Equivalence between two-dimensional cell-sorting and one-dimensional generalized random walk, – spin representations of generating operators–.

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Abstract

The two-dimensional cell-sorting problem is found to be mathematically equivalent to the one-dimensional random walk problem with pair creations and annihilations, i.e. the adhesion probabilities in the cell-sorting model relate analytically to the expectation values in the random walk problem. This is an example demonstrating that two completely different biological systems are governed by a common mathematical structure. This result is obtained through the equivalences of these systems with lattice spin models. It is also shown that arbitrary generation operators can be written by the spin operators, and hence all biological stochastic problems can in principle be analyzed utilizing the techniques and knowledge previously obtained in the study of lattice spin systems.

Keywords: cell-sorting, random walk, lattice spin models, equivalence

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1 Introduction

Lattice models are important in biology when one needs to introduce a spatial structure. It has been shown that lattice models are often equivalent to spin models, which are lattice models for magnetic materials. Spin models have long been studied as a purely statistical mechanical subject, and various models on various lattices with different types of interactions have been investigated in detail. Approximation methods and techniques for numerical calculations have been extensively developed. Some models have been solved and the analytic expressions for physical quantities such as energy, specific heat, susceptibility, or correlation functions have been obtained. Some of the solvable models are known to be equivalent to each other, i.e. analytic relations between the quantities of the models are found under some specific relations of parameters.

In this study, it is shown that models for biological systems (or ecosystems, or organismic systems) are sometimes governed by a common mathematical structure, even though the models seem to differ completely from other. We show that the two-dimensional cell-sorting is equivalent to a generalized one-dimensional random walk in the following manner. The two-dimensional cell-sorting model on a square grid is equivalent to the two-dimensional Ising model which is one of the most typical statistical mechanical models for magnetism. Prior study have shown the two-dimensional Ising model is equivalent to the one-dimensional XY model, the Hamiltonian of which can be interpreted as the generation matrix of the random walk problem with pair creations and annihilations.

In Section 2, the spin models are briefly reviewed. In Section 3, a cell-sorting model is reviewed and its equivalence to the Ising model is considered. In Section 4, the analytic relations between the adhesion probabilities in the cell-sorting problem on a two-dimensional square grid and the expectation values in the random walk problem with pair creations and pair annihilations are derived.

In Section 5, relations between the stochastic movements, particularly those of the molecular motors, and spin Hamiltonians are considered. Molecular motors are protein molecules that are vital to biological motion especially for internal material transport such as muscle contraction, bacterial motion, cell division, intracellular transport along the axons of nerve cells, and genomic transcription. Several important families of motor proteins such as ribosomes, kinesins, dyneins, myosins and RNA polymerase have been identified. They move along periodically structured molecular tracks and show stochastic movements on an one-dimensional template. In this study, I will consider the random walk problem with hard-core interaction, the movements of ribosomes on a mRNA, and the movements of kinesins. Finally I
will show that generation rules for stochastic movements appearing in biological problems can always be represented by the Hamiltonians of spin models.

2 Lattice spin models and their equivalences

**Lattice spin models:** Magnetic materials are composed of atoms that have their own magnetic moment. The atoms interact with each other energetically, and these interactions are completely quantum mechanical in nature. Spin models are the mathematical models for magnets in which spin operators are assigned to every lattice point and interact with each other. Quantum spin is a kind of angular momentum and is defined through the following commutation relations:

\[
[s^x_l, s^y_l] = is^z_l, \quad [s^y_l, s^z_l] = is^x_l, \quad [s^z_l, s^x_l] = is^y_l,
\]

where \([A, B] = AB - BA\), \(i^2 = -1\), and \(s^x_l, s^y_l, s^z_l\) are the \(x, y, z\) components of the spin operator at site \(l\), respectively.

Assume the spin at site \(i\) and the spin at site \(j\) energetically interact with each other. Let the interaction energy be \(-J(s^x_is^x_j + s^y_is^y_j + \Delta s^z_is^z_j)\), where \(J\) is the coupling constant and \(\Delta\) is the anisotropic parameter. The Hamiltonian of the system is written as

\[
H = -J \sum_{\langle i, j \rangle} [s^x_is^x_j + s^y_is^y_j + \Delta s^z_is^z_j],
\]

which is the sum of the interaction energies over all the spin pairs \(\langle i, j \rangle\) that interact each other. The eigenvalues of \(H\) are the energies which can be realized in this system. The model (2) is called the XXZ model, its isotropic case \(\Delta = 1\) is called the Heisenberg model.

Spin operators are classified by the spin magnitude \(S\). Possible values of \(S\) are 0, 1/2, 1, 3/2 and \(m/2\) where \(m\) is a natural number. Let us consider the most typical case: \(S = 1/2\). In this case, there are two eigenstates of \(s^z_i\) with the eigenvalues 1/2 and −1/2. We call them the spin up state \(|+\rangle_i\) and the spin down state \(|-\rangle_i\), respectively. Generally there exist \(n = 2S + 1\) eigenstates of the spin operator \(s^z_i\) when its magnitude is equal to \(S\).

Then we find that the energy contribution from the last term in (2) is obtained from the product of the eigenvalues of interacting two spins. We call this factor the Ising interaction. Spin model with only the Ising interaction is called the Ising model.

The one-dimensional Ising model

\[
H = -J \sum_{i=1}^{N} s^z_is^z_{i+1}
\]
was first solved by Ising (1925). When we consider the Ising model with \( N \) sites, there are \( 2^N \) possible configurations of spin up and down states, because two states are possible for each site \( i (i = 1, 2, \ldots, N) \).

The total energy is a function of the configurations. Thus the energy can be written as \( E_k (k = 1, 2, \ldots, 2^N) \) where each \( k \) denotes a configuration. Following the statistical mechanics, the probability to find a configuration with an energy \( E_k \) is \( \exp(-E_k/k_B T)/Z \), where \( T \) is the temperature, \( k_B \) is the Boltzmann constant, and \( Z = \sum_{k=1}^{2^N} \exp(-E_k/k_B T) \) is the normalization factor called the partition function. Then the expectation value of the energy, for example, is obtained as

\[
\langle E \rangle = \frac{\sum_{k=1}^{2^N} E_k \exp(-\beta E_k)/Z}{Z} = \frac{1}{Z} \frac{\partial}{\partial (-\beta)} \log Z
\]

which can also be written as

\[
\langle E \rangle = \frac{1}{Z} \frac{\partial}{\partial (-\beta)} \sum_{k=1}^{2^N} \exp(-\beta E_k) = \frac{\partial}{\partial (-\beta)} \log Z.
\]

We then introduce the Gibbs free energy \( F \) by the relation \(-\beta F = \log Z\). The expectation value of the total energy \( E \), and other quantities like magnetization, specific heat and susceptibility, are obtained as the derivatives of \( F \). Models are usually said to be solved when their Gibbs energies are analytically obtained in a closed form.

