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ENDOGENOUS ELECTROMAGNETIC FORCES IN LIVING CELLS: IMPLICATIONS FOR TRANSFER OF REACTION COMPONENTS

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ABSTRACT

The mechanisms of order in living cells and in particular of the space–time order of chemical reactions are largely unknown. Directed transport of components to a reaction region cannot be explained by Brownian motion, which is disordered and increases entropy of the system. Besides transport by the motor proteins along microtubules, the endogenous electromagnetic field can provide translation motion of reaction components. This forced translation motion can have a high degree of certainty to reach the target region.

INTRODUCTION

In living cells the many thousands of different chemical reactions carried out simultaneously and successively are closely coordinated. The reactions are linked together in chains and networks in space and time. Not all cellular reactions occur within the same intracellular compartment. Each of the many different molecules that takes part in reactions in a cell moves from enzyme to enzyme along a specific reaction pathway. The sum of all these pathways determines the cell's chemistry. Active transport of molecules across the cell membrane and inside the

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cell depends on the generation of force and movement. The production of force and movement enables the cytoplasmic contents of the cell to become organized and the cells themselves to move and assemble into tissues. These processes play a vital part in establishing biological order (1,2). The origin, nature, and properties of the ordering forces are largely unknown.

Before the components of reactions can bind to each other, they must encounter and come into close contact. Then, the interaction surfaces have to adjust their mutual positions. Therefore, we have to distinguish three stages of chemical reactions producing new compounds: a) translation motion of the components to the reaction region; b) short range motion in the reaction region bringing the surfaces of interacting components together and adjusting necessary space positions (''lock and key'' positions); and c) formation of chemical bonds (1).

First, we will discuss the concept of chemical bonds and, in this context, affinity (1,3). Affinity was introduced as an empirical quantity used for assessment of the strength of the bonding between two components in chemical reactions (and is a useful index of the specificity of their interaction). The equilibrium constant for the reaction is used as a measure of affinity (the equilibrium constant is determined by the ratio of the association rate constant to the dissociation rate constant). The equilibrium constant and, therefore, also the affinity are related directly to the difference of the free energy of the system before and after reaction. (This aspect connects affinity with the energy of the chemical bond.) The equilibrium constant has to be determined under standard conditions (which include concentration of the components and their equilibrium space distribution). We may assume that at the initial time the components of a reaction are separated in different compartments. In this case, the correct value of the equilibrium constant may be determined after some measured time when the components have achieved uniform distribution. If only a small number of each of the components exist in a large space, the probability of the reaction within a certain time interval depends on the probability of encounter of the components. Under standard conditions, encounter of the components is a certain event. Therefore, affinity in its classical form cannot elucidate the mechanism of order of chemical reactions, in particular, directional transport of reaction components between different space compartments.

Chemical bonds depend on electronegativity as introduced by Pauling (3a) to assess the capability of particular atoms or some groups of atoms to bind the valence electron. We present electronegativities of some elements and molecular radicals that are important in biological systems. The electronegativities of P, H, S, C, N, and O atoms are 2.1, 2.15, 2.6, 2.6, 3.0, and 3.5, respectively. The molecular radicals $-CH_3$, $-SH$, $-CHO$, $-COOH$, $-NH_2$, $-C{\equiv}CH$, $-C{\equiv}N$, and $-OH$ have the electronegativities 2.5, 2.7, 2.8, 2.9, 3.2, 3.2, 3.4, and 3.5, respectively (3). Asymmetry of charge distribution in a molecule, depending on the electronegativities of its parts, can explain the molecular dipole moments. We will not go into the details of covalent and noncovalent bonding; we will only mention some characteristic features of them. Covalent bonds depend on the over-

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lap of electron orbitals, and their effective distance of action is on the order of 0.1 nm. Attraction of opposite charges (which is the basis of ionic bonds) is screened by mobile ions in a biological medium within a distance of about 1 nm. Besides ionic bonds, noncovalent bonds in biological systems are the hydrogen bonds, bonds based on van der Waals forces (caused by the fluctuation electric charges) and on hydrophobic expulsion forces (1,4).

