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Introduction to the physics of Brownian motors

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1 Introduction

Can useful work be extracted out of unbiased random fluctuations if all acting forces and temperature gradients average out to zero? As far as macroscopic fluctuations are concerned, the task can indeed be accomplished by various kinds of mechanical or electrical rectifiers, such as a windmill or a self-winding wristwatch. On the other hand, in the case of microscopic fluctuations, i.e. Brownian "noise", this question has provoked debates ever since the early days of Brownian motion theory [1–4]: Prima facie speaking, there seems indeed no obvious reason why a periodically working device with a broken inversion symmetry (ratchet device) should not preferentially loop in either one or the other direction under the action of unbiased random perturbations. In the absence of any such prohibitive a priori reason, and in view of the fact that, after all, the symmetry of the system is broken, the manifestation of such a preferential direction of motion appears indeed to be an almost unavoidable educated guess, though a rigorous proof can hardly be given. This very postulate that if a certain phenomenon is not ruled out by symmetries then it will generically occur, is known as *Curie's principle* [5].

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Yet, as already argued by Smoluchowski in 1912 [2] and popularized later by Feynman [4, 6], in spite of the broken symmetry, no preferential direction of motion is possible if only equilibrium fluctuations are at work. Otherwise, such a device would constitute a Maxwell-demon type perpetuum mobile of the second kind [1, 7], which is in contradiction to the second law of thermodynamics. Note that this conclusion does not undermine Curie's principle: A necessary condition for a system to be at thermal equilibrium can also be expressed in the form of a symmetry condition, namely the so-called *detailed balance* symmetry [8, 9]. However, in contrast to what we have called above an obvious prohibitive reason for a preferential direction of motion, detailed balance symmetry is a rather subtle probabilistic concept which in certain situations is at odds with one's own intuition. Nevertheless, its main physical content is rather simple, expressing in a formal manner the reversibility (time-inversion symmetry) of a stationary equilibrium process, which in turn immediately leads us back to the impossibility of a preferential direction of motion. We finally note that reversibility is not sufficient for a system to be at equilibrium, as can be exemplified by stationary non-equilibrium systems which satisfy detailed balance symmetry.

2 Basics

In order to quantify and develop further these considerations, we focus on a Brownian particle in one dimension with coordinate $x(t)$ and mass m, which is governed by a Newtonian equation of motion of the form

$$m\ddot{x}(t) + V'\big(x(t)\big) = -\eta\dot{x}(t) + \xi(t) \ , \quad (1)$$

where $V(x)$ is a periodic potential with period L,

$$V(x+L) = V(x) \ , \quad (2)$$

which exhibits broken spatial symmetry (a so-termed ratchet potential). A typical example reads

$$V(x) = V_0\,[\sin(2\pi x/L) + 0.25\,\sin(4\pi x/L)] \ , \quad (3)$$

which is depicted in Fig. 1.

The left-hand side in (1) represents the deterministic, conservative part of the particle dynamics, while the right-hand

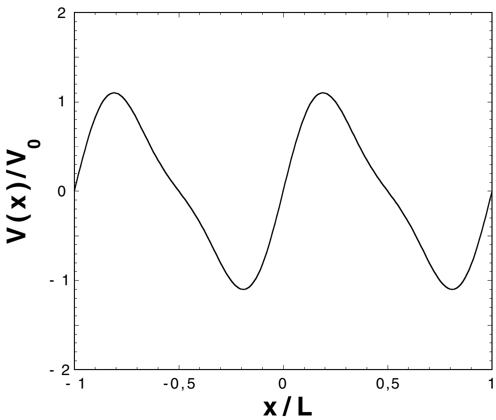

FIGURE 1 Typical example of a ratchet potential $V(x)$: It is periodic in space with period L and possesses a broken spatial symmetry. Plotted is the example from (3) in dimensionless units

side accounts for the effects of the thermal environment. These are energy dissipation, modeled in (1) as viscous friction with a friction coefficient η, and randomly fluctuating forces in the form of the thermal noise $\xi(t)$. These two terms are not independent of each other, because they both have the same origin, namely the interaction of the particle $x(t)$ with a huge number of microscopic degrees of freedom of the environment. In fact, our assumption that the environment is an equilibrium heat bath at temperature T, whose effect on the system can be modeled in the form of the phenomenological ansatz appearing on the right-hand side of (1), completely fixes all statistical properties of the fluctuations $\xi(t)$ without the need to refer to any microscopic details of the environment [10]. Namely, in order not to allow for a perpetuum mobile of the second kind, the fluctuations $\xi(t)$ are bound to be a Gaussian white noise of zero mean,

$$\langle \xi(t) \rangle = 0 \, , \tag{4}$$

satisfying the fluctuation–dissipation relation [11–13]

$$\langle \xi(t)\xi(s) \rangle = 2\eta k_{\mathrm{B}} T \delta(t-s) \, , \tag{5}$$

where k_{B} is Boltzmann's constant, i.e. the noise $\xi(t)$ is uncorrelated in time.

The state variable $x(t)$ in (1) will usually be referred to as a "Brownian particle" and in many relevant instances indeed describes the position of a true physical particle. More generally, it may also represent some quite different type of collective degree of freedom or other relevant (slow) state variable of the system under investigation. Examples appearing in other contributions to the present special issue include a chemical reaction coordinate, geometric configuration coordinates, or some internal degrees of freedom of cellular transport enzymes as they occur in the modeling of molecular motors and pumps, the Josephson phase in a superconducting quantum interference device, and alike. In these typically very small systems the fluctuation dynamics is often to a good approximation governed by an *overdamped* Langevin dynamics, that is, the inertia term $m\ddot{x}(t)$ then becomes negligible [9, 14]. We thus arrive at the following *minimal equilibrium ratchet model*:

$$\eta \dot{x}(t) = -V'(x(t)) + \xi(t) \, . \tag{6}$$

The quantity of foremost interest in the context of transport in periodic systems is the average particle current in the long-time limit (after initial transients have died out), i.e.