The Gibbs free energy of the one-dimensional Ising model have also been obtained in a sophisticated way in introducing the transfer matrix method (Kramers and Wannier 1941; Kubo 1943). Let \( s_i \) be the eigenvalue of \( s_i^z \). The partition function of this model is written as

\[
Z = \sum_{m=\pm \frac{1}{2}} \exp(-\beta E_k)
\]

where the periodic boundary condition \( m_{N+1} = m_1 \) is assumed. When one introduce \( 2 \times 2 \) matrix \( (V)_{mm'} = \exp(\beta J m m') \), i.e. \( (V)_{\frac{1}{2}, \frac{1}{2}} = (V)_{\frac{1}{2}, -\frac{1}{2}} = \exp(+\beta J/4) \) and \( (V)_{\frac{1}{2}, -\frac{1}{2}} = (V)_{-\frac{1}{2}, \frac{1}{2}} = \exp(-\beta J/4) \), the
The partition function is written as
\[
Z = \sum_{m_1 = \pm \frac{1}{2}} \sum_{m_2 = \pm \frac{1}{2}} \cdots \sum_{m_N = \pm \frac{1}{2}} (V)_{m_1 m_2} (V)_{m_2 m_3} \cdots (V)_{m_N m_1}
\]
\[
= \sum_{m = \pm \frac{1}{2}} (V^N)_{mm}
\]
\[
= \text{Tr} V^N = \lambda_1^N + \lambda_2^N = \lambda_1^N (1 + \frac{\lambda_2^N}{\lambda_1^N}),
\]
where \(\lambda_1\) and \(\lambda_2\) are the eigenvalues of the matrix \(V\): \(\lambda_1 = 2 \cosh(\beta J/4)\), \(\lambda_2 = 2 \sinh(\beta J/4)\). The free energy per site in the thermodynamic limit is
\[
f = \lim_{N \to \infty} \frac{1}{N} F = \lim_{N \to \infty} \frac{1}{N - \beta} \log[\lambda_1^N (1 + \frac{\lambda_2^N}{\lambda_1^N})] = \frac{1}{-\beta} \log \lambda_1.
\]
Effects coming from the boundary vanish when one take the thermodynamic limit \(N \to \infty\). Hence the free energy is obtained if the maximum eigenvalue of the transfer matrix \(V\) is obtained.

When we consider the two-dimensional Ising model on a square lattice with the size \(M \times N\), we have to introduce a \(2^M \times 2^M\) transfer matrix. This huge matrix have been diagonalized and the free energy have been obtained (Onsager 1944).

All the spin operators \(s^z_i\) in the Ising Hamiltonian commute with each other: \([s^z_i, s^z_j]\) = 0. Then the system is called a classical model because there exist no quantum effect coming from non-commutativity of operators.

Next let us introduce \(s^\pm_i = s^x_i \pm is^y_i\). From the commutation relation (1), it is derived that \(s^+_i\) maps the spin down state to the spin up state, \(s^-_i\) maps the spin up state to the spin down state, and otherwise it works as the zero operator:
\[
s^+_i |\downarrow_i\rangle = |\uparrow_i\rangle, \quad s^-_i |\uparrow_i\rangle = |\downarrow_i\rangle, \quad s^+_i |\uparrow_i\rangle = 0, \quad s^-_i |\downarrow_i\rangle = 0.
\]
The sum of the first two terms in (2) is equal to \((s^+_i s^-_j + s^-_i s^+_j)/2\), and this term transfers the spin up state from site \(j\) to \(i\), or from site \(i\) to \(j\):
\[
s^+_i s^-_j |\downarrow_i\rangle |\uparrow_j\rangle = |\uparrow_i\rangle |\downarrow_j\rangle, \quad s^-_i s^+_j |\uparrow_i\rangle |\downarrow_j\rangle = |\downarrow_i\rangle |\uparrow_j\rangle.
\]
Contributions coming from the other states are zero: \(s^+_i s^-_j |\uparrow_i\rangle |\downarrow_j\rangle = 0\) and \(s^-_i s^+_j |\downarrow_i\rangle |\uparrow_j\rangle = 0\). Thus the sum of the first two terms in (2) is the two-body flip operation, in which \(+\) moves from the right to the left, or from the left to the right. Therefore the Hamiltonian (2) is the sum

5
of the two-body flips and the products of the eigenvalues of interacting two spins.

The spin model interacting via \( s^x_i s^x_j \) and \( s^y_i s^y_j \),

\[
H = -J \sum_{\langle i,j \rangle} [(1 + \gamma) s^x_i s^x_j + (1 - \gamma) s^y_i s^y_j] - h \sum_i s^z_i , \tag{4}
\]
is called the XY model, where \( \gamma \) is the anisotropy parameter. The factor \( h \) in the last term is an external magnetic field applied to the \( z \) direction, which will become important to consider the equivalence. The interaction is a sum of the two-body flips and hence it is not trivial to find the eigenstates, in contrast with the fact that the eigenstates of the Ising model is obtained immediately. In the one-dimensional case, the XY model have been solved exactly (Lieb et al. 1961; Katsura 1962; Niemaijer 1967).

The Ising model with an external field applied to the \( x \) direction, \( -h^x \sum_i s^x_i \), is called the transverse Ising model. The transverse susceptibility at \( h^x = 0 \) for the one-dimensional case with \( S = 1/2 \) have been exactly calculated (Fisher 1960). The transverse susceptibility at \( h^x = 0 \) for the two-dimensional case with \( S = 1/2 \) have also been obtained (Fisher 1963). The exact free energy for the one-dimensional case have been obtained (Katsura 1962; Pfueyt 1970). The transverse term is expressed as \( s^x_i = (s^+_i + s^-_i) / 2 \), and thus it represents independent one-body flip of each spin with the probability proportional to \( h^x \). The transverse susceptibility at \( h^x = 0 \) of the one-dimensional transverse Ising model with arbitrary spin magnitude \( S \) have been exactly obtained (Minami 1996). The susceptibility and the specific heat for general Ising type interactions \( (s^z_i)^m (s^z_j)^n \) have also been exactly obtained (Minami 1998).

The Hamiltonians of the XY model and the transverse Ising model are the sums of operators which do not always commute with each other. Non-commutatibity of operators induce quantum effects, and these models are typical examples of the quantum spin system.