The short range mechanisms acting in the reaction region include the recognition of reaction components and their reaction sites, the close approach of the components, their rotations, and the back-and-forth movements to prepare linking the components with respect to each other. London dispersion forces (interaction due to a mutual polarization of the two components by each other), the thermal vibrations, rotations, and Brownian motion are assumed to be responsible for the short-range ''arrangements'' in the reaction region. Nevertheless, forces generated by polarization vibrations of the reaction components, surrounding components, and structures have to be taken into account also. These forces may be highly specific and very strong in the vicinity of the source. Similar rationales may be applied to long-range translation motion.

Long-range transport aimed at a certain target can considerably increase the probability of encounter and contribute to the organization of chemical reactions. Transport of organelles, vesicles, and other types of cargo mediated by kinesins and dyneins along microtubules is aimed at certain regions. The information system governing this transport is still unknown.

Measurement of electromagnetic activity of living cells is described, e.g., in (5–8). An electromagnetic field with a fundamental electric component can play a role in organization and order. As the cytoskeleton structures are polar (9–13), even thermal vibrations are accompanied by polarization waves and generate an electromagnetic field around them (14,15). We assume that the electric oscillating field generated by the microtubules (and also by the actin filaments) can play an important role not only in the organization of the cytoskeleton, but also in the transport of components of reactions (2). The field is inhomogeneous and can exert forces on electric dipoles and multipoles as well as dielectrophoretic forces on neutral particles and molecules, resulting in translation motion. The oscillating electric field generated by microtubules and by actin filaments can induce electric vibrations in molecules and structures in their vicinity and in this way activate secondary generators in protein molecules and structures that generate secondary force fields around them.

Analysis of the electric oscillation field generated by the microtubules may be found, e.g., in (2,14,15). The oscillations may exist in a wide range of frequencies. The intensity of the electric field in the close vicinity of a microtubule can be of the order of 10^8 V/m or even higher (given a value for relative permittivity of about 1). The force $\boldsymbol{F}_d$ exerted on an electric dipole by the generated field is equal to the gradient of the scalar product of the dipole moment $\boldsymbol{p}$ and the intensity $\boldsymbol{E}$ of the electric field, i.e., $\boldsymbol{F}_d = \nabla (\boldsymbol{p}.\boldsymbol{E})$. In an inhomogeneous electric field where the intensity of the electric field decreases from 10^7 to 10^6 V/m within a distance

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of 10 nm, the force $F_d = 10^{-13}$ N for a dipole moment $p = 10^{-28}$ Cm. An inhomogeneous electric field can exert force on and cause translation motion of neutral dielectric particles. The dielectrophoretic force depends on the difference of permittivities of the particle (ε_p) and of the ambient medium (ε_m), on the volume of the particle (V), and on the gradient of the square of the intensity of the electric field [as is derived in (16)], i.e.,

$$\boldsymbol{F}_\varepsilon = V\frac{\varepsilon_m}{2(\varepsilon_p + 2\varepsilon_m)}(\varepsilon_p - \varepsilon_m)\,\nabla \boldsymbol{E}^2.$$

For the same electric field as in the previous case for the electric dipole, this relation yields the force $F_\varepsilon = 10^{-14}$ N ($V = 10^{-25}$ m^3, $\varepsilon_p - \varepsilon_m = 10\varepsilon_0$). These values of F_d and of F_ε can exist only in limited space regions.

We will examine the effect of endogenous forces of electromagnetic nature on the transport of particles and evaluate the probability that the particle will reach the region in which the reaction takes place.

Random and Deterministic Motion

Brownian motion resulting from random collisions in the microscopic world can be treated as the Wiener-Lévy process (17). The Wiener-Lévy process is a limited form of the random walk. The probability density (the density function) of three-dimensional Brownian motion may be given by the relation

$$f(r, t) = \sqrt{\frac{2}{\pi(\alpha t)^3}}r^2\, exp\left(-\frac{r^2}{2\alpha t}\right) \tag{1}$$

where

$$r = \sqrt{x^2 + y^2 + z^2} \geq 0,$$

is the radial distance from the point where the particle was at time $t = 0$. Assuming a spherical particle of radius a and using Stokes's law, the coefficient α (which is related to the spectrum of white noise) may be expressed in the form

$$\alpha = \frac{kT}{3\pi\eta\alpha}, \tag{2}$$

where k is the Boltzmann constant, T is the temperature (in K), and η is the dynamic viscosity. The Brownian motion process is characterized by a zero mean value and a time dependent variance αt. The maximum of probability density moves from the center with increasing time.