$$\langle \dot{x} \rangle := \left\langle \lim_{t\to\infty} \frac{x(t)-x(0)}{t} \right\rangle \, . \tag{7}$$

It is intuitively plausible, and it can also be readily confirmed by a more rigorous formal calculation, that – as far as the velocity $\dot{x}(t)$ is concerned – the infinitely extended state space in (6) can be substituted by a circle, i.e. we can identify $x+L$ with x. Accordingly, the probability density $P(x,t)$ associated with a statistical ensemble of independently sampled random processes (6) inherits the spatial periodicity L and is normalized on the unit cell $[0, L]$. Moreover, one can infer that the average particle current (7) can be rewritten in the form

$$\langle \dot{x} \rangle = -\lim_{t\to\infty} \frac{1}{t} \int_0^t \mathrm{d}t' \int_0^L \mathrm{d}x \frac{V'(x)}{\eta} P(x,t') \, . \tag{8}$$

The time evolution of $P(x,t)$ is quantitatively described by a so-called Fokker–Planck equation [9, 14]. For our present, archetype dynamics in (6), this equation yields in the long-time limit – as one would have expected – a Boltzmann-type, steady-state solution $P^{\mathrm{st}}(x)$ of the form

$$P^{\mathrm{st}}(x) = \frac{\exp[-V(x)/k_{\mathrm{B}}T]}{\int_0^L \mathrm{d}y \exp[-V(y)/k_{\mathrm{B}}T]} \, . \tag{9}$$

With (8) this implies for the particle current the result

$$\langle \dot{x} \rangle = 0 \, . \tag{10}$$

In other words, we find once again that *at thermal equilibrium*, in a spatially periodic potential there arises – in spite of the system intrinsic asymmetry – *no preferential direction of the random Brownian motion*.

Finally, we complement our minimal ratchet model (6) by an additional homogeneous, static force F:

$$\eta \dot{x}(t) = -V'\big(x(t)\big) + F + \xi(t) \, . \tag{11}$$

It is instructive to incorporate the ratchet potential $V(x)$ and the force F into a single effective potential $V_{\mathrm{eff}}(x) := V(x) - xF$, which the Brownian particle (11) experiences. For example, for a negative force, $F<0$, pulling the particles to the left, the effective potential will be like in Fig. 1, but now tilted to the left. In view of the result (10) for $F=0$, it is suggested that in such a tilted potential the particles will move on average "downhill", i.e. $\langle \dot{x} \rangle < 0$ for $F<0$, and similarly $\langle \dot{x} \rangle > 0$ for $F>0$. This conclusion can also be confirmed with detailed quantitative calculations along similar lines to the above discussed case for $F=0$. Here, we content ourselves with the remark that detailed balance symmetry is broken when $F \neq 0$, suggesting according to Curie's principle the emergence of a non-zero current. Such a current can then only point in the same direction as F, in order not to yield a perpetuum mobile of the second kind.

The appearance of a non-vanishing current $\langle \dot{x} \rangle$ furthermore signals that the ratchet system is driven away from thermal equilibrium by the static force F in (11) with the concomitant possibility for a motor action.

2.1 *Proof-of-principle device: Brownian motor driven by temperature oscillations*

Next we turn to the central issue of this section, namely the phenomenon of noise-induced, directed transport in a spatially periodic, asymmetric system away from thermal equilibrium. This so-called "ratchet effect" is very often illustrated by the example of an on–off ratchet model, as originally devised by Bug and Berne [15] and independently by Ajdari and Prost [16] (see also Sect. 4 below). Here, we will elucidate the prominent physics with a different example, namely the so-called *temperature ratchet* model [17]. This Brownian motor model, however, actually turns out to be closely related to the on–off ratchet model. We emphasize that the choice of this example is not primarily based on its historical significance but rather on the authors' personal taste and research activities. Moreover, this example is particularly suitable for the purpose of illustrating – besides the ratchet effect per se – also several other basic physical concepts, upon which we will elaborate in more detail in the following subsections.

In order to illuminate the mechanism of a Brownian motor, we consider as an extension of the model in (11), the situation where the noise strength, as represented by the temperature T of the Gaussian white noise $\xi(t)$ in (5), is subjected to periodic, temporal modulations with period $\mathcal{T}$ [17], i.e.

$$\langle \xi(t)\xi(s) \rangle = 2\eta k_{\mathrm{B}} T(t) \delta(t-s) \,, \tag{12}$$

$$T(t) = T(t+\mathcal{T}) \,. \tag{13}$$

Two typical examples which we will adopt for our numerical investigations below are

$$T(t) = \overline{T}\,\{1 + A\,\mathrm{sign}\,[\sin(2\pi t/\mathcal{T})]\} \,, \tag{14}$$

$$T(t) = \overline{T}\,[1 + A \sin(2\pi t/\mathcal{T})]^2 \,, \tag{15}$$

where $\mathrm{sign}(x)$ denotes the signum function and $|A| < 1$. With the first realization in (14) the temperature thus jumps between $T(t) = \overline{T}[1+A]$ and $T(t) = \overline{T}[1-A]$ at every half period, $\mathcal{T}/2$. Due to these permanent changes of the temperature, $T(t)$, the system approaches a periodic long-time asymptotics, which in general can only be handled numerically.

We next come to the pivotal feature of the temperature ratchet model (11)–(13): In the case of the statically tilted model with a time-independent temperature T we have seen above that for a given force, say $F < 0$, the particle will move "downhill" on average, i.e. $\langle \dot{x} \rangle < 0$. This fact holds true for *any fixed* (non-zero) value of T. Returning to the temperature ratchet with T being now subjected to periodic temporal variations, one therefore should expect that the particles still move "downhill" on average. The numerically calculated "load curve" depicted in Fig. 2 demonstrates [17] that the opposite is true within an entire interval of negative F values. Surprisingly indeed, the particles are climbing "uphill" on average, thereby performing work against the load force, F. This upward directed motion is apparently triggered by no other source than the white thermal noise $\xi(t)$.