**Equivalences:** It has been derived that some of these spin models are equivalent to each other in the following sense (Suzuki 1971). The two-dimensional Ising model is solved using the transfer matrix \( V \), where the free energy is obtained from the maximum eigenvalue of \( V \). Let \( |\phi_0 \rangle \) be the eigenstate of \( V \) corresponding to the maximum eigenvalue. With an appropriate choice of parameters, the Hamiltonian \( H \) of the one-dimensional XY model commutes with the transfer matrix \( V \) of the two-dimensional Ising model: \([H, V] = HV - VH = 0\). Hence these models have a common set of eigenstates: \( H \) and \( V \) can be diagonalized simultaneously. In particular, the eigenstate \( |\phi_0 \rangle \) corresponding to the maximum eigenvalue of \( V \) and the eigenstate for the smallest eigenvalue
of the one-dimensional XY model are the same. This structure implies that the expectation values in the two-dimensional Ising model and the expectation values in the lowest energy state (i.e. the ground state) of the one-dimensional XY model analytically relate to each other.

The two-dimensional Ising model and the one-dimensional XY model are equivalent to each other, where an anisotropic limit of the XY model with an external field is the transverse Ising model. The energy of the two-dimensional Ising model is determined from the simple product of the eigenvalues of interacting two spins. The interaction is simple but the model is not easy to solve because it is defined on the two-dimensional square grid. The interaction of the one-dimensional XY model is the two-body flip and it is not trivial to find the eigenstates, though the lattice is a one-dimensional chain and simpler than the square lattice. The interaction of the transverse Ising model is simple Ising interaction, however there exists an external magnetic field in the $x$ direction, which does not commute with the Ising interaction.

It is derived that the correlation functions in the two-dimensional Ising model and those in the lowest energy state of the one-dimensional XY model satisfy the following relation:

$$\langle s^x_{ji} s^x_{ik}\rangle_{2D\text{ Ising}} = \cosh^2 K^*_1 \langle s^x_{ji} s^x_{ik}\rangle_{1D\text{ XY}} - \sinh^2 K^*_1 \langle s^y_{ji} s^y_{ik}\rangle_{1D\text{ XY}}.$$  \hspace{1cm} (5)

The parameters are assumed to satisfy $\cosh 2K^*_1 = 1/\gamma$, $\tanh 2K^*_2 = (1 - \gamma^2)^{1/2}/h$, and $\sinh 2K^*_1 \sinh 2K^*_2 = 1$, $K^*_i = \beta J^*_i$ ($i = 1, 2$), where $J^*_1$ and $J^*_2$ are the vertical and horizontal coupling constants of the square lattice Ising model, respectively (Suzuki 1971, in which the Ising model is written in terms of the Pauli operator $\sigma^x_j$ where $s^x_j = \sigma^x_j/2$).

The expectation value of a quantity $Q$ in the state $|\phi\rangle$ is calculated using the operator $\hat{Q}$ which corresponds to $Q$, and using the expansion $|\phi\rangle = \sum_k c_k |k\rangle$ as

$$\langle Q \rangle = \langle \phi | \hat{Q} | \phi \rangle = \sum_{kk'} c_k^* c_{k'} \langle k' | \hat{Q} | k \rangle,$$  \hspace{1cm} (6)

where $c_{k'}^*$ is the complex conjugate of $c_{k'}$ and $|k'\rangle$ is the dual state of $|k\rangle$.

Many other examples of equivalences of lattice spin models have been investigated. The six-vertex model, which is a two-dimensional lattice model, is equivalent to the one-dimensional XXZ model. The eight-vertex model is equivalent to the one-dimensional XYZ model. General formula for equivalences between $d$-dimensional classical systems and $(d+1)$-dimensional quantum systems have also been obtained (Suzuki 1976).
3 A model for cell-sorting and equivalence to the Ising model

Cell sorting problem: Among the processes involved in the formation of an animal, one of the most important phenomena is the self-rearrangement of cells leading to the formation of functional structures. Starting from a random mixture of cells from different origins, the cells reassemble themselves, begin to form clusters of cells of the same type, and simulate their normal histological patterns. These movements are directed, spontaneous, and proceed in the absence of external forces. This pattern formation phenomenon is known as cell-sorting.

The mechanisms that determine why cells adhere to one another, i.e. the forces that drive cell movement during the relevant processes, are an important area of research. Steinberg made two assumptions to explain certain kinds of cell rearrangements. He assumed that cell-sorting required spontaneous progressions of motile and mutually adhesive cells to configurations that have minimum adhesive free energy (Steinberg 1962a; b; c; 1963; 1970). His assumptions are i) any contact between cells has an adhesion energy depending on the cell types, and ii) cells are mobile and can reach a global energy minimum configuration independent of their initial condition. These assumptions indicate that differential intercellular adhesion and random movement of cells are the basic mechanisms of this self-organizing phenomenon.

This differential adhesion hypothesis has been checked against various spatial restrictions, and various additional assumptions on the movement of cells have been developed. The cell assumed to move on either a two-dimensional square grid or a three-dimensional cube, has been investigated analytically, tested through numerical simulations, and applied to real systems (Goel et al. 1970; Goel and Leith 1970; Leith and Goel 1971; Goel and Rogers 1978; Rogers and Goel 1978; Mochizuki et al. 1996; 1998; Mochizuki 2002). Cell movement on a hexagonal grid has also been considered (Antonelli et al. 1973; 1975; Rogers and Sampson 1977). Cells are represented by not only hexagons but also general \( n \)-gons (Matela and Fletterick 1979; 1980), Voronoi polygons (Sulis et al. 1984), or polygonal cells (Graner and Sawada 1993). Cells are represented by the large-Q Potts model, in which each cell can take Q internal states (Graner and Glazier 1992; Glazier and Graner 1993, Nakajima and Ishihara 2011). A viscous liquid model with interfacial tension was considered (Gordon et al. 1972). Steinberg’s theory was modified using dynamical equations of a molecular nature, and cell-sorting was found to occur in a near-liquid state (Greenspan 1981). A continuous mathematical model was proposed to analyze cell-sorting in Dictyostelium discoideum (Umeda 1989; Umeda and Inouye 1999; 2004).
In the present study, I concentrate on the model introduced by Mochizuki et al. (1996) on the two-dimensional square lattice. This model is directly equivalent to the Ising model, which has been exactly analyzed as a model for magnetic materials.

**Model and the equivalence:** Let us consider two kinds of cells distinguished by color: black and white. The cells are assumed to form a regular square lattice. Let $\lambda_{BB}$ be the strength of adhesion per cell contact between black and black cells, and $\lambda_{WW}$ and $\lambda_{BW}$ be the strength between white and white, and black and white cells, respectively. One can estimate the total adhesion $\Lambda_k$ when the configuration $k$ of the black and white cells is known: $\Lambda_k$ is the sum of all the strength of adhesion between cells. Cells exchange their positions between nearest neighbors. Let $m$ be the rate of exchange of the location. It is assumed the probability of finding a configuration having total strength equal to $\Lambda_k$ is proportional to $\exp(\Lambda_k/m)$.