Equation (1) holds in the case where the probabilities of the random walk steps in all directions are equal. In this case the probability density is symmetrical with respect to the origin $r = 0$. If the probabilities are not equal, symmetry is obviously disturbed. For instance, if the probability p_{x+} for steps in the positive

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direction is greater then the probability p_{x-} for steps in the negative direction along the x axis (but their difference is small and, therefore, $4p_{x+}p_{x-} \approx 1$), then for the random variable r in Equation (1) we can derive

$$r = \sqrt{(x - vt)^2 + y^2 + z^2}, \tag{3}$$

where v is the velocity of the translation motion along the x axis in its positive direction (this velocity depends on the difference of the probabilities $p_{x+} - p_{x-}$). The center of the probability space moves. We can consider the effect of a deterministic force as the change of probabilities. In the case of the deterministic force F the v value for a spherical particle can be derived in the form

$$v = \frac{F}{6\pi\eta\alpha}. \tag{4}$$

(Mesoscopic and macroscopic expression of the effects of random collisions in the microscopic world is diffusion; the diffusion constant $D = \alpha/2$.)

We may use this concept in the case in which the number of particles in the medium is large. For instance, if the concentration of ATP molecules in cytosol is about 1 mM, then the average distance between them is of the order of 10 nm.

Transport along the microtubules is deterministic in nature. Motor proteins—kinesins and dyneins—carry cargo (organelles, vesicles, etc.) along the microtubule toward the periphery of the cell and inside the cell toward the centrosome, respectively. The rate at which the motor proteins move along the microtubule varies over a wide range. For instance, axonal kinesin steps toward the periphery at approximately 2 μm/s and a *Drosophila* kinesin called Ncd moves toward the centrosome at about 0.1 μm/s (1). The probability of reaching the target point by the transport along the microtubule has a high degree of certainty (we may assume that the probability $P = 1$).

Probability of Transport to the Target

We will determine the probability of finding a particle in any certain region. Figure 1 shows two-dimensional Brownian motion of a particle computed as a random walk with equal and nonequal probabilities of steps (4×10^6 steps of 0.1 nm each). The trajectory of the Brownian motion is determined for equal probabilities of steps in all directions (a), for different probabilities of steps along the x axis (b, c); Figure 1b shows the trajectory for $p_{x+} = 0.505$ and $p_{x-} = 0.495$; and Figure 1c for $p_{x+} = 0.51$ and $p_{x-} = 0.49$. For the probabilities $p_{x+} = 0.6$ and $p_{x-} = 0.4$ the trajectory extends about 40 μm to the right hand site (not shown in Fig. 1). We can conclude that even a small imbalance in probabilities results in significant translation motion which is similar to the translation caused by a deterministic force.

The probability density of three-dimensional Brownian motion (with and without a deterministic force) given by Equations (1)–(4) is shown in Figure 2.

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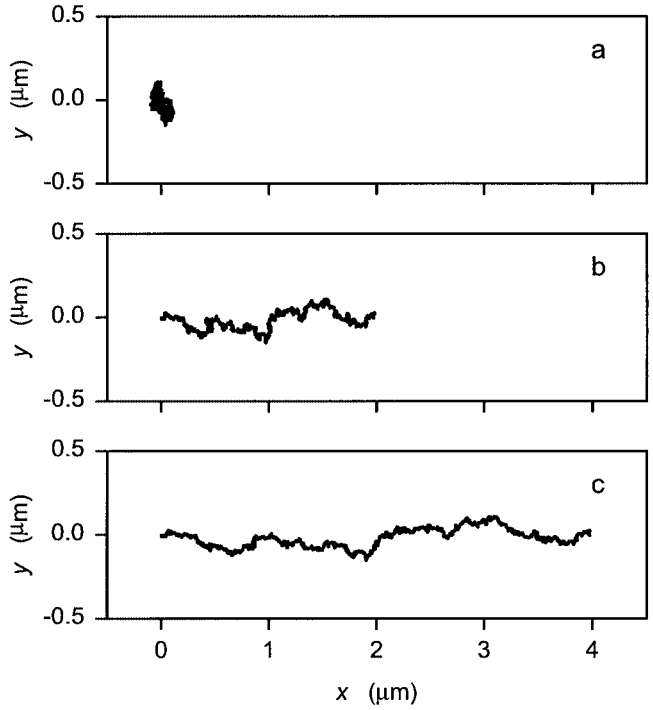


Figure 1. Two-dimensional trajectory of the random walk process (the Brownian motion) with equal (a) and non-equal (b,c) probabilities of the steps in the x direction.