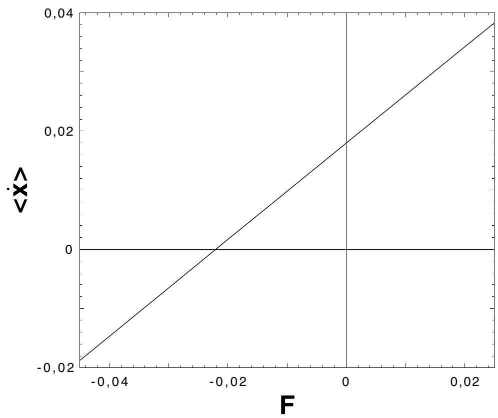

FIGURE 2 Numerically determined time- and ensemble-averaged particle current $\langle \dot{x} \rangle$ in the long-time limit versus the force F for the temperature ratchet model (3), (11), (12) and (14). Using dimensionless units, the parameter values are $\eta = L = \mathcal{T} = k_{\mathrm{B}} = 1$, $V_0 = 1/2\pi$, $\overline{T} = 0.5$ and $A = 0.8$

A conversion (or rectification) of random fluctuations into useful work as exemplified above is termed the "*ratchet effect*". For a setup of this type, the names *thermal ratchet* [18], *Brownian motor* [19], *Brownian rectifier* [20] (mechanical diode [21]), *stochastic ratchet* [22], or simply ratchet are in use.[1] Because the average particle current $\langle \dot{x} \rangle$ usually depends continuously on the load force F it is for a qualitative analysis sufficient to consider the case $F = 0$: the occurrence of the ratchet effect is then tantamount to a finite current,

$$\langle \dot{x} \rangle \neq 0 \quad \text{for} \quad F = 0 \,, \tag{16}$$

i.e. the unbiased Brownian motor implements a "particle pump".

In order to understand the basic physical mechanism behind the ratchet effect at $F = 0$, we focus on strong, i.e. $|A| \lesssim 1$, dichotomous periodic temperature modulations from (14). During an initial time interval, say $t \in [\mathcal{T}/2, \mathcal{T}]$, the thermal energy $k_{\mathrm{B}}T(t)$ is kept at a constant value, $k_{\mathrm{B}}\overline{T}[1-A]$, much smaller than the potential barrier ΔV between two neighboring local minima of $V(x)$. Thus, all of the particles will have accumulated in the close vicinity of the potential minima at the end of this time interval, as sketched in the lower panel of Fig. 3. Then, the thermal energy jumps to a value $k_{\mathrm{B}}\overline{T}[1+A]$ much larger than ΔV and remains there during another half period, say $t \in [\mathcal{T}, 3\mathcal{T}/2]$. Because the particles then hardly feel the potential any more in comparison to the violent thermal noise, they spread out in a manner which is typical for the case of free thermal diffusion (upper panel in Fig. 3). Finally, $T(t)$ jumps back to its original low value of $\overline{T}[1-A]$, and the particles slide downhill towards the respective closest local minima of $V(x)$. Due to the asymmetry of

[1] The notion "molecular motor" should be reserved for models focusing specifically on intracellular transport processes. Similarly, the notion "Brownian ratchet" has been introduced in a rather different context, namely as a possible operating principle for the translocation of proteins across membranes [23].

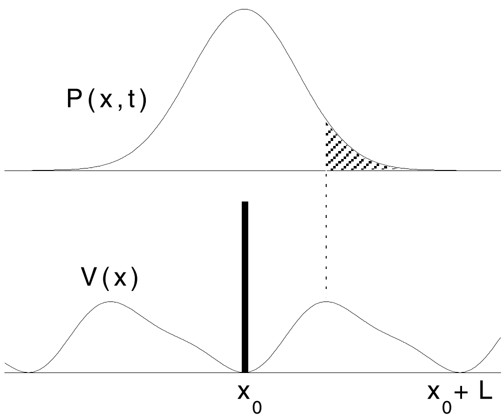

FIGURE 3 The basic working mechanism of the Brownian motor model (11), (12) and (14). The figure illustrates how Brownian particles, initially concentrated at x_0 (*lower panel*), spread out when the temperature is switched to a very high value (*upper panel*). When the temperature jumps back to its initial low value, most particles are captured again in the basin of attraction of x_0, but also substantially in that of $x_0 + L$ (*hatched area*). A net current of particles to the right, i.e. $\langle \dot{x} \rangle > 0$ results. Practically the same mechanism is at work when the temperature is kept fixed and instead the potential is turned "on" and "off" (on–off ratchet) [15, 16]. Especially, in both cases a finite amount of thermal noise is indispensable for a non-zero particle current

$V(x)$, the original population of one given minimum is redistributed asymmetrically, yielding a net average displacement after one temporal period $\mathcal{T}$.

In the case where $V(x)$ has exactly one minimum and maximum per period, L (as in Fig. 3), it is quite obvious that if the local minimum is closer to its adjacent maximum to the right (Fig. 3) a positive particle current, $\langle \dot{x} \rangle > 0$, will arise. Put differently, upon inspection of the lower part of Fig. 3, it is intuitively clear that during the cool-down cycle the particles must diffuse a long distance to the left and only a short distance to the right, yielding a net transport against the steep hill towards the right. All these predictions rely on our assumptions that $\overline{T}[1 - A]$ and $\overline{T}[1 + A]$ are much smaller and larger than ΔV, respectively, and that the time period $\mathcal{T}$ is sufficiently large. For more general temperature modulations, the direction of the current becomes much less obvious to predict, as will be demonstrated in Sect. 2.4 below.

2.2 *Modifications and applications*

In contrast to the explanation of the direction of the current in Fig. 3, the ratchet effect (16) itself obviously persists for very general temperature modulations $T(t)$ due to Curie's principle. For the same reason, the ratchet effect is also robust with respect to modifications of the potential shape [17] and is recovered even for random instead of deterministic modulations of $T(t)$ [24–26], a modified dynamics with a discretized state space [27], and in the presence of a finite inertia [28].