Let us introduce the differential adhesion $A = \lambda_{BB} + \lambda_{WW} - 2\lambda_{BW}$. The total adhesion $\Lambda_k$ changes its value by $A$ as an unit when two cells change their locations, and hence the system is controlled not through the energies $\lambda_{BB}$, $\lambda_{WW}$ and $\lambda_{BW}$ independently, but through the differential adhesion $A$. Typical equilibrium configurations are calculated by Mochizuki et al., where one can find a pattern in which black and white cells appear situated like a checker-board for $A/m = -2$, the pattern seems almost random when $A/m = 0$, and it appears segregated when $A/m$ is positive and large.

This model of cell-sorting is equivalent to the Ising model when $\lambda_{BB} = \lambda_{WW}$. One can introduce a direct correspondence in which a black cell at site $i$ corresponds to the spin up state $|+\rangle_i$, and a white cell at site $i$ corresponds to the spin down state $|\rangle_i$. The interaction energy between two up states, or two down states, is equal to $-J/4$, and that between up and down states is equal to $+J/4$. Let us introduce a constant $J_0$ and set

$$\lambda_{BB} = \lambda_{WW} = -(-J/4 + J_0),$$
$$\lambda_{BW} = -(+J/4 + J_0).$$

The overall minus signs are introduced because the probability to find a configuration with total adhesion strength $\Lambda_k$ is proportional to $\exp(\Lambda_k/m)$ in the case of the cell-sorting model, though the probability to find a configuration with total energy $E_k$ is proportional to $\exp(-E_k/k_B T)$ in the case of the Ising model. It is easy to check that the contributions from $J_0$ cancel in the calculations of expectation values. The Hamiltonian is $H = -J \sum_{\langle ij \rangle} s_i^z s_j^z + \frac{1}{2} z N J_0$, where $N$ is the total number of sites and $z$ is the number of interacting pairs $\langle ij \rangle$ from each site $i$, e.g. $z = 2$ in the one-dimensional linear chain and $z = 4$ in
the two-dimensional square lattice. The parameters in the cell-sorting model and those in the Ising model are related by $A = J$ and $m = k_B T$, and hence $A/m = J/k_B T$. The probability of re-arrangement increases as the temperature increases. The correspondence is consistent with the facts that $J$ is the coupling constant which determines the unit of energy scale in the Ising model, and $A$ is the the difference adhesion which determines the unit of the total adhesion in the cell-sorting problem.

As a model of magnetism, $A/m = -2$ indicates that the Ising model is an antiferromagnet. The checkerboard-like pattern is that called the Néel order. The case with $A/m = 0$ corresponds to a paramagnet, where there is no interaction between spins, and each spin flips independently. The cases with positive $A/m$ correspond to ferromagnets, where the spin of the nearest-neighbors tends to become parallel and tend to form clusters. In the case studied by Mochizuki et al., the number of the black cells and the number of the white cells are fixed to be the same.

The two-dimensional Ising model has a critical point $T_c$ at a non-zero and finite value of temperature. Below $T_c$, clusters of spin up states appear, which corresponds to the existence of cell-sorting phenomena, whereas above $T_c$ there is no cell-sorting. In the case of the one-dimensional Ising model, the critical temperature is equal to zero.

The quantities studied in the cell-sorting problem correspond to quantities in the Ising model. Let us assume the periodic boundary condition. Following the notations in Mochizuki et al., let $\rho_B$ be the fraction of the black cells and $\rho_W$ be the fraction of the white cells, then $\rho_B + \rho_W = 1$. Let $q_{BB}$ be the fraction of black cells in the neighborhood of a randomly chosen black cell, $q_{WW}$ the fraction of white cells in the neighborhood of a randomly chosen white cell, $q_{WB}$ the fraction of white cells in the neighborhood of a randomly chosen black cell, and $q_{BW}$ the fraction of black cells in the neighborhood of a randomly chosen white cell. Then $q_{BB} + q_{WB} = 1$ and $q_{WW} + q_{BW} = 1$. The two-body correlation function in the Ising model is the expectation value of the product of eigenvalues $\pm 1/2$ of corresponding two sites. Thus, by definition, the nearest-neighbor correlation function is written using the probabilities as

$$\langle s^z_i s^z_j \rangle_{\text{Ising}} = \frac{1}{2^2} \rho_B q_{BB} + \frac{-1}{2^2} \rho_B q_{WB} + \frac{-1}{2^2} \rho_W q_{BW} + \frac{-1}{2^2} \rho_W q_{WW}$$

$$= \frac{1}{4} \rho_B (2q_{BB} - 1) + \frac{1}{4} \rho_W (2q_{WW} - 1)$$

$$= \frac{1}{4} (2\rho_B q_{BB} + 2\rho_W q_{WW} - 1).$$

(7)

The magnetization $\langle s^z_i \rangle_{\text{Ising}}$ is the expectation value of the eigenvalue associated to each site, and obviously is equal to $\frac{1}{2} \rho_B + (-\frac{1}{2}) \rho_W$. How-
ever, it can also be written in terms of the probabilities $\rho_B q_{BB}$ and $\rho_W q_{WW}$. The probability that the two cells in a randomly chosen nearest-neighbor pair are both black is $\rho_B q_{BB}$, the probability that one of the two cells is black and the other cell is white is $\rho_B q_{WB} + \rho_W q_{BW}$, and the probability that the two cells are both white is $\rho_W q_{WW}$. Considering the average magnetization per pair, we obtain

$$
\langle s_i^z \rangle_{\text{Ising}} = \frac{1}{2} \left( \frac{1}{2} + \frac{1}{2} \right) \rho_B q_{BB} + \left( \frac{1}{2} - \frac{1}{2} \right) (\rho_B q_{WB} + \rho_W q_{BW}) + \left( - \frac{1}{2} - \frac{1}{2} \right) \rho_W q_{WW} \\
= \frac{1}{2} (\rho_B q_{BB} - \rho_W q_{WW})
$$

From (7) and (8), $\rho_B q_{BB}$ and $\rho_W q_{WW}$ are expressed by the correlation functions in the Ising model as

$$
\rho_B q_{BB} = \langle s_i^z s_j^z \rangle_{\text{Ising}} + \frac{1}{4} + \langle s_i^z \rangle_{\text{Ising}},
$$

$$
\rho_W q_{WW} = \langle s_i^z s_j^z \rangle_{\text{Ising}} + \frac{1}{4} - \langle s_i^z \rangle_{\text{Ising}},
$$

This argument can be generalized to obtain probabilities for other types of spin pairs. When the site $i$ and $j$ locate in the next-nearest-neighbors (or in other specific locations) each other, $q_{BB}$ etc. should be redefined as the fraction to find cells of corresponding colors in the next-nearest-neighbors (or in the other specific locations). Then (9) is still valid. With the open boundary, (9) is also valid except boundary terms, which vanish when one assume the periodic boundary condition.