At initial time 0 the particle is at the center point $r = 0$ (the origin). The spherical particle has a radius $a = 2.5$ nm and the dynamic viscosity of the medium $\eta = 1.002 \times 10^{-3}$ Pa.s (these values will also be used in further models). As the dispersion depends on time, the probability density $f(r, t)$ flattens with increasing time, and the maximum of the curve shifts to the greater values of r (Fig. 2a). The probability density has spherical symmetry (with the center $r = 0$). Figures 2a and 2b show the probability density in the case where the deterministic forces 10^{-14} and 10^{-13} N, respectively, are applied in the direction of the positive x axis. The center of the probability density function is shifted nearly 2 μm along the x axis in 1 ms (Fig. 2c). The shift represents translation motion of particles, and the rate of transfer can be on the order of 1 mm/s.

We will now show the probability of finding a particle in a certain region of space as a function of time. First, we will assess the radius r_P of a sphere in which we can find the particle with probability P. Only Brownian motion is assumed. At initial time, the particle is in the center $r = 0$ (the origin). The r_P's as a function of time for P from 0.01 to 0.99 are shown in Figure 3. With increasing time the particle may be found at greater distances from the origin. The uncertainty increases with time. After 1 ms the r_P value for $P = 0.99$ is of the order of 1 μm.

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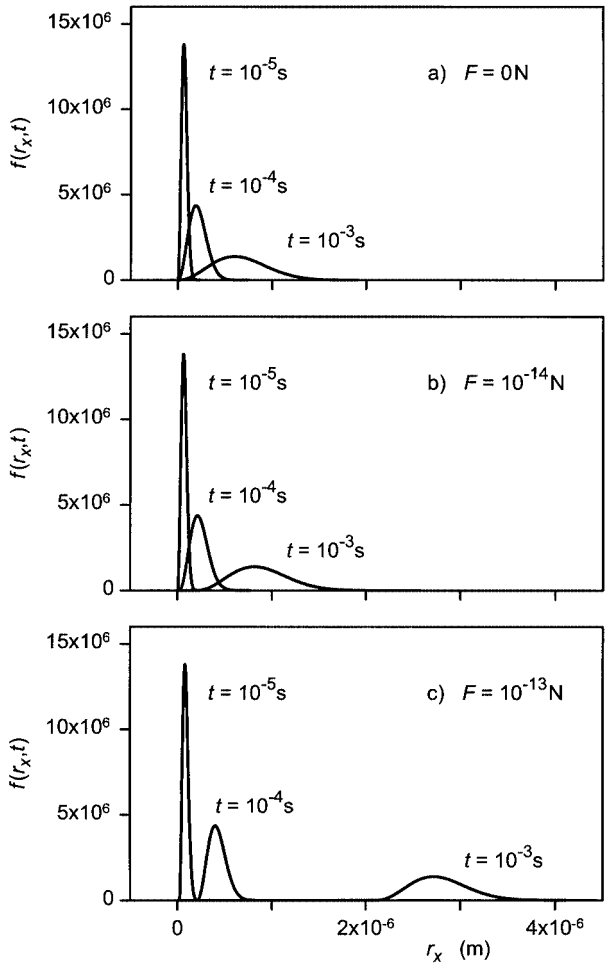


Figure 2. Probability density $f(r_x, t)$ of the three dimensional Brownian motion (a) and of Brownian motion and motion caused by the deterministic force parallel with the x axis (b, c) as a function of the distance r_x along the x axis for various values of time given in seconds.

We will now assess the probability P of finding a particle in a target region after elapse of a given time. We will assume that the target region is a spherical volume with the radius 30nm, the center of which is positioned on the x axis at a distance $X = 100$ nm from the origin (position of the particle at time $t = 0$). Figure 4 shows the probability P as a function of time t for Brownian motion and the motion caused by a uniform deterministic force in the direction of the positive x axis. The deterministic forces are 10^{-14} and 10^{-13} N. If this deterministic force acts on the particle, the P value may be about one order greater than P for the Brownian motion. Nevertheless, the P value is small (on the order of 10^{-2} as the Brownian motion causes scattering in directions perpendicular to the x axis.