In all these cases, the particle current is bound to approach zero in the adiabatic limit (i.e. asymptotically slow temperature modulations) according to the finding in (10). A similar conclusion can be reached for asymptotically fast temperature modulations. Interestingly enough, a more detailed perturbative analysis of the periodic case (13) reveals that the current actually approaches zero in both asymptotic regimes remarkably fast, namely as $\mathcal{T}^{-2}$ and $\mathcal{T}^{2}$, respectively [17]. Thus, the temperature ratchet turns out to be in some sense rather reluctant to obey Curie's principle in the asymptotic regimes.

In practice, the required magnitudes and time scales of the temperature variations may be difficult to realize *experimentally* by directly adding and extracting heat; it may, however, become feasible indirectly, e.g. by pressure variations. A possible exception to this general rule is a situation involving point contact devices with a defect tunneling incoherently between two states [24]. Furthermore, it has been suggested in [29] that microorganisms living in convective hot springs may be able to extract energy out of the permanent temperature variations they experience; the temperature ratchet is a particularly simple mechanism which could accomplish the task. Moreover, a temperature-ratchet-type modification of the experimental work put forward in [30] has been proposed in [31]. Finally, it is known that certain enzymes (*molecular motors*) in living cells are able to travel along polymer filaments by hydrolyzing ATP (adenosine triphosphate) [32]. The interaction (chemical "affinity") between molecular motor and filament is spatially periodic and asymmetric, and thermal fluctuations play a significant role on these small scales. Roughly speaking, the ATP hydrolyzation energy is quickly converted into a very irregular vibrational motion of the numerous fast (irrelevant) internal degrees of freedom of the enzyme, giving rise to a locally increased apparent temperature. As this excess heat spreads out (diffuses away), the temperature decreases again. In other words, hydrolyzing an ATP molecule may be viewed as converting a certain amount of chemical energy into heat. Overall, we thus recover all the necessary ingredients of a temperature ratchet. The idea that local temperature variations may assist intracellular transport has been hinted at in terms of Feynman-type ratchet devices as early as in 1990 [18]. Admittedly, modeling the molecular motor as a Brownian particle without any relevant internal degree of freedom (apart from $T(t)$) and the ATP hydrolysis as mere production of heat is a gross oversimplification from the biochemical point of view, but may still be acceptable as a primitive sketch of the basic physics. Especially, quantitative estimates in [33, 34] indicate that the real temperature variations are probably not sufficient to account for the observed traveling speed of molecular motors. For a more detailed discussion of the modeling of molecular motors, we also refer to the article by Astumian in the present special issue.

A cute game theoretic re-interpretation of the ratchet effect has been devised by Parrondo [35, 36] (see also http://seneca.fis.ucm. es/parr/). Namely, for each of the two possible temperatures in (14), the random dynamics (6) may be considered as a game of chance, and by construction each of these two games in itself is fair (unbiased). The astonishing phenomenon of the ratchet effect then translates itself into the surprising observation that by randomly switching between two fair games one ends up with a game which is no longer fair.

2.3 *What characterizes a Brownian motor?*

We begin by emphasizing once more that the ratchet effect as exemplified for the temperature ratchet model of Fig. 2 is not in contradiction to the second law of thermodynamics, because we may consider the temperature changes in (14) as being caused by two heat baths at two different temperatures. From this viewpoint, our Brownian motor is nothing else than an extremely primitive and small heat engine. The fact that such a device can produce work is therefore not a miracle – but is still amazing.

However, there is also one distinct difference between the conventional types of heat engines and a Brownian motor as exemplified by the temperature ratchet. To this end we first note that the two "relevant state variables" of our present system are $x(t)$ and $T(t)$. In the case of an ordinary heat engine, these state variables would always cycle through one and the same periodic sequence of events ("working strokes"). In other words, the evolutions of the state variables $x(t)$ and $T(t)$ would be tightly coupled (interlocked and synchronized). As a consequence, a single suitably defined effective state variable (e.g. the continuation of an index, labelling the above-mentioned periodic sequence of events) would actually be sufficient to describe the system. In contrast to this standard scenario, the *relevant state variables* of a genuine Brownian motor are *loosely coupled*. Of course, some degree of interaction is indispensable for the functioning of the Brownian motor, but while $T(t)$ completes one temperature cycle, $x(t)$ may evolve in several very different ways ($x(t)$ is not "slaved" by $T(t)$).

The loose coupling between state variables is a salient point which makes the Brownian motor concept more than just a fancy new look at certain very small and primitive, but otherwise quite conventional, thermo-mechanical or even purely mechanical engines. Accordingly, the presence of some amount of (not necessarily thermal) random fluctuations is an indispensable ingredient of a genuine Brownian motor (exceptionally, deterministic chaos may be a substitute for noise). Especially, we note that, obviously, symmetry breaking and some time-dependent forcing are necessary requirements for any type of directed transport, supplemented by a certain periodicity if a cyclically operating device is involved. Yet, it is not justified to sell every such little "engine" under the new fashionable label "ratchet" or "Brownian motor", especially if the governing (deterministic) transport principle is completely trivial, as, for example, for a purely mechanical ratchet in the original sense (such as a lifting jack), for interlocked mechanical gears, or for Archimedian and other "screw-like" pumping and propulsion devices. Rather, one distinguishing feature of a Brownian motor is that (random or deterministic) *noise plays a non-negligible or even the dominating role*, with the consequence that, in general, not even the direction of transport is obvious (see also Sect. 2.4 below). A second essential requirement is that all acting forces are unbiased, i.e. after averaging over time, space, and ensemble, no systematic component remains.

The issue of whether the coupling between relevant state variables is loose or tight has been widely discussed in the context of molecular motors [37–39] under the name of *mechanochemical coupling*. The general fact that such couplings of non-equilibrium enzymatic reactions to mechanical currents play a crucial role for numerous cellular transport processes has long been known [40, 41]. The possibility of a *loose* mechanochemical coupling is one of the main conceptually new aspect of the "ratchet paradigm" as compared to "traditional" biological models for molecular motors. Whether or not this coupling is indeed to some extent loose is still under debate, but only if the answer turns out to be positive can we expect a significant impact of the Brownian motor approach to the modeling and understanding of the physics that reigns a molecular motor dynamics.