In the one-dimensional Ising model, there is no spontaneous symmetry breaking, and hence $\langle s_i^z \rangle_{\text{Ising}} = 0$, thus $\rho_B = 1/2$. The nearest-neighbor correlation function of this case is immediately calculated by the transfer matrix method and one obtains $q_{BB} = 2 (\tanh(J/4kT)/4 + 1/4 + 0) = (\tanh(A/4m) + 1)/2$, which is consistent with the result obtained for the cell-sorting model.

### 4 Equivalences between biological systems

The cell-sorting model with adhesion strength is equivalent to the Ising model in each dimension. The two-dimensional Ising model on the square lattice is equivalent to the one-dimensional XY model with an external magnetic field, and it is also equivalent to the one-dimensional transverse Ising model. The XY model and the transverse Ising model are equivalent to systems with two-body flip, or independent one-body flip, with the energy estimated as the product of eigenvalues of two states. Next I consider a stochastic process that corresponds to the XY model.
Let us consider identical particles on the one-dimensional lattice. Each particle locate on a lattice point \( x \), where \( x \) is integer. The particles move right or left in each step with the rate \( p_R \) and \( p_L \), respectively. The particles interact with the hard-core interactions: they cannot move into the space already occupied by other particles. Let us introduce the following notation

\[ |−\cdots,+−\cdots+⟩ = |−⟩_1 \cdots |+⟩_j |−⟩_{j+1} \cdots |+⟩_m, \quad \text{etc.} \]

Operators \( s^+_j \) and \( s^{-}_{j+1} \) work nontrivially only on the \( j \)-th and \( j+1 \)-th sites as

\[ s^-_j s^+_{j+1} |\cdots,+−\cdots⟩ = |\cdots,−,+−\cdots⟩, \]

\[ s^+_j s^-_{j+1} |\cdots,+−\cdots⟩ = |\cdots,+−\cdots⟩, \] (10)

When we regard + as a particle and − as an empty site, operations (10) are the mappings in which a particle moves to one of its nearest neighbors. The matrix representations of the operators are

\[
s^-_j s^+_{j+1} = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0
\end{bmatrix}_{jj+1}, \quad s^+_j s^-_{j+1} = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0
\end{bmatrix}_{jj+1},
\] (11)

where the basis set used to represent the matrix is

\[
\{|+⟩_j|+⟩_{j+1}, |−⟩_j|−⟩_{j+1}, |+⟩_j|−⟩_{j+1}, |−⟩_j|+⟩_{j+1}\}.
\]

The matrix \( [\cdot]_{jj+1} \) operates on the site \( j \) and \( j+1 \), and operates as an identity on the other sites. Then the contributions from the random hoppings are written as

\[
H = \sum_{j=1}^{N} [p_R s^-_j s^+_{j+1} + p_L s^+_j s^-_{j+1}]
\] (12)

\[
= \sum_{j=1}^{N} \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & p_L & 0 \\
0 & 0 & p_R & 0
\end{bmatrix}_{jj+1}.
\] (13)

Let \( \{x_1, x_2, \ldots, x_m\} \) be a configuration of the particles, in which the sites \( x_1, x_2, \ldots, x_m \) are occupied and the other sites are empty. Let \( \{x_i\}_k \ (k = 1, \ldots, 2^N) \) be the possible \( 2^N \) configurations, where each \( k \) denotes one configuration. Let \( P(\{x_i\}_k; n) \) be the probability that the configuration of the particles is \( \{x_i\}_k \) after the \( n \)-th step. Let us introduce the probability vector \( \mathbf{P}_n \), in which the \( k \)-th element of \( \mathbf{P}_n \)
is \((P_n)_k = P(\{x_i\}_k; n)\). Then the random hoppings are generated by 
\[ P_{n+1} = HP_n. \] This process conserves the number of particles. In the case of 
\( p_R = p_L = 1/2 \), the operator \( (12) \) is reduced to the Hamiltonian
of the XY-model \( (4) \) with \( \gamma = 0 \) and \( h = 0 \).

When one introduce nearest-neighbor pair creation and annihilation processes with the probability \( p_U \) and \( p_D \), respectively, and also multiply the weights \(-h/2\) and \( h/2\) for the nearest-neighbor pair particles
and pair of the empty sites, respectively, \( H \) becomes
\[
H = \sum_{j=1}^{N} \begin{bmatrix}
-h/2 & p_U & 0 & 0 \\
p_D & h/2 & 0 & 0 \\
0 & 0 & p_L & 0 \\
0 & 0 & p_R & 0
\end{bmatrix}_{j,j+1}.
\] (14)

This operator \( (14) \) is written by the spin operators as
\[
H = \sum_{j=1}^{N} \left[ p_R s_j^- s_{j+1}^+ + p_L s_j^+ s_{j+1}^- + p_U s_j^+ s_{j+1}^+ + p_D s_j^- s_{j+1}^- - \frac{h}{2} (s_j^z + s_{j+1}^z) \right].
\] (15)

When \( p_R = p_L = 1/2 \) and \( p_U = p_D = \gamma/2 \), \( (15) \) is reduced to the Hamiltonian of the anisotropic XY-model \( (4) \) with an external field \( h \).

The first \( 2 \times 2 \) block element in \( (14) \) represents the following processes. Two particles meet and annihilate with the rate \( p_D \), a nearest-neighbor pair of particles are created with the rate \( p_U \). The weight of each state varies spontaneously: multiplied by the factor which is the sum of \(-h/2\) and \( h/2\) associated to each nearest-neighbor pair of particles and each nearest-neighbor pair of empty sites, respectively.

Let \( p_U = p_D = \gamma/2 \), and assume \( \gamma > 0 \). All the matrix elements in the first block in \( (14) \) can become non-negative by a rotation as
\[
R^{-1} \begin{bmatrix}
-h & \gamma \\
\gamma & h
\end{bmatrix}_{j,j+1} R = \lambda \begin{bmatrix}
0 & 1 \\
1 & 0
\end{bmatrix}_{j,j+1},
\]
where \( \lambda = \sqrt{\gamma^2 + h^2}/2 \) and
\[
R = \begin{bmatrix}
\cos \theta & -\sin \theta \\
\sin \theta & \cos \theta
\end{bmatrix}_{j,j+1}, \quad \tan \theta = \frac{h - \gamma + \sqrt{\gamma^2 + h^2}}{h + \gamma + \sqrt{\gamma^2 + h^2}}, \quad |\theta| < \frac{\pi}{4}.
\]

Thus the pair creation and annihilation processes with the spontaneous change \(-h/2\) and \( h/2\) can also be regarded as a simple reflection multiplied by the factor \( \lambda \), in the above two rotated basis.

