starts with a burst of energy in the depot, indicated by the larger peak in $e(t)$, Fig. 8, which is used for the acceleration of the particle. The the amount of the energy bursts, the time when the energy depot is filled and the area covered by trajectories, depend remarkably on the conversion parameter, d_2 as discussed in more detail in (Schweitzer *et al.*, 1997b).

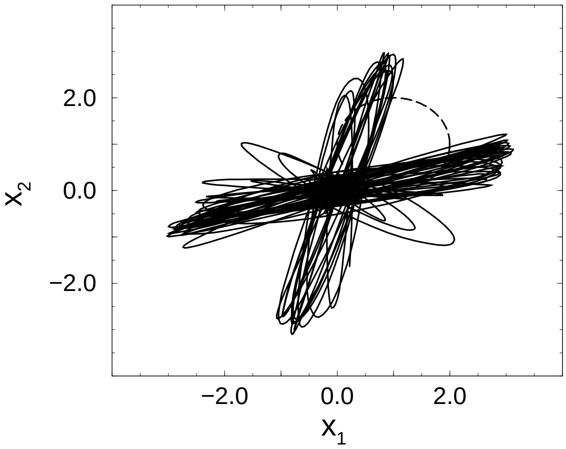

Figure 7: Trajectories in the x_1, x_2 space for the stochastic motion of the active Brownian particle. The circle (cooordinates (1,1), radius 1) indicates the "feeding area". (parameters: $q_0 = 10$, $d_2 = 1$, $\gamma_0 = 0.2$, $c = 0.01$, $D = 0.01$, initial conditions: $(x_1, x_2) = (0, 0)$, $(v_1, v_2) = (0, 0)$)

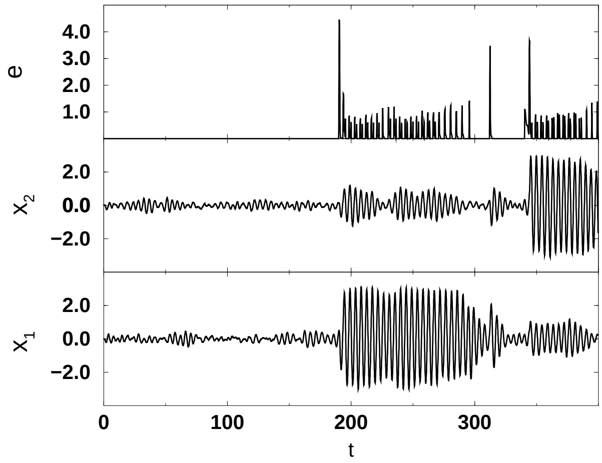

Figure 8: Internal energy depot, e and space coordinates x_1, x_2 vs. time for the stochastic simulation presented in Fig. 7.

The cases discussed in Sect. 3 and 5, describe basic types of motion for active Brownian particles with an internal energy depot. Of course, the model provided can also be specified to describe other situations with respect to the "nest" and the "food". We just want to mention the case of many "nests" which can be easily implemented into the potential $U(\underline{r})$. On the other hand, we can also assume many separated food sources, randomly distributed on the surface, which means a specification for $q(\underline{r})$.

Finally, we can generalize the situation by considering that the availablility of energy is both space and time dependent, which means additional conditions for the foraging function $q(\underline{r}, t)$. Let us consider a situation, where food grows with a given flow density $\Phi(\underline{r}) = \eta q_f(\underline{r})$, with η being a dimensional constant. Then, we assume that the change of the foraging function may depend both on the increase and the decrease of food, i.e:

$$\dot{q}(\underline{r}, t) = \Phi(\underline{r}) - \eta q(\underline{r}, t) = \eta[q_f(\underline{r}) - q(\underline{r}, t)] \tag{38}$$

The formal solution for the foraging function yields:

$$q(\underline{r}, t) = e^{-\eta t} q(\underline{r}, 0) - \eta \int_{-\infty}^{t} d\tau \, e^{-\eta(t-\tau)} q_f(\underline{r}(\tau), \tau)) \tag{39}$$

As we see, the actual value of the energy influx now depends on the whole prehistory of the motion of the particle and reflects a certain kind of memory. However, throughout this paper those memory effects in foraging will be neglected, which means $\eta \to \infty$.

6 Discussion

The objective of this paper was to study active Brownian motion as a simplified model of active biological motion. The complexity of the biological creature has been reduced to the physics of pumped Brownian particles with energy depots, but we have shown in this work that several basic ingredients of active biological motion could be also featured in this very simple model.