A further closely related question in this context concerns the efficiency of a Brownian motor. This issue has recently developed into an entire subfield of its own right and is treated in more detail in the contribution by Parrondo and Jiménez de Cisneros to the present special issue.

2.4 *Tailoring current reversals: a new paradigm for particle separation*

In this section we show that under more general conditions than those depicted in Fig. 2 the sign of the current $\langle \dot{x} \rangle$ may be already very difficult to understand on simple intuitive grounds, not to mention its quantitative value. This leads us to another basic phenomenon in Brownian motor systems, namely the inversion of the current direction upon variation of a system parameter. Early observations of this effect have been reported in [42–47]; here we illustrate it once more for our standard example of the temperature ratchet [17].

Our starting point is the observation that in the absence of a static tilt, i.e. $F = 0$, the current $\langle \dot{x} \rangle$ of the temperature Brownian motor in (11) and (12) is inverted if one goes over from the potential $V(x)$ to its mirror image $V(-x)$. It follows [48] that by continuously deforming $V(x)$ into $V(-x)$ in such a way that spatial periodicity and asymmetry is always maintained, there must exist some intermediate step where $\langle \dot{x} \rangle = 0$. From the viewpoint of Curie's principle this is called a non-generic situation: since no "systematic" symmetry reason for the absence of current can be figured out, we may speak of an *accidental symmetry* in this case. In other words, Curie's principle thus postulates the absence of accidental symmetries in the generic case. That is, an accidental symmetry may still occur as an exceptional coincidence, or by a fine-tuning of parameters; typically, however, it will not occur. Accidental symmetries are structurally unstable – an arbitrarily small perturbation destroys them – while a broken symmetry is a structurally stable situation. Consequently, upon slightly changing *any* parameter of the model, the immediate re-appearance of a finite current can be expected, implying the existence of a so-called "current reversal" of $\langle \dot{x} \rangle$ as a function of that specific model parameter. An example of a potential $V(x)$ exhibiting such a current reversal is plotted in Fig. 4, and the resulting current is depicted as a function of the specific model parameter η in Fig. 5. When compared to the example from Fig. 1, the modification of the ratchet potential in Fig. 4 looks rather harmless. In particular, compared with Fig. 3, the explanation of a positive current, $\langle \dot{x} \rangle > 0$, for a large temporal period $\mathcal{T}$ still applies. However, for the rather small $\mathcal{T}$ value used in Fig. 5, this innocent-looking modification of the potential has obviously a very drastic effect on the value and the *sign* of the resulting current.

According to Fig. 5, Brownian particles with different friction coefficients η move in opposite directions when exposed to the same thermal environment and the same ratchet

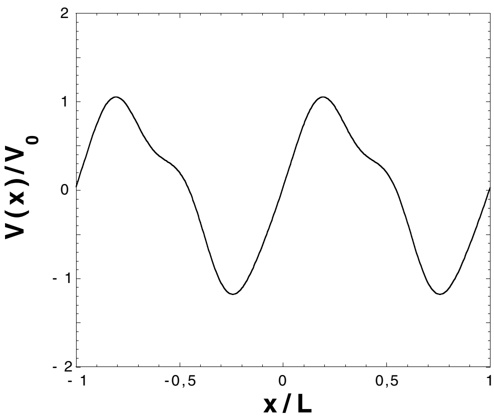

FIGURE 4 The ratchet potential $V(x) = V_0\{\sin(2\pi x/L) + 0.2\sin[4\pi(x/L - 0.45)] + 0.1\sin[6\pi(x/L - 0.45)]\}$ plotted in dimensionless units

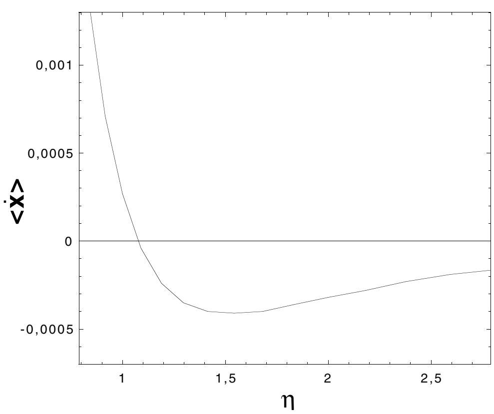

FIGURE 5 Numerically determined time- and ensemble-averaged particle current $\langle \dot{x} \rangle$ in the long-time limit versus the friction coefficient η for the Brownian motor model (11), (12) and (15) with the ratchet potential $V(x)$ from Fig. 4. Using dimensionless units, the parameter values are $F = 0$, $L = k_B = 1$, $V_0 = 1/2\pi$, $\overline{T} = 0.1$, $A = 0.7$ and $\mathcal{T} = 0.17$

potential. This is, for example, the case for spherical particles of different diameters in a liquid with the corresponding friction coefficients given by Stokes law. Had we not neglected the inertial effects $m\ddot{x}(t)$ in (1), such a particle separation mechanism also would occur with respect to the mass parameter, m. This can be inferred along the very same line of reasoning as above; it similarly holds true for any other dynamically relevant particle property!

Promising *applications* of such current reversal effects for particle separation methods that are based on the ratchet effect involve the modes of pumping, separating and shuttling of particles of differing size, mass, charge, etc. Moreover, the separation mechanism is acting continuously in time without the need to stop and start again a separation device in order to add or extract the corresponding particle yields. Another interesting aspect of current inversions arises from the observation that structurally very similar molecular motors may travel in opposite directions on the same intracellular filament. If we accept the temperature ratchet as a crude qualitative model in this context (see Sect. 2.2), then also the latter feature can be reproduced: If two types of molecular motors are known to differ in their ATP consumption rate $1/\mathcal{T}$, or in their friction coefficient η, or in any other parameter appearing in our temperature-ratchet model, then one can tailor a ratchet potential $V(x)$ in the above-described manner such that they will indeed move in opposite directions.