Therefore the Hamiltonian of the XY-model can be regarded as the generator of the following two processes, 1) random walk process with hard-core interactions, and 2) pair creations and pair annihilations with spontaneous change of weights which are determined from the
number of pair particles and "pair vacuums". The second process 2) is also regarded as the rotated reflections with the rate \( \sqrt{\gamma^2 + h^2}/2 \).

In the relation (5), the expectation values \( \langle \cdot \rangle_{1D \text{XY}} \) are estimated in the ground state \( |\phi_0\rangle \) of the XY model with the coupling constant \( J > 0 \), and thus \( -J < 0 \). The state \( |\phi_0\rangle \) is the eigenstate corresponding to the maximum eigenvalue of \( \Lambda_0 \) because the sign of the coupling is now \( -J = 1 > 0 \). When we consider the matrix \( H + cI \) where \( I \) is the unit matrix and \( c > 0 \) is sufficiently large, all the matrix elements of \( H + cI \) are non-negative, and the eigenstates of \( H + cI \) are simultaneously the eigenstates of \( H \). From the Perron-Frobenius theorem, it is derived that all the coefficients in \( |\phi_0\rangle \) are non-negative.

Let \( \lambda_0 \) be the maximum eigenvalue of \( H \). The maximum eigenvalue of the matrix \( \hat{H} = H/\lambda_0 \) is equal to 1. Let \( \Lambda_i \) be an eigenvalue of \( \hat{H} \) and \( |\phi_i\rangle \) be an eigenstate corresponding to \( \Lambda_i \): \( \hat{H}|\phi_i\rangle = \Lambda_i|\phi_i\rangle \). Then all the eigenvalues satisfy \( |\Lambda_i| \leq |\Lambda_0| = 1 \). Therefore the state \( |\phi_0\rangle \) survives in the limit where the operator \( \hat{H} \) is iteratively applied: \( \hat{H}^n|\phi_0\rangle = |\phi_0\rangle \).

In the one-dimensional XY model, there exist a critical field \( h_c \), which corresponds to the critical temperature \( T_c \) of the two-dimensional Ising model. The ground state is unique for \( h > h_c \) and two-fold degenerate for \( h \leq h_c \) in the thermodynamic limit \( N \to \infty \). In the case of the two-dimensional Ising model, the eigenstate of the transfer matrix corresponding to the maximum eigenvalue is unique for \( T > T_c \) and two-fold degenerate for \( T \leq T_c \), and there exists a spontaneous symmetry breaking and the magnetization becomes non-zero below \( T_c \). This implies that the global minimum of the free energy is realized with \( \rho_B = 1/2 \) for \( T > T_c \), and with \( \rho_B \neq 1/2 \) for \( T \leq T_c \). The corresponding cell-sorting model below \( T_c \) is, therefore, a generalized model which includes the effect of gathering of one kind of cells from outside.

If the process represented by \( \hat{H} \) is fully stochastic, the matrix \( \hat{H} \) should satisfy the conservation of probability: \( \langle \hat{H} \rangle_{ij} \geq 0 \) and \( \sum_i \langle \hat{H} \rangle_{ij} = 1 \). The matrix \( \hat{H} \) does not satisfy this condition. However, the state \( |\phi_0\rangle \) is a steady state and the conservation of probability is satisfied in \( |\phi_0\rangle \). Let

\[
|\phi_0\rangle = \sum_{\{x_i\}} P_0(x_1, x_2, \ldots, x_{m_p}; n)|x_1, x_2, \ldots, x_{m_p}\rangle,
\]

where \( |x_1, x_2, \ldots, x_{m_p}\rangle \) is the direct product of the states \( |+\rangle_j \) \( (j = x_1, x_2, \ldots, x_{m_p}) \) and \( |\rangle_j \) \( (j \neq x_1, x_2, \ldots, x_{m_p}) \), i.e., the state where the sites \( x_1, \ldots, x_{m_p} \) are occupied and the other sites are empty. The coefficient \( P_0(x_1, x_2, \ldots, x_{m_p}; n) \) is the probability that the system is in the state \( |x_1, x_2, \ldots, x_{m_p}\rangle \). The probability distribution \( \{P_0(x_1, x_2, \ldots, x_{m_p}; n)\} \) is invariant under the operations of \( \hat{H} \) and satisfies the conservation of probability. This means that \( \hat{H} \) is stochastic in the subspace corresponding to the maximum eigenvalue.
In the case of the cell-sorting problem on the square grid, from (5), (9), and from the relations
\[ \langle s^z_{ij} \rangle_{2D Ising} = \frac{1}{2} \rho_B + \left( -\frac{1}{2} \right) \rho_W, \]
\[ \rho_B + \rho_W = 1, \]
and \( \cosh 2K^* = \frac{1}{\gamma} \), one obtains
\[ \rho_B q_{BB} = \langle s^z_{ij} s^z_{ik} \rangle_{2D Ising} + \left( \frac{1}{4} \right) \rho_B + \left( \frac{1}{4} \right) \rho_W = \gamma \langle s^+_{ij} s^-_{ik} \rangle_{1D XY} - \sinh 2K^* \langle s^y_j s^y_k \rangle_{1D XY} + \left( \frac{1}{4} \right) \rho_B - \left( \frac{1}{2} \right) \]
(16)

The probability \( q_{BB} \) in (16) is that for the two cells locating \((i, j)\) and \((i, k)\). The parameter \( \gamma \) is specified from the restriction \( K_1 = K_2 = \beta J = A/m \). The expectation values are calculated in principle from \( \langle \cdot \rangle_{1D XY} = \langle \phi_0 | \cdot | \phi_0 \rangle \), the expansion (10), and the normalization conditions \( \langle + | + \rangle = 1, \langle - | - \rangle = 1, \langle + | - \rangle = 0 \) and \( \langle - | + \rangle = 0 \) for each site \( i \). The magnetization \( \langle s^z_i \rangle_{2D Ising} \) below \( T_c \) have been calculated by Yang (1952). The correlation functions \( \langle s^z_l s^z_k \rangle_{1D XY} \) have been analytically calculated in the context of the one-dimensional XY model (McCoy et al., 1971; Tonegawa, 1981), and \( \langle s^z_0 s^z_{jk} \rangle_{2D Ising} \) have also been calculated in the context of the equivalent two-dimensional Ising model (Wu et al. 1976; McCoy et al. 1977), both for arbitraly \( j \) and \( k \). In conclusion, the adhesion probability in the two-dimensional cell-sorting problem is analytically expressed by the expectation values in the steady state of the one-dimensional generalized random walk problem.