Our model of active Brownian motion is based on particles with the ability to take-up energy from the surrounding, to store it in an internal energy depot and to convert the stored energy into kinetic energy for movement. The internal energy depot is crucial for active motion, since it allows the particle to overcome periods where no external energy supply is possible. Since these conditions allow to reach out into larger parts of the surrounding area, the internal energy depot provides a new degree of freedom for the moving object. This is also realized in biological creatures, where, during the search for food, the depot provides the energy to move by converting internal into kinetic energy, further it allows the metabolism of the creature.

In our model, the internal depot can be filled at certain places ("feeding areas") which do not have a long-range attraction to the particles, and thus are hit by chance. Further a "nest" is modeled by a potential, which originates a certain force driving the particle back to its "nest". Assuming a LANGEVIN-type motion of the particle, we found for different "foraging functions" a stationary motion of the particle on limit cycles. Moreover, an oscillatory motion of the object between "nest" and "food" has been observed for the case of spatially localized supply with energy. Here, the take-up of energy inside the food circle determines how far the particle can reach out from the nest again. Due to stochastic influences, the oscillatory regime may break down after a certain time, but new cycles are possible.

Considering the active motion of microscopic biological objects, like cells, the case of a continuous supply of energy seems to be valid, but the active motion (or self-motion) of the object still results from the transfer of internal energy into kinetic energy. The energetic description of the object, with respect to energy input, conversion of energy, loss of energy (due to metabolism and friction) and energy output (motion in a potential), reminds us of a simple kind of a micro–motor. We are not going to explain the operation of this micro–motor, however taking into account the energy balance, we are able to discuss the efficency ratio, which is included in our model.

Based on the assumptions discussed in previous sections, the efficency ratio, σ, is defined as the ratio between the input of energy per time intervall, dE_{in}/dt, and the output of energy per time intervall, dE_{out}/dt. The input is simply given by the "foraging function" $q(r)$, which describes the take-up of external energy per time intervall. Other energy sources, like active friction or stochastic forces, are neglected here. The output is defined as the amount of energy available from the depot, $d(\underline{v})\ e(t)$, which is the amount that can be converted into the mechanical energy of the object (kinetic and potential energy), with a loss of energy due to metabolism and friction. With the ansatz for $q(\underline{r})$ (eq. 14) and $d(\underline{v})$ (eq. 1), the efficiency ratio can be expressed as follows:

$$\sigma = \frac{dE_{out}/dt}{dE_{in}/dt} = \frac{d(\underline{v})\ e(t)}{q(\underline{r})} = \frac{d_2\ e\ v^2}{q_0} \tag{40}$$

Assuming again a very fast relaxation of the internal energy depot, which then can be described by eq. (23), eq. (40) is modified to:

$$\sigma = \frac{d_2\ v^2}{c + d_2\ v^2} \tag{41}$$

Here, we see that the metabolism of the object, which results in energy dissipation, leads to a decrease of the efficiency ratio, which is now less than 1.

Inserting the expression for stationary velocity, eq. (33), we find for the efficiency ratio in the stationary limit:

$$\sigma = 1 - \frac{c\ \gamma_0}{d_2\ q_0} \tag{42}$$

Eq. (42) concludes the discussions above. The efficiency ratio, which is 1 only in the ideal case, decreases if the dissipative processes, like (passive) friction (γ_0) and metabolism (c), are taken into account. Moreover, σ is larger than zero only if the foraging function is above the critical value q_0^{crit} (eq. 35).

We would like to mention that our considerations are based on a deterministic description of the moving object. However, for microscopically small objects, the influence of noise, e.i. the stochastic force D as another source of energy, could not be neglected; which may result in a modification of eqs. (40-42).

A final remark is devoted to the problem of the directed motion of biological micro-objects. Our model has shown the existence of a periodic forth-and backward movement for very simple situations. On the other hand, there are many circumstances where biological objects, like bacterias, cells, social insects, perform a directed movement by responding e.g. to chemical gradients (Alt, 1980, Calenbuhr and Deneubourg, 1991, Dickinson and Tranquillo, 1993, Schweitzer and Schimansky-Geier, 1994, Schweitzer *et al.*, 1997b). In order to take into account these additional effects, our model could be improved assuming a non-linear coupling between different moving particles. This would lead to a more complex sketch of the objects discussed in order to approach biological features.

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