Multiple current reversals have been exemplified in [49–58]. In this case, particles with parameter values within a characteristic "window" may be separated from all the others. The first systematic investigation of such multiple inversions from [58] suggests that it may even be possible to tailor an arbitrary number of current reversals at prescribed parameter values.

2.5 *Generalized reversibility and supersymmetry*

While, in accordance with Curie's principle, current inversions, i.e. $\langle \dot{x} \rangle = 0$, are interesting exceptional situations, they are atypical in the sense that they require fine-tuning of parameters. From this viewpoint, the *absence* rather than the *presence* of directed transport in spite of a broken spatial symmetry is the truly astonishing situation away from thermal equilibrium. In this section, an entire class of such intriguing exceptional cases is identified which, in particular, do not require fine-tuning of model parameters.

As usual, we exemplify the general principle at work by way of our temperature-ratchet model (11), (12) and (13) in the unbiased case where $F = 0$. Our first observation is that when we replace the potential $V(x)$ by $V(-x)$ the average current $\langle \dot{x} \rangle$ changes its sign. As a consequence, if there exists a Δx such that $V(-x) = V(x + \Delta x)$, i.e. the potential is symmetric, we can conclude that $\langle \dot{x} \rangle = 0$. In the same way, one can infer that the average current $\langle \dot{x} \rangle$ also changes its sign if one considers $x(-t)$ in place of $x(t)$ and at the same time replaces $V(x)$ and $T(t)$ by $-V(x)$ and $T(-t)$, respectively. As a consequence, we can again conclude that $\langle \dot{x} \rangle = 0$ if there exist quantities Δx, ΔV, and Δt such that

$$-V(x) = V(x + \Delta x) + \Delta V \,, \tag{17}$$

$$T(-t) = T(t + \Delta t) \,. \tag{18}$$

In fact, under these symmetry conditions, the Brownian motor model (11)–(13) exhibits reversibility in the sense that $x(-t)$ is again a solution of the model dynamics (up to irrelevant shifts of the time and space origins). In other words, it is impossible to decide whether a movie of the process runs forward or backward in time, with the immediate consequence that $\langle \dot{x} \rangle = 0$. In this respect, we are dealing here with a natural extension of the concepts of time-inversion symmetry and detailed balance symmetry as discussed at the end of Sect. 1.

As far as the detailed formal proof of the above conclusions is concerned, we refer to [48, 59]. Related considerations for the case with inertia can be found in [60]. We also mention that a potential with the property (17) is traditionally called supersymmetric [59]. Here, we borrow this previously established notion of *supersymmetry* without further discussing its connection with quantum-mechanical concepts. For an example of a supersymmetric potential see Fig. 6. A corresponding example for time-inversion symmetry (18) is provided by (14) or (15).

In other words, the quite surprising result of our above considerations is that if *both* the potential $V(x)$ *and* the temperature $T(t)$ satisfy their respective symmetry conditions,

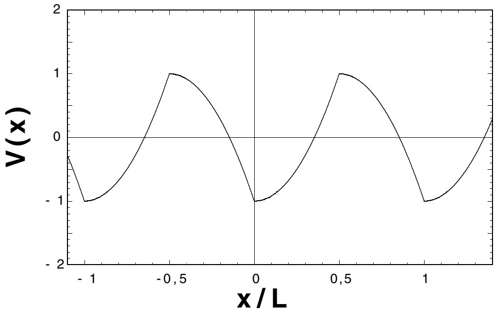

FIGURE 6 Example of a supersymmetric potential $V(x)$ (in arbitrary units) of the type (17) with $\Delta x = L/2$ and $\Delta V = 0$

(17) and (18), then, in spite of the broken spatial symmetry, the temperature-ratchet model (11)–(13) with $F = 0$ exhibits zero current for any choice of the friction η, the period L, and the characteristic amplitude and time scale of the temperature modulations, for example, in (14) and (15). In contrast to usual current inversions, no fine-tuning of those parameters is thus required in order that $\langle \dot{x} \rangle = 0$.

Note that this conclusion is no contradiction to Curie's principle, since a *generic* variation within the entire class of admitted ratchet models also involves a change of $V(x)$ and $T(t)$ such that the symmetry conditions (17) and (18) are no longer strictly satisfied. In fact, as we have seen above, the very same situation also arises for a symmetric instead of a supersymmetric $V(x)$ in combination with an arbitrary $T(t)$. In other words, we find that for both "systematic" and "accidental" symmetries the result $\langle \dot{x} \rangle = 0$ is unstable with regard to completely general, generic variations of the model, while the property $\langle \dot{x} \rangle \neq 0$ is robust with regard to such variations, i.e. "a finite current is the rule".

3 Typology

The essential ingredient of the ratchet effect from Sect. 2.1 has been a modification of the equilibrium ratchet model (6) so as to permanently keep the system away from thermal equilibrium (detailed balance). We have exemplified this procedure by a periodic variation of the temperature (13), but there clearly exists a great variety of other types of non-equilibrium perturbations. The general considerations throughout the preceding Sect. 2 lead to the following guiding principles which should also be observed in the design of a more general *Brownian motor*:

- Use of spatial (or cyclic) periodicity.
- All acting forces and gradients have to vanish after averaging over space, time, and statistical ensembles.
- Random forces (of thermal, non-thermal, or even deterministic (chaotic) origin) should play a prominent role.
- Breaking of detailed balance symmetry (thermal equilibrium).
- Symmetry breaking.

Regarding the last requirement, there are essentially three different ways in which it can be accomplished: First, the spatial inversion symmetry of the periodic system itself may be broken *intrinsically*, that is, already in the absence of the non-equilibrium perturbations. This is the most common situation and typically involves some kind of periodic and asymmetric, so-termed ratchet potential. A second option consists in the use of asymmetric non-equilibrium perturbations $f(t)$: On the one hand, these may be stochastic fluctuations $f(t)$, possessing non-vanishing, higher-order odd multi-time moments – notwithstanding the requirement that they must be unbiased, i.e. the first moment vanishes. On the other hand, such an asymmetry can also be created by unbiased (deterministic) periodic non-equilibrium perturbations $f(t)$. Both variants in turn induce a spatial asymmetry of the dynamics. Yet a third possibility arises via a collective effect in coupled, perfectly symmetric non-equilibrium systems, namely in the form of *spontaneous* symmetry breaking [61, 62]. Note that in the latter two cases we speak of a Brownian motor dynamics even though a ratchet potential is not necessarily involved.

The first main class of Brownian motors are so-called *tilting ratchets* [63] of the general form

$$\eta \dot{x}(t) = -V'\big(x(t)\big) + f(t) + \xi(t) \; . \tag{19}$$

In other words, the minimal equilibrium ratchet model (6) is perturbed by an additive, unbiased non-equilibrium force $f(t)$ and the homogeneous, static load force F from (11) has been omitted, see (16). Furthermore, one mostly focuses on perturbations $f(t)$ which are either a stationary *stochastic* process or a *periodic* function of time. When $V(x)$ is a ratchet potential, these two options are referred to as *fluctuating force* ratchet or *rocking* ratchet [47], respectively. Note that the latter represents a particularly natural situation in many experimental systems. Coming to symmetric potentials $V(x)$, we have already mentioned above that the (periodic or stochastic) non-equilibrium process $f(t)$ now has to carry the spatial asymmetry of the dynamics without introducing an obvious a priori bias, suggesting the name *asymmetrically tilting* ratchet [48, 64].

A second main class – called fluctuating potential ratchets – are of the form

$$\eta \dot{x}(t) = -V'\big(x(t)\big)[1 + f(t)] + \xi(t) \; . \tag{20}$$

The summand 1 is a matter of convention, reflecting a kind of "unperturbed" contribution to the total potential. The class of fluctuating potential ratchets contains as a special case the *on–off* ratchets, for which $f(t)$ can take on only two possible values, one of them being -1 (potential "off"). In this case, it turns out [48] that an asymmetric ratchet potential, together with finite thermal noise $\xi(t)$ is indispensable for directed transport, independent of any further details of the periodic or stochastic driving $f(t)$, see also Fig. 3.

More general time-dependent variations of the potential shape, without affecting its spatial periodicity, which are induced by the non-equilibrium perturbation $f(t)$ may be referred to as *pulsating* ratchets. A specific subclass thereof, called *travelling potential* ratchets [48, 65–67], have potentials of the form $V\big(x - f(t)\big)$. The most natural choice, already suggested by the name "travelling potential", are functions $f(t)$ with a systematic long time drift, e.g. $f(t) = ut$ with a constant "travelling speed" u. A modification are functions $f(t)$ which proceed in discrete jumps so that the relevant potential $V\big(x - f(t)\big)$ switches between several spatially shifted but otherwise identical static potentials. The operating principle of a great variety of important (largely mechanical) engines is based on a travelling potential ratchet mechanism. Yet, many of them are close or even beyond the borderline between the realm of genuine Brownian motors and that of conventional engines and pumps as discussed in Sect. 2.3.

A further important class of ratchets is given by models of the form (5), but, in contrast to the temperature ratchet (12), with a space-dependent temperature profile $T(x)$ of the same periodicity L as the potential $V(x)$. The close similarity of such a model to the Seebeck effect suggests the name *Seebeck* ratchet [48].

Much like for the illustrative example of the temperature ratchet – discussed in Sects. 2.1 and 2.4 – and also for many of the above more general ratchet models, predicting by simple arguments the actual direction of the transport is already far from obvious, not to mention its quantitative value. In particular, while the occurrence of a ratchet effect is the rule according to Curie's principle, exceptions with zero current are still possible. For instance, such a non-generic situation may be created by fine-tuning of some parameter. Usually, the direction of transport then exhibits a change of sign upon variation of this parameter, i.e. a current reversal. As in Sect. 2.4, these current inversions can often be imposed in a well-controlled manner by tailoring the shape of the potential and/or the properties of the non-equilibrium driving $f(t)$. By generalizing the line of reasoning from Sect. 2.5, another type of exception can be traced back to symmetry reasons with the characteristic signature of zero current without fine-tuning parameters.

Clearly, there are many further possible combinations and generalizations of the above compiled very simple basic ratchet models. Extensions that come to mind, to name but a few [48], include: a simultaneously pulsating and tilting scheme; taking into account finite inertia effects $m\ddot{x}(t)$ (cf. (1)); two instead of one spatial dimensions; time- or space-dependent friction; deviations from spatial periodicity in the form of some quenched spatial disorder; the superposition of several periodic contributions with incommensurate periods; models with spatially discretized state variables; quantum-mechanical effects, i.e. the class of "quantum Brownian motors" [68, 69]; and collective effects for many interacting Brownian motors [35, 61, 62, 70–74]. In particular, the most promising avenues for future new research on Brownian motors are situations that involve a coupling among many Brownian motors and the shuttling or control of directed transport of quantum objects such as electrons or spin degrees of freedom in quantum dot arrays, stylized nanoscale devices and molecular wires (molecular electronics).

An enormous amount of work has been devoted in recent years to the detailed theoretical exploration of all these numerous interesting specific models. Moreover, a quite appreciable and rapidly growing number of experimental studies and biological as well as technological applications have been established. A basically complete list of relevant publications up to 1994 is contained in the following section. Since then, the literature has grown by several hundred items. A systematic review even of the most important among them goes far beyond the scope of our present pedagogical introduction. A selection of short review articles includes [20, 39, 63, 73, 75], feature articles on an elementary level are [76–78], and a special issue devoted to the subject is [79]. A comprehensive recent review, on which also the present article is largely based, is the work in [48].

4 Genealogy

Progress in the field of Brownian motors has evolved via contributions from various physical directions including also repeated re-discoveries of the same basic principles in different contexts. For this reasons, a brief historical tour d'horizon seems appropriate here. At the same time, this provides a flavor of the wide variety of applications of Brownian motor concepts.

Though certain aspects of the ratchet effect are contained implicitly already in the works of Archimedes, Seebeck, Maxwell, Curie, and others, Smoluchowski's Gedankenexperiment from 1912 [2], regarding the prima facie quite astonishing absence of directed transport in spatially asymmetric systems in contact with a single heat bath, may be considered as the first sizable major contribution. The next important step forward was Feynman's famous recapitulation and extension [4] to the case of two thermal heat baths at different temperatures.

Brillouin's paradox [3] from 1950 may be viewed as a variation of Smoluchowski's counterintuitive observation. This paradox refers to the non-trivial objective of a consistent modeling of the non-linear thermal fluctuations in the presence of a non-linear relaxation dynamics. Such a situation occurs, for example, in a thermal system with non-linear conductance. For a more detailed elucidation of such a subtle fluctuation analysis in an electric circuit containing a linear capacitance and a non-linear resistance being in contact with a thermal heat bath, we refer the reader to Sect. 6.2 in [9]; in particular, the non-linear thermal fluctuations are then not capable of providing an average finite voltage. Likewise, Feynman's prediction that in the presence of a second heat bath a ratchet effect will manifest itself has its Brillouin-type correspondence in the Seebeck effect, discovered by Seebeck in 1822 without having in mind, of course, any idea about the underlying microscopic ratchet effect.

Another root of Brownian motor theory leads us into the realm of intracellular transport research, specifically the biochemistry of molecular motors and molecular pumps. In the case of molecular motors, the concepts which we have in mind here have been unraveled in several steps, starting with A. Huxley's ground-breaking 1957 work on muscle contraction [80] and continued in the late 1980s by Braxton and Yount [81] and in the 1990s by Vale and Oosawa [18], Leibler and Huse [33, 82], Cordova, Ermentrout, and Oster [83], Magnasco [21, 37], Prost, Ajdari, and collaborators [73, 84], Astumian and Bier [39, 85], Peskin, Ermentrout, and Oster [86, 87] and many others (see [32] for a review). In the case of molecular pumps, the breakthrough came with the theoretical interpretation of previously known experimental findings [88] as a ratchet effect in 1986 by Tsong, Astumian and coworkers [89]. While the general importance of asymmetry-induced rectification, thermal fluctuations, and the coupling of non-equilibrium enzymatic reactions to mechanical currents for numerous cellular transport processes is well known [40, 41], the above works introduced for the first time a quantitative microscopic modeling beyond the linear response regime close to thermal equilibrium. Especially, in the biophysical literature [40, 41] the notion of Curie's principle has previously been mostly used for its implications in the special case of linear response theory (transport close to equilibrium) in isotropic systems, stating that a force can couple only to currents of the same tensorial order.

On the physical side, a ratchet effect in the form of voltage rectification by a dc-SQUID in the presence of a magnetic field and an unbiased, slow ac current (i.e. an adiabatic tilting ratchet scheme) was experimentally observed and theoretically interpreted as early as 1967 by De Waele, Kraan, de Bruyn Ouboter, and Taconis [90]. Further, directed transport induced by unbiased, temporally periodic driving forces in spatially periodic structures with broken symmetry has been the subject of several hundred experimental and theoretical papers since the mid-1970s. In this context the 1974 paper by Glass, von der Linde, and Negran [91] on the so-called photovoltaic and photorefractive effects in non-centrosymmetric materials, presents a ground-breaking experimental contribution. The general theoretical framework was elaborated a few years later by Belinicher, Sturman and coworkers, and reviewed – together with the above-mentioned numerous experiments – in their capital works [92, 93]. Especially, they identified as the two main ingredients for the occurrence of the ratchet effect in periodic systems the breaking of the thermal equilibrium (detailed balance symmetry) and of the spatial symmetry.

The possibility of producing a dc output by use of two superimposed sinusoidal ac inputs at frequencies ω and 2ω (i.e. a harmonic mixing mechanism) in a spatially periodic, symmetric system, exemplifying an asymmetrically tilting ratchet mechanism, was observed experimentally 1978 by Seeger and Maurer [94]. Theoretical analysis of the experimental results was put forward as early as 1979 by Wonneberger [95], without realizing at that time, however, its potential function as a Brownian motor. The occurrence of a ratchet effect was theoretically predicted in 1987 by Bug and Berne [15] for the simplest variant of a pulsating ratchet scheme, termed an on–off ratchet (see Sect. 3). A ratchet model with a symmetric periodic potential and a state-dependent temperature (multiplicative noise) with the same periodicity but out of phase, i.e. a simplified microscopic model for the Seebeck effect, has been analyzed by Büttiker [96] and Van Kampen [97].

The independent re-inventions of the on–off ratchet scheme in 1992 by Ajdari and Prost [16] and of the tilting ratchet scheme in 1993 by Magnasco [21] together with the seminal 1994 works [37, 44–47, 84–86, 98–101] provided the inspiration for a whole new wave of ample theoretical and experimental activity. Moreover, the topic of Brownian motors has ignited progress within the statistical physics community, as documented in more detail in the other contributions to the present special issue and reviewed, for example, in [20, 39, 48, 63, 73, 75–79]. While initially the modeling of molecular motors has served as one of the main motivations, the scope of Brownian motor studies has subsequently been extended to an ever-increasing number of physical and technological applications, along with the re-discovery of the numerous pertinent works before 1992. As a result, a much broader and profound unified conceptual basis has been achieved; new theoretical tools have been developed which have led to the discovery of many novel interesting and quite astonishing phenomena together with a large variety of exciting new experimental realizations.

Within the realm of noise-induced or -assisted non-equilibrium phenomena, an entire family of well-established major fields are known under the labels of stochastic resonance [102], noise-induced transitions [103] and phase transitions [104, 105], reaction rate theory [106–108], and driven diffusive systems [109], to name but a few examples. The present special issue clearly documents the fact that the important recent contributions of many workers to the theory and application of Brownian motors has given rise to another full-fledged member to this family.

ACKNOWLEDGEMENTS This work was supported by the DFG-Sachbeihilfe HA1517/13-4 and the Graduiertenkolleg GRK283.

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