5 Correspondences of stochastic processes with lattice spin models

The matrix \( H \) (and \( \bar{H} \)) corresponding to the XY model is not itself fully stochastic for all the possible states of the particles. In this section, first I formulate the most general form of the stochastic matrix for the one-dimensional random walk process with creations and annihilations, and next consider three examples to show the close relation between biological systems and lattice spin systems, and finally prove that the stochastic processes in biological systems can always be written in terms of the spin Hamiltonians.

Let us consider the operator

\[ H = \sum_{j=1}^{N} \begin{bmatrix} w_3 & p_U & 0 & 0 \\ p_D & w_4 & 0 & 0 \\ 0 & 0 & w_1 & p_L \\ 0 & 0 & p_R & w_2 \end{bmatrix}_{jj+1}. \]
The element $p_D$ in the matrix $[|jj+1\rangle]_j$ is the rate of the pair annihilation $|+\rangle_j|+\rangle_{j+1} \rightarrow |-\rangle_j|-\rangle_{j+1}$. The element $w_3$ is the rate of the pair to be invariant $|+\rangle_j|+\rangle_{j+1} \rightarrow |+\rangle_j|+\rangle_{j+1}$, and the other elements are defined as the rates of the following transitions:

\[
\begin{align*}
    p_U & : |-\rangle_j|-\rangle_{j+1} \rightarrow |+\rangle_j|+\rangle_{j+1}, \\
    p_R & : |+\rangle_j|-\rangle_{j+1} \rightarrow |-\rangle_j|+\rangle_{j+1}, \\
    p_L & : |-\rangle_j|+\rangle_{j+1} \rightarrow |+\rangle_j|-\rangle_{j+1}, \\
    w_1 & : |+\rangle_j|-\rangle_{j+1} \rightarrow |+\rangle_j|-\rangle_{j+1}, \\
    w_2 & : |-\rangle_j|+\rangle_{j+1} \rightarrow |-\rangle_j|+\rangle_{j+1}, \\
    w_4 & : |-\rangle_j|-\rangle_{j+1} \rightarrow |+\rangle_j|+\rangle_{j+1}.
\end{align*}
\]

First let us assume the periodic boundary condition, and consider the case $w_i = 0 (i = 1, 2, 3, 4)$. Starting from the state $|+\rangle_1|+\rangle_2 \cdots |+\rangle_N$ = $|+ \cdots +\rangle$. $N$ kind of pair annihilations which result in the states with successive two minus, $| - + \cdots +\rangle$, $| + - \cdots +\rangle$, etc., are possible. Thus the conservation of probability is satisfied with the condition $Np_D = 1$. Starting from other states such as $| - + \cdots +\rangle$, $| + - \cdots +\rangle$, etc., it is straightforward to convince that two $p_D$'s (or two $p_U$'s) are always replaced by a pair formed by $p_R$ and $p_L$ in the calculations of the total probability, and thus the conservation of probability is satisfied with $2p_D = p_R + p_L$, $2p_U = p_R + p_L$. Similarly in the case of $p_D$, the condition for $p_U$ is $Np_U = 1$. Thus we obtain $p_D = p_U = 1/N$, and $p_R + p_L = 2/N$. Let us introduce the rates $w_i (i = 1, 2, 3, 4)$, then $p_D$, $p_U$, $p_R$, and $p_L$ should be replaced by $p_D + w_3$, $p_U + w_4$, $p_R + w_1$, and $p_L + w_2$, respectively, in the calculations of the total probability. Therefore the conservation of probability is satisfied iff

\[
\begin{align*}
    p_D + w_3 = p_U + w_4 = \frac{1}{N}, \\
    (p_R + w_1) + (p_L + w_2) = \frac{2}{N}.
\end{align*}
\]

When we assume the open boundary condition, $s_{N+1}^x \neq s_1^x$, then the number of spin pairs $(j, j+1)$ is $N$, and the condition (18) remains true though the number of sites now being $N+1$. The condition (19) should be satisfied for $2 \leq j \leq N - 1$. At $(j, j+1) = (1, 2)$ and $(N, N+1)$, the probability is conserved iff

\[
p_R + w_1 = p_L + w_2 = \frac{1}{N}.
\]

The condition (19) is satisfied when we assume (20). Thus (18) and (20) are the conditions in the case of the lattice with open boundary. These are the general form of the one-dimensional stochastic matrix for random walk processes, with pair creations and pair annihilations.
The matrix (17) is written by the spin operators as

\[ H = \sum_{j=1}^{N} \left[ p_R s_j^- s_{j+1}^+ + p_L s_j^+ s_{j-1}^- + p_U s_j^+ s_{j+1}^+ + p_D s_j^- s_{j-1}^- \right] \]

\[ + \Delta s_j^z s_{j+1}^z \frac{h}{2} (s_j^z + s_{j+1}^z) + c_0 I + \frac{c}{2} (s_j^z - s_{j+1}^z) \], \quad (21) \]

where \( I \) is the identity operator and

\[ \Delta = w_3 + w_4 - w_1 - w_2, \quad h = w_4 - w_3 \]

\[ c_0 = \frac{1}{4} (w_3 + w_4 + w_1 + w_2), \quad c = w_1 - w_2. \] \quad (22)

When one assume the periodic boundary condition \( s_{N+1}^z = s_1^z \), the last term in (21) vanishes: \( \sum_{j=1}^{N} (s_j^z - s_{j+1}^z) = 0 \), and thus \( H \) is independent of \( c \). It is easy to check that \( w_3, w_4 \) and \( w_1 + w_2 \) do not depend on \( c \), and hence the process remains stochastic, i.e. satisfy (18) and (19), with \( c \) being a free parameter. This is a result which comes from the translational invariance of the system.

Next let us consider one-body creations and annihilations of the particles. Let us introduce an operator \( n_j = \frac{1}{2} + s_j^z \). \quad (23)

In our notation, the eigenstate of \( s_j^z \) with the eigenvalue \( +1/2 \) (the eigenvalue \( -1/2 \)) corresponds to the state with a particle (without a particle) at site \( j \). The operator \( n_j \) takes the value 1 or 0 when the site \( j \) is occupied by a particle or the site \( j \) is empty, respectively. Thus \( n_j \) is called the number operator. Let us consider the case where a particle is added at site \( j \). The new state with the added particle is created by \( s_j^+ \), and the old state without the particle is removed by \( -(1 - n_j) \):

\[ \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix} - \begin{bmatrix} 0 & 0 \\ 0 & 1 \end{bmatrix} = s_j^+ - (1 - n_j). \]

(Note that these operators work non-trivially only in the subspace where \( n_j = 0 \), states in which the site \( j \) is empty, and otherwise they work as the zero operator.) Thus the term \( \Delta H_j^+ = \alpha_j [s_j^z - (1 - n_j)] \) should be added to the Hamiltonian \( H \) in (21), where \( \alpha_j \) is the rate of creation at site \( j \). Similarly, if a particle at site \( j \) is annihilated with the rate \( \beta_j \), the term \( \Delta H_j^- = \beta_j [s_j^z - n_j] \) should be added to (21). (These operators work only in the subspace where \( n_j = 1 \), states with a particle at site \( j \).) Because \( s_j^\pm = s_j^x \pm is_j^y \), these terms are the transverse and parallel magnetic fields applied to the site \( j \). Thus we find
that external fields induce the spontaneous creations and annihilations (attachments and displacements) of the particles.

Random walk with hard-core interaction: From (13) and (18) + (22), the fully stochastic random walk process with hard-core interactions is written as

\[ H_{\text{RW}} = \frac{1}{N} \sum_{j=1}^{N} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & \eta_L \\ 0 & 0 & \eta_R & 0 \end{bmatrix}_{jj+1}, \]  

(24)

where \( \eta_R/N = p_R \), \( \eta_L/N = p_L \) and \( \eta_R + \eta_L = 2 \). This operator is written by the spin operators as

\[ H_{\text{RW}} = \frac{2}{N} \sum_{j=1}^{N} \left[ \frac{1}{2}(\eta_R s_j^- s_{j+1}^+ + \eta_L s_j^+ s_{j+1}^-) + s_j^z s_{j+1}^z + \frac{1}{4} I \right]. \]  

(25)

When \( \eta_R = \eta_L = 1 \), the operator (25) is the Hamiltonian of the XXZ model (2) with \( \Delta = 1 \), i.e. the Hamiltonian of the Heisenberg model. This case is a kind of the hard-core boson system, which is originally proposed as a model for helium superfluidity (Matsubara and Matsuda, 1956).

The anisotropy \( \eta_R \neq \eta_L \) can be removed by an unitary transformation (Henkel and Schütz 1994, in which the eigenstate with the eigenvalue \( -1/2 \) is regarded as the state with a particle) provided \( \eta_R \eta_L \neq 0 \). Let

\[ V = \exp[(\log q) \sum_{j=1}^{N} j n_j], \]  

(26)

where \( n_j \) is given by (23). The commutation relation \([n_j, s_j^\pm] = \pm s_j^\pm\) and the expansion

\[ e^L A e^{-L} = A + \frac{1}{1!} [L, A] + \frac{1}{2!} [L, [L, A]] + \frac{1}{3!} [L, [L, [L, A]]] + \cdots, \]

yield \( V s_j^\pm V^{-1} = q^{\pm j} s_j^\pm \) and \( V s_j^z V^{-1} = s_j^z \). Let \( q = \sqrt{\eta_L/\eta_R} \) and one obtains

\[ V H_{\text{RW}} V^{-1} = V \left[ \frac{2}{N} \sum_{j=1}^{N} \frac{\sqrt{\eta_R \eta_L}}{2} (q^{-1} s_j^- s_{j+1}^- + q s_j^+ s_{j+1}^+) + s_j^z s_{j+1}^z + \frac{1}{4} I \right] V^{-1} = \frac{2}{N} \sqrt{\eta_R \eta_L} \sum_{j=1}^{N} \left[ \frac{1}{2} (s_j^- s_{j+1}^- + s_j^+ s_{j+1}^+) + (s_j^z s_{j+1}^z + \frac{1}{4} I) \right]/\sqrt{\eta_R \eta_L}. \]
Hence it is derived that the anisotropy of the hopping rates in the random walk process can be handled as the anisotropy $\Delta = 1/\sqrt{\eta_R/\eta_L}$ of the quantum coupling in an uniform spin chain.

**Ribosome moving on mRNA:** A ribosome is a large, complex molecule that synthesizes a protein molecule using the genetic message coded on mRNA as the template. RNA comprises four kinds of nucleotides, and a triplet of nucleotides constitutes a codon. Each possible type of codon corresponds to one species of amino acid: 61 kinds of codon lead to 20 species of amino acid, whereas three special codons indicate termination of translation. The information enclosed in the codon sequence is translated by the ribosome into the amino acid sequence of the encoded proteins.

A ribosome binds to an mRNA and begins to synthesize the protein by adding an amino acid (this is referred to as initiation). After a biochemical reaction for the elongation of the protein, the ribosomes moves forward on the track by one codon (i.e. one elongation has occurred). Finally, the ribosome reaches the termination codon and leaves the mRNA, releasing the protein (this is referred to as termination).

A number of ribosomes can be simultaneously attached to one mRNA template. A ribosome can move forward on the track provided that the next codon is not captured by another ribosome, i.e. ribosomes are moving on the mRNA template interacting via hard-core interactions. A ribosome is often treated as a molecular motor, and this collective movement process along the mRNA chain shows a correspondence with a one-dimensional driven lattice gas, or with vehicular traffic on a road.

MacDonald et al. introduced a stochastic process now known as the asymmetric simple exclusion process (ASEP), as a model for the movement of ribosomes on a mRNA (MacDonald et al. 1968; MacDonald and Gibbs 1969). The model was first introduced in the biophysical literature, and later studied from a purely theoretical viewpoint (see for example Derrida 1998).

The actual movement of a ribosome is closely coupled to its internal mechanochemical processes to synthesize a protein. Accounting for these processes, the ASEP has been generalized to have seven (Basu and Chowdhury 2007), five (Garai et al. 2009), or two (Ciandrini et al.) distinct biochemical states in each cycle. The ribosome movement is also characterized by a pause and translocation, which defines the time of its residing at a corresponding codon. The ASEP has been generalized to have one or more slow codon bottlenecks (Kolomeisky 1998; Chou and Lakatos 2004; Dong et al. 2007a; Dong et al. 2007b). The ASEP with different hopping rates associated with each site has been considered (Shaw et al. 2003; Shaw et al. 2004; Romano et al. 2009). A ribosome recycling mechanism has been introduced (Chou
2003), in which a part of the ribosome detaches at the termination site and part of them diffuses back to the initiation site. The ASEP comprising open boundaries with random particle attachments and detachments was also introduced (Parmeggiani et al. 2003, Pierobon et al. 2006). A stochastic model with a secondary structure of mRNA was introduced by von Heijine et al. (1977).

Now, let us introduce the ASEP, which is a random walk process with specified moving rates and with a continuous time variable. Let us consider a one-dimensional lattice. Each site \( j \in \mathbb{Z} \) is empty or occupied by a particle which corresponds to a ribosome. Each particle stochastically move forward or backward interacting via the hard-core interactions i.e. a particle at site \( j \) moves to the site \( j+1 \) with the rate \( p_R \) provided that the site \( j+1 \) is empty, and a particle at site \( j+1 \) moves to the site \( j \) with the rate \( p_L \) provided that the site \( j \) is empty.

Let us first assume the periodic boundary condition and consider the stochastic matrix \((17)\) with \( p_U = