100 years of Einstein's Theory of Brownian Motion: From Pollen Grains to Protein Trains – 2.

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In this part, rotational Brownian motion and Brownian shape fluctuations of soft materials are discussed. This is followed by an elementary introduction to two of the hottest topics in this contemporary area of interdisciplinary research, namely, stochastic resonance and Brownian ratchet

1. Beyond Translation: Rotation and Shape Fluctuations

In undergraduate mechanics courses in colleges (or universities), normally, a student first learns Newtonian mechanics of point particles which also describes the motion of the center of mass of extended objects. Then, one learns to deal with the rotational motion of rigid bodies. Finally, a student is exposed to the mechanics of deformable bodies, i.e., elastic solids and fluids. In the first part of this article, we considered only the translational motion of the center of mass of the Brownian particles. In this section we shall consider rotational Brownian motion of rigid particles and the shape fluctuations of soft materials caused by the Brownian motion of these deformable bodies.

1.1 *Rotational Brownian Motion of Rigid Bodies*

To the best of our knowledge, one of the earliest direct experimental observations of the rotational Brownian motion was made by Gerlach [1] using a tiny mirror fixed on a very fine wire; some of the fundamental questions on this problem were addressed theoretically soon thereafter by Uhlenbeck and Goudsmit [2]. This is a relatively simple problem because the rotation involves only a single angle θ which measures the angular deflection. The corresponding Langevin equation has the form

$$I\left(\frac{d^2\theta}{dt^2}\right) = \mathcal{T}_{ext} - G\theta - \alpha\left(\frac{d\theta}{dt}\right) + \mathcal{T}_{br}, \qquad (1)$$

where I is the moment of inertia of the oscillator, α is the friction coefficient, G is the torsional elastic constant of the fiber, $\mathcal{T}_{ext}$ is the external torque and $\mathcal{T}_{br}$ is the Brownian (i.e., random) torque. Each term of this Langevin equation is the rotational counterpart of the corresponding term in the Langevin equation (7, Part 1) for translational Brownian motion.

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Interestingly, three quarters of a century later the problem of rotational Brownian motion of a mirror was reinvestigated by replacing air by a fluidized granular medium. In this novel experiment [3] the torsion oscillator was immersed in a container filled with glass beads and the noisy vertical vibration of the container took place at frequencies much higher than the natural frequency of the torsion oscillator.

The Langevin equation for the more general cases of rotation of a rigid body in three dimensions has a more complex form. Recall that the rotational motion of a macroscopic asymmetrical object is given by the Euler equation. The corresponding Euler–Langevin equation for rotational Brownian motion has the general form

$$\frac{d\vec{L}}{dt} + \vec{\omega} \times \vec{L} = \mathcal{T}_{ext} - \Gamma\omega + \mathcal{T}_{br}(t), \qquad (2)$$

with $\vec{L} = I\omega$, where I is the moment of inertia of the body and ω is its angular velocity; $\mathcal{T}_{ext}$ is the externally imposed torque while $\mathcal{T}_{br}(t)$ is the random noise torque. For the sake of simplicity one often assumes a Gaussian white noise torque $\mathcal{T}_{br}(t)$. The Fokker–Planck equation corresponding to the Euler-Langevin equation (2) is a deterministic equation that describes the time evolution

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of a probability density for the angular orientation (measured in terms of Euler angles) and the angular velocities of the body which executes the rotational Brownian motion.

The problem of rotational Brownian motion of a sphere was briefly mentioned in a paper published by Einstein in 1906 [4]. Investigaton of the rotational Brownian motion in the context of dielectric relaxation was initiated by Peter Debye and extended by many authors in the second half of the twentieth century [5].

Another related problem is the relaxational dynamics of large single-domain magnetic particles in rocks [6]. Each of these particles consists of a large number of individual moments all aligned parallel to each other such that the particle posseses a giant magnetic moment. Since the particle is embedded in a solid matrix, it cannot rotate physically but the direction of the magnetic moment can undergo Brownian rotation. A collection of such single-domain particles will be aligned parallel to the externally applied magnetic field. Then, after the field is switched off, the remanent magnetization M_r will vanish as

$$M_r = M_s e^{-t/\tau}, \tag{3}$$

where M_s is the magnetization of a non-relaxing particle, t is the time elapsed after the field is switched off and

$$\tau = \tau_0 e^{AV/k_\mathrm{B} T} \tag{4}$$

is the relaxation time where V is the volume of the particle and $\tau_0 \sim 10^{-9}$ sec. Therefore, varying V and/or T, the relaxation time τ can be made to vary from 10^{-9} sec to millions of years.

It was pointed out by Louis Néel that, at a given temperature T, the particle magnetization will appear 'blocked' (i.e., frozen in time) in any dynamic experiment where the frequency of the measurement ω_m is such that $\tau \gg \omega_m^{-1}$.

Blocking of the magnetization of the super-paramagnetic particles finds important applications in paleomagnetism (geomagnetism), as the history of the earth's magnetic field remains frozen in the rocks. During the early stage of the formation of the rock at a relatively higher temperature, the magnetic particles exist in thermal equilibrium with the earth's magnetic field, but later, as the rock cools, the magnetization of these particles get blocked and they retain the memory of the direction of the earth's magnetic field.

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1.2 *Brownian Motion of Deformable Bodies: Shape Fluctuations*

A linear polymer is a simple example of a deformable body which is, effectively, one dimensional. The Brownian forces acting on such an object in aqueous medium can give rise to random *wiggling*, i.e., random fluctuations in its shape. The random Brownian forces tend to induce wiggles in the polymer chain while the bending stiffness tends to restore its linear shape. These two competing effects determine the overall conformation of the polymer chain. One of the most important effects of this Brownian wiggling is that, even in the absence of any energy cost for creating such wiggles, the polymer behaves, effectively, as a spring where its spring constant is temperature-dependent and the corresponding restoring force it exerts is of purely entropic origin [7].

Similarly, Brownian motion of a soft membrane, e.g., the plasma membrane of a red-blood cell, manifests as 'flickering' of the effectively two-dimensional elastic sheet. The Brownian shape fluctuations of soft membranes have many important consequences. For example, consider a stack of such membranes which have a tendency to stick to each other because of the ubiquitous Van der Waals attractions. However, at all non-zero temperatures the Brownian shape fluctuations cause the membranes to bump against each other; the higher the temperature, the stronger the effectively repulsive entropic force. As a consequence of this competition between the two forces, an unbinding phase transition takes place in the system at a characteristic temperature as the temperature is raised from below.

2. Brownian Motion in External Static Potential

Translational Brownian motion of a particle under the influence of an external *linear* potential of the form $U(x) = ax$ is relevant, for example, in the context of sedimentation of colloidal particles under gravity [10, Part 1]. Brownian motion of a harmonically bound particle [8], i.e., a particle subjected to a *quadratic* potential of the form $U(x) = ax^2$, is a reasonably good model for the dynamics of a tiny spherical dielectric particle trapped by an optical tweezer. In order to satisfy the law of equipartition of energy in thermodynamic equilibrium, $< x^2 >$ approaches the value $k_BT/(m\omega^2)$ in the limit of extremely long times; Uhlenbeck and Ornstein [8] derived the exact expression valid for all times and, hence, showed how $< x^2 >$ approaches the asymptotic value with the passage of time.

The potential $U(x) = -ax^2 + bx^4$ has two equally deep minima which are separated from each other by an energy barrier; Brownian motion of a particle subjected to such a potential leads to noise assisted transitions, back and forth, from one well to the other. The average waiting time T_K between two successive noise-induced transitions increases exponentially with the increase of the barrier height. Noise-induced transitions in bistable systems have found applications in a wide variety of systems; we shall call T_K as the Kramers time in honor of Hendrik Kramers who considered such problems first in the context of chemical reaction rate theory in his classic paper entitled 'Brownian motion in a field of force and the diffusion model of chemical reactions' [9,10].

Kramers was not the first to consider noise-induced transitions from a potential well. In fact, in 1935, Becker and Döring studied the problem of noise-assisted hopping of a barrier to escape from a metastable state. The problem of noise-induced transitions in systems with metastable, bistable or multistable systems has a long history with abundant examples of unintentional rediscoveries and rederivation of results by experts from different disciplines, often using different terminologies [11]. Nevertheless, this shows the breadth of coverage of this multidisciplinary umbrella and the wide range of applicability of the concepts and techniques.

3. Brownian Motion in Time-dependent Potential

In the preceeding section we have considered Brownian motion in static (time-independent) external potential. However, two of the hottest topics in the area of Brownian motion which have kept many physicists busy for the last quarter of a century, are related to Brownian motion in time-dependent potentials. In the following two subsections we briefly discuss these two phenomena, namely, stochastic resonance and Brownian ratchet.

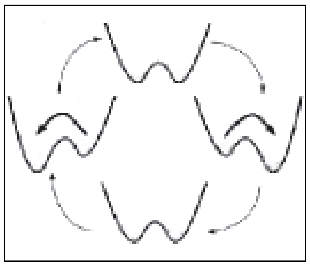
3.1 *Stochastic Resonance and Applications*

Let us begin with a Brownian particle subjected to a bistable potential. Suppose a small amplitude periodic forcing is added so that the left and the right wells periodically exchange their relative stability as shown in *Figure* 1. Let $T_p = 2\pi/\Omega_p$ be the time period of the periodic forcing. Then, the potential $U(x)$ is given by

$$U(x,t) = \frac{a}{2}x^2 - \frac{b}{4}x^4 - A_0 x \; cos(\Omega_p t). \qquad (5)$$

Note that the periodic forcing is too weak to induce transition in the position of the particle from one well to the other without assistance from noise. However, in the presence of noise, even in the absence of forcing,

Figure1. The back and forth tilting of the bistable potential in one cycle of the periodic forcing. (Copyright: Indrani Chowdhury; reproduced with permission).



Contrary to naive expectations, noise can have a constructive effect in enhancing the signal over an appropriately chosen window of noise intensity.

noise-induced transition from one well to the other goes on. Now, extending the concept of resonance, we introduce the concept of stochastic resonance by the condition $2T_K(D) = T_p$ where T_K is the Kramers time and it depends on the strength D of the noise [12,13].

The phenomenon of stochastic resonance has been demonstrated directly in laboratory experiments [14]. A micron-size dielectric bead is used as the Brownian particle and a bistable potential is created using two optical (laser) traps. The most important quantity characterizing a stochastic resonance is the signal-to-noise (SNR) ratio. The signature of a stochastic resonance is that the SNR, which vanishes in the absence of noise, rises with the increase of noise intensity and exhibits a maximum at an optimum level of noise intensity; on further increase of noise intensity, SNR decreases because of the randomization caused by the noise. In other words, contrary to naive expectations, noise can have a constructive effect in enhancing the signal over an appropriately chosen window of noise intensity. Not surprisingly, it finds applications in electrical engineering. Moreover, many organisms seem to use stochatic resonance for sensory perception; these include, for example, electro-receptors of paddlefish, mechano-receptors of crayfish, etc.

Stochastic resonance has been evoked to explain the periodic occurrence of Ice age on earth; the period is estimated to be approximately $100,000$ years. Suppose the ice-covered and water-covered earth correspond to the two local minima. Eccentricity of the earth's orbit (and, therefore, incoming solar radiation) varies periodically with a period of about $T_p \simeq 100,000$ years. But, this variation is too weak to cause the transition from ice-covered to water-covered earth and vice versa. It has been suggested that random noise in the climatic conditions can give rise to a stochastic resonance causing a transition between the two local minima with a period of about 100,000 years.

3.2 *Brownian Ratchet and Applications*

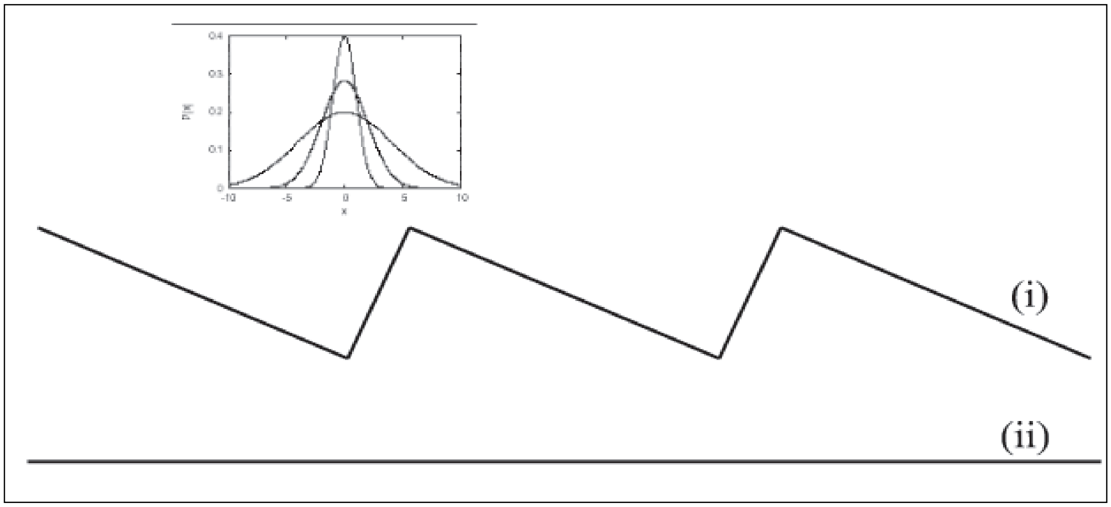
Let us now consider a Brownian particle subjected to a *time-dependent* potential, in addition to the viscous drag (or, frictional force). The potential switches between the two forms (i) and (ii) shown in *Figure* 2. The sawtooth form (i) is spatially *periodic* where each period has an *asymmetric* shape. In contrast, the form (ii) is flat so that the particle does not experience any external force imposed on it when the potential has the form (ii). Note that, in the left part of each well in (i) the particle experiences a rightward force whereas in the right part of the same well it is subjected to a leftward force. Moreover, the spatially averaged force experienced by the particle in each well of length ℓ is

$$< F >= -\frac{1}{\ell}\int_0^\ell \left(\frac{\partial U}{\partial x}\right) dx = U(0) - U(\ell) = 0 \qquad (6)$$

because of the spatially periodic form of the potential (i). What makes this problem so interesting is that, in spite of vanishing average force acting on it, the particle can still exhibit directed, albeit noisy, rightward motion.

In order to understand the underlying physical principles, let us assume that initially the potential has the

Figure 2. The two forms of the time-dependent potential used for implementing the Brownian ratchet mechanism. (Copyright: Indrani Chowdhury; reproduced with permission).



The concept of Brownian ratchet was popularized by Feynman through his lectures.

shape (i) and the particle is located at a point on the line that corresponds to the bottom of a well. Now the potential is switched off so that it makes a transition to the form (ii). Immediately, the free particle begins to execute Brownian motion and the corresponding Gaussian profile of the probability distribution begins to spread with the passage of time. If the potential is again switched on before the Gaussian profile gets enough time for spreading beyond the original well, the particle will return to its original initial position. But, if the period during which the potential remains off is sufficiently long, so that the Gaussian probability distribution has a non-vanishing tail overlapping with the neighbouring well on the right side of the original well, then there is a small non-vanishing probability that the particle will move forward towards right by one period when the potential is switched on.

In this mechanism, the particle moves forward not because of any force imposed on it but because of its Brownian motion. The system is, however, not in thermal equilibrium because energy is pumped into it during every period in switching the potential between the two forms. In other words, the system works as a rectifier where the Brownian motion, in principle, could have given rise to both forward and backward movements of the particle in multiples of ℓ. However the backward motion of the particle is suppressed by a combination of (a) the time dependence and (b) spatial asymmetry (in form (i)) of the potential. In fact, the direction of motion of the particle can be reversed by replacing the potential (i) by the potential (iii) shown in *Figure* 3.

The mechanism of directional movement discussed above is called a 'Brownian ratchet' [15] for reasons which we shall now clarify. The concept of Brownian ratchet was popularized by Feynman through his lectures [16] although, historically, it was introduced by Smoluchowski [17]. Consider the ratchet and pawl arrangement shown

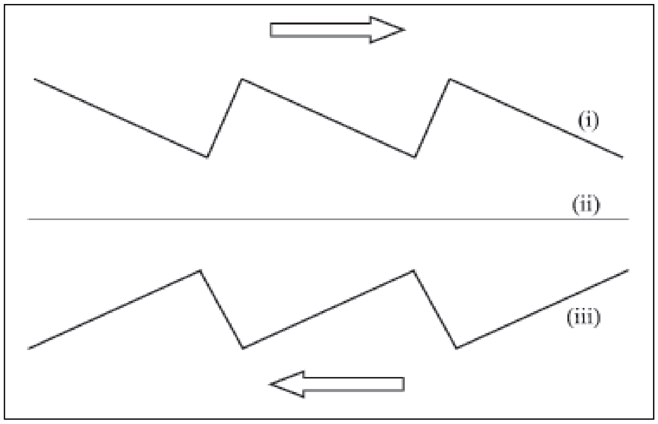


Figure 3. The direction of the motion of the particle in a Brownian ratchet is determined by the form of the asymmetry of the potential in each period. (Copyright: Indrani Chowdhury; reproduced with permission).

in *Figure* 4. The random bombardment of the vanes by the air molecules gives rise to torques which fluctuate randomly both in magnitude and direction. Because of the asymmetric shape of each of the teeth, it may appear that the ratchet would move countercloclowise more easily than clockwise (when viewed from the left side) leading to its directed counterclockwise, albeit noisy, rotation. In principle, it should then be possible to exploit such directed rotation to perform mechanical work. However, any such device, if it really existed, would violate the second law of thermodynamics because it would extract thermal energy from its environment, by cooling the environment spontaneously, and convert that energy into mechanical work. Feynman resolved the apparent paradox by pointing out that both the clockwise and counterclockwise rotations are actually equally likely because the pawl also executes random Brownian motion because of the random extension and compression of the spring that keeps it pressed against the wheel

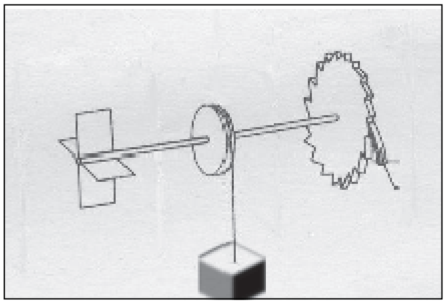


Figure 4. Feynman's ratchet and pawl arrangement; the wheel on the right is the ratchet and its clockwise rotation is hindered by the touching pawl. (Copyright: Indrani Chowdhury; reproduced with permission).

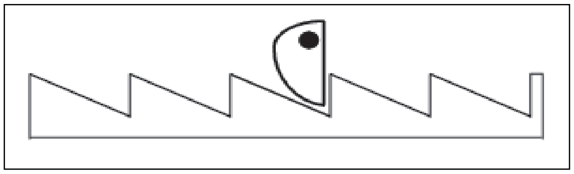


Figure 5. A linear ratchet and pawl arrangement. (Copyright: Indrani Chowdhury; reproduced with permission).

of the ratchet. A linear design of the Brownian ratchet is shown in *Figure* 5.

The Brownian ratchet has its counterpart in the abstract theory of games. In particular, Juan Parrondo [18] proposed a game with two separate rules, say A and B, of the game. Even in situations where both the rules will ruin the gambler, Parrondo showed that the gambler can win by using the rules A and B alternately. It is not difficult to map this problem onto the Brownian ratchet mechanism depicted in *Figure* 2 and the winning of the gambler corresponds to the directed movement of the Brownian particle in *Figure* 2.

The ratcheting via time-dependent potential discussed above is not merely a theoretical possibility but nature exploits this for driving a class of molecular motors inside cells of living organisms; this includes KIF1A, a family of kinesin motor proteins [19]. Such molecular motors move along microtubule filaments just as trains move along their tracks.

A mechanism based on the Brownian-ratchet has been proposed [20] for translocation of proteins across membranes. This is easy to understand using a picture similar to the ratchet shown in *Figure* 5. Proteins are known to unfold before translocation through a narrow pore in the membrane. Once the tip of the protein successfully penetrates the membrane, it can translocate through Brownian motion provided there exists some mechanism to rectify its backward movements. Several possible mechanisms for such rectification have been proposed including binding of chaperonins at designated binding sites along the translocated part of the macromolecule [19].

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ATP is the energy currency of almost all eukaryotic cells and the cell synthesizes ATP from the raw materials using a machine, called ATP synthase, which is bound to the mitochondrial (chloroplast) membrane of animal (plant) cells. To my knowledge, this is the smallest among all the natural and man-made rotary motors. This complex motor actually consists of two reversible parts, namely F_0 and F_1, which are coupled to each other. A Brownian-ratchet mechanism has been suggested [21] for the rotary motor F_0. Detailed structure and function of this natural nano-motor will be considered in a separate article [19].

What started as a curiosity of microscopists, who were baffled by the random movements of the pollen grains in water, turned out to be one of the most challenging scientific problems.

4. Summary and Conclusion

What started as a curiosity of microscopists, who were baffled by the random movements of pollen grains in water, turned out to be one of the most challenging scientific problems that could not be solved by anybody till the beginning of the twentieth century. It was Albert Einstein who, in one of his three revolutionary papers of 1905, published the correct theory of Brownian motion. His theoretical predictions were confirmed by a series of experiments on colloidal dispersions by Jean Perrin and his collaborators. These investigations of Brownian motion in collidal dispersions not only helped in silencing the critics of the molecular kinetic theory of matter but also laid down the foundation of nonequilibrium statistical mechanics.

By the end of the first quarter of the twentieth century, quantum theory became the darling of the majority of the physicists and the science of colloids lost its appeal. Over the next quarter of a century progress was rather slow but steady. However, in the second half of the twentieth century, motivated partly by the industrial demand for novel materials, physicists and engineers discovered the great potential of soft materials [22], including colloids which gradually regained its past glory [23]. Moreover, revolution in optical microscopy in the last ten years has provided a glimpse of the cellular interior, a wonderland dominated by Brownian motion. Preliminary explorations in this new frontier of research indicate that, instead of being a nuisance, the Brownian motion is, perhaps, fully exploited by Nature to its advantage not merely to survive but to thrive. Brownian motion of pollen grains does not arise from any process of life but some of the least understood processes of life, including the train-like motion of the biomolecular motors on the filamentary tracks, may not be possible without Brownian motion!

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