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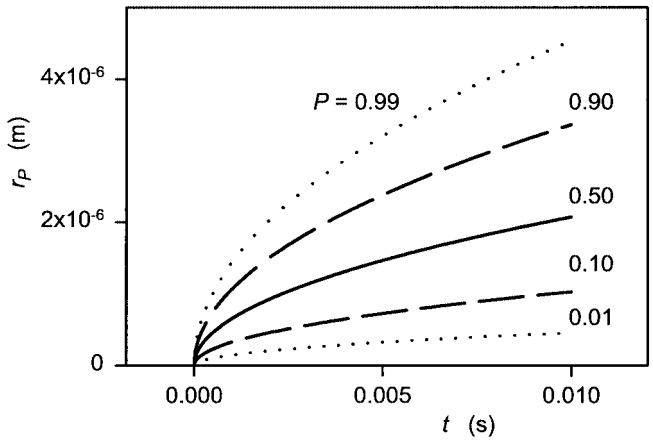


Figure 3. Radius r_P of a sphere (inside which is the particle with probabilities 0.01, 0.1, 0.5, 0.9, and 0.99) versus time t.

Effects of Central Forces

Chemical reactions between two components may begin if the components are at a certain minimal distance where ''reaction forces'' put the components together. We will assess the probability P of finding a particle in the reaction (target) region after elapse of a given time. We assume that the target region is

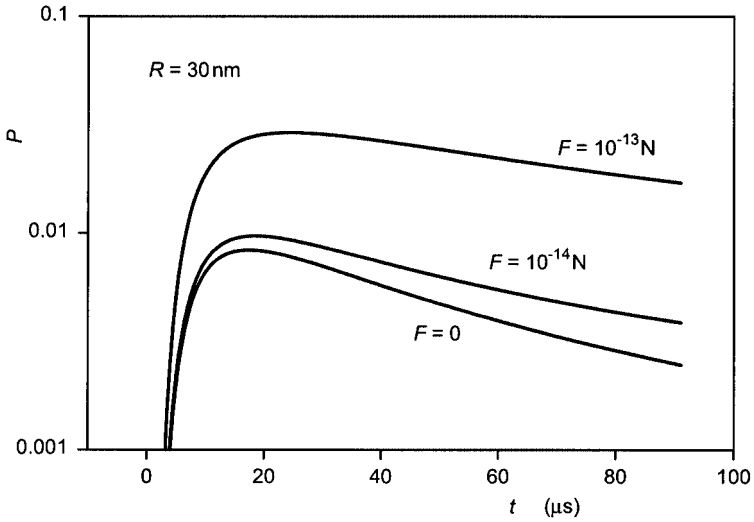


Figure 4. Probability P of finding the particle in the target region as a function of time evaluated for a three-dimensional model. The distance X of the center of the target region ($R = 30$ nm) from the origin is 100 nm. Besides the Brownian motion, the particle is subject to the motion caused by a parallel force field along the x axis (the force is a parameter).

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a spherical volume with radii of $R = 30$ and $R = 10$ nm, the center of which is positioned on the x axis at the distance X from the origin.

First, we will use a one-dimensional approximation with a mathematical framework that was set up by Einstein. The density of probability of finding a particle in any place at an instant t is $f(x, t)$. Probability is spread from any elementary part dx of the space to all other elementary parts, and vice versa. The function transferring the probability denoted as $\varphi(\tau, y)$ is symmetric in space with respect to $y = 0$. For the time interval from t to $t + \tau$ ($\tau > 0$) we obtain

$$f(x, t + \tau) = \int_{-\infty}^{+\infty} f(x - y, t)\varphi(\tau, y)dy. \tag{5}$$

The function $\varphi(\tau, y)$ has to satisfy the relation

$$\int_{-\infty}^{+\infty} y^2\varphi(\tau, y)dy = \alpha\tau \tag{6}$$

and, therefore

$$\varphi(\tau, y) = \frac{1}{\sqrt{2\pi\alpha\tau}}\exp\left(-\frac{y^2}{2\alpha t}\right). \tag{7}$$

We will now evaluate the probability that a spherical particle whose radius is $a = 2.5$ nm and position $x = 0$ at initial time $t = 0$ reaches a one-dimensional target space with radius R at distance $X = 100$ nm. If central force F acts on the particle, the probability transfer is altered and the function $\varphi(\tau, y)$ is not symmetric. For a force acting in the direction of the positive (negative) x axis we have

$$\begin{aligned} &\varphi(\tau, y \mp \Delta y) \quad \text{for} \quad y < x \\ &\varphi(\tau, y \pm \Delta y) \quad \text{for} \quad y > x \end{aligned} \tag{8}$$

where $\Delta y = v\tau$ and v is given by Equation (4). Figure 5 shows the probability P as a function of time for $R = 30$ nm (a) and $R = 10$ nm (b). The force F is a parameter. The central force causes a large increase of the probability that the particle reaches the target region. The probability may be close to 1.

We will now analyze the motion of an harmonically bound particle, i.e., the effect of external force $-qx(t)$ on particle movement. The equation of motion is given by (17):

$$\frac{d^2x}{dt^2} + \beta\frac{dx}{dt} + \omega_0^2 x = n(t) \tag{9}$$

where the spectrum of the normal white noise $n(t)$ is

$$\overline{\alpha} = \frac{2kTf}{m^2},$$

$\beta = f/m$, $\omega_0^2 = q/m$, $f = 6\pi\eta\alpha$, and m is the mass of the particle.

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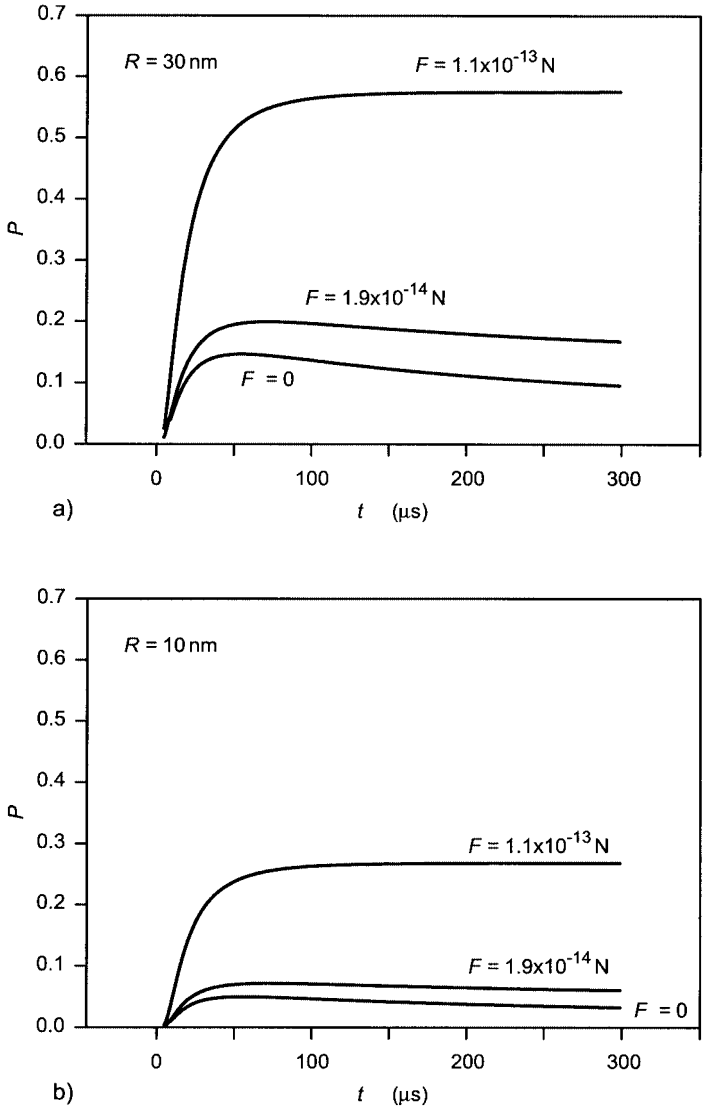


Figure 5. Probability P of finding the particle in the target region as a function of time evaluated for a one-dimensional model. The distance X of the target region from the origin is 100 nm. The radius of the target region is 30 nm (a) and 10 nm (b). Besides the Brownian motion the particle is subject to the motion caused by a central force field along the x axis; the central force does not depend on the distance from the center (the force is a parameter).

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The probability density for one-dimensional motion is given by the relation (17):

$$f(x) = \omega_0\sqrt{\frac{\beta}{\pi\bar{\alpha}}}\exp\left(-\frac{\beta\omega_0^2}{\bar{\alpha}}x^2\right) \tag{10}$$

and for the three-dimensional motion one may derive

$$f(x, y, z) = \omega_0^3\left(\frac{\beta}{\pi\bar{\alpha}}\right)^{3/2}\exp\left[-\frac{\beta\ \omega_0^2}{\bar{\alpha}}(x^2 + y^2 + z^2)\right]. \tag{11}$$

We can also determine the conditional probability density for a particle that is at a distance X from the center $x = 0$ at time $t = 0$. The one-dimensional conditional probability density is given by the relation (17):

$$f(x/X) = \frac{1}{\sqrt{2\pi e}}\exp\left[-\frac{(x - bX)^2}{2e}\right], \tag{12}$$

where for $\beta^2 - 4\omega_0^2 > 0$ (the overdamped motion) we get

$$b = \exp\left(-\frac{\beta\tau}{2}\right)\left[\cosh(\omega\tau) + \frac{\beta}{2\omega_0}\sinh(\omega\tau)\right]$$

$$e = \frac{\bar{\alpha}}{2\beta\omega_0^2} \tag{13}$$
$$\left\{1 - \exp(-\beta\tau)\left[1 + \left(\frac{\beta^2}{4\omega^2} + 1\right)\sinh^2(\omega\tau) + \frac{\beta}{2\omega}\sinh(2\omega\tau)\right]\right\}$$

where

$$\omega = \sqrt{\frac{\beta^2}{4} - \omega_0^2}.$$

From Equations (10) and (12) we get the three-dimensional conditional probability density in the form:

$$f(x|X, y, z) = \frac{\omega_0^2\beta}{\bar{\alpha}\sqrt{2\pi^3 e}}\exp\left[-\frac{(x - bX)^2}{2e} - \frac{\beta\omega_0^2}{\bar{\alpha}}(y^2 + z^2)\right] \tag{14}$$

Probability P versus time that a particle reaches the spherical target region (at distance 100 nm from its position at initial time) with $R = 30$ and $R = 10$ nm is shown in Figures 6a and 6b, respectively. The elastic force constant q is a parameter. The greatest probability for Brownian motion is about 10^{-4} ($R = 10$ nm) and 10^{-2} ($R = 30$ nm). The central force strongly increases the probability, which might be one or two orders greater than that in the case of Brownian motion alone. The probability can reach a value close to 1, which means a certain event.

If the deterministic force is a central force emanating from the center of the

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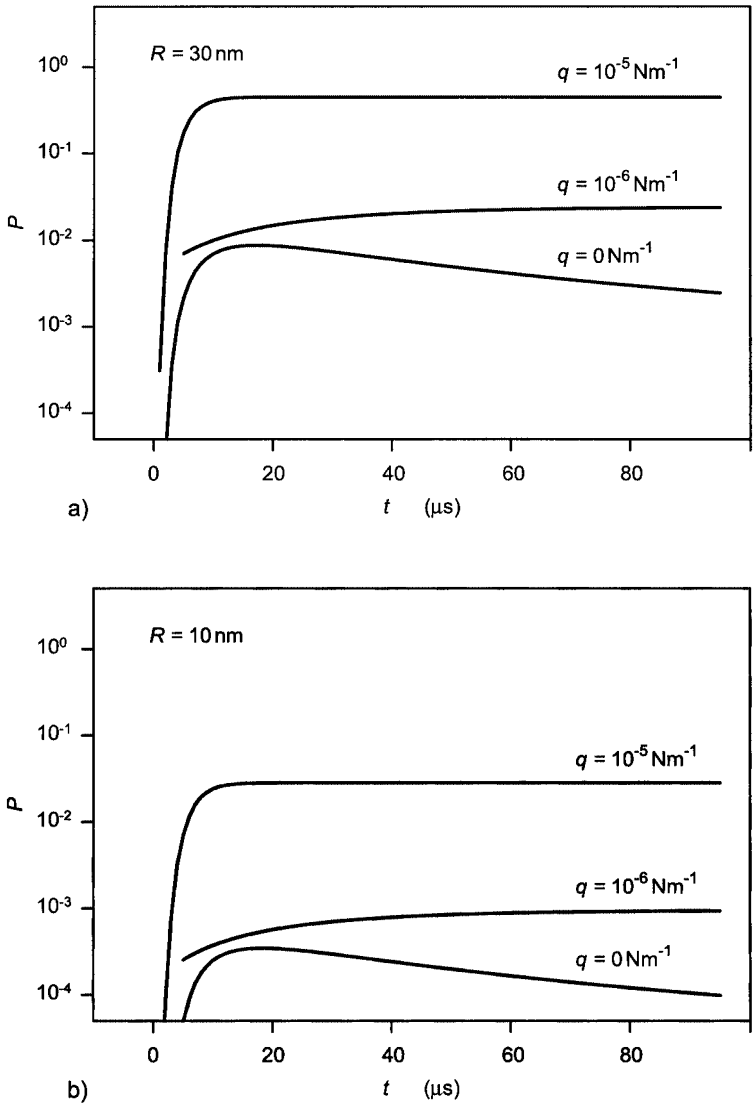


Figure 6. Probability P of finding the particle in the target region as a function of time evaluated for a three-dimensional model. The distance X of the target region from the position of the particle in the initial time is 100 nm. The radius of the target region is 30 nm (a) and 10 nm (b). Besides the Brownian motion, the particle is subject to the motion of a central force field with the center in the target region (the force is a parameter).

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target region, the probability P of finding the particle inside it is considerably greater than in the case of forces acting along the x axis.

DISCUSSION

It is well known that random motion of Brownian type cannot explain directional transport and organization of chemical reactions in biological matter. Brownian motion increases entropy. We analyzed the translation motion caused by deterministic forces and assumed that these forces are of electromagnetic origin. A uniform field of parallel forces in a certain direction is not as effective in bringing a particle to any certain position as is a field of central forces. Nevertheless, if the field of parallel forces is not uniform, and the direction of its gradient is perpendicular to the x axis, the dielectrophoretic force can pull the particle toward the x axis.

Spherical particles with radius $a = 2.5$ nm are assumed in the analysis of transport toward the target. The velocity of a particle depends on its size as well as on its shape. Therefore, the time dependence of the probability to reach the target is also a function of these parameters.

As the transport of one reaction component is independent of the transport of other components of the same kind, then the total probability that at least one of them would reach the target region is given by a sum of the particular probabilities. If the number of the components is of about $10–10^2$, then the sum of the individual probabilities of the order of $10^{-1}–10^{-2}$ is great enough to provide a high degree of certainty that the product of the reaction would be formed.

We may compare the probabilities of bringing a particle to the target region by different mechanisms and under various conditions. Transport along microtubules has a high degree of certainty, and can carry ''cargo'' over long distances, but the rate is low. Transport by deterministic forces is comparatively fast (can be realized within several μs) but very likely over smaller distances than microtubule transport (we evaluate the probability for the distance 0.1 μm).

We point out that transport of reaction components governed by endogenous forces together with transport along microtubules has a high degree of certainty, and can explain directional transport and organization of biochemical reactions in living cells.

An electromagnetic field may be generated by intracellular polar structures, e.g., by actin filaments and by microtubules. Microtubules are composed of subunits that are strong electric dipoles. In interphase, the microtubules emanate from the centrosome (which generally lies next to the nucleus near the center of the cell) toward the periphery of the cell. Each of the microtubules generates an electromagnetic field around itself (elementary electromagnetic field). The total electromagnetic field in any place in the cell consists of elementary fields. Therefore, the total field is given by a sum of a large number of different space–time vectors representing the elementary fields. Due to the dynamic instability of microtubules,

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these vectors have random character. The sum of random vectors with different amplitudes, space orientations, and phases was evaluated in (18–20).

CONCLUSIONS

We present a theoretical analysis of the transport of the reaction components to their target region. The ubiquitous Brownian motion can transfer reaction components, but cannot be responsible for effective transport aimed at a target, because of its randomness. Diffusion may be important for the transport of components with high concentration such as ATP (leading to uniform distribution). The guided transport of organelles and vesicles along microtubules has an high degree of certainty but its velocity is low. Nevertheless, it is very likely important for long range transport. The force field of electromagnetic nature could have an essential deterministic function in the short range and medium range transport of reaction components. A field of central force seems to be more effective than is that of a parallel field. This type of transport of reaction components may be important in biological systems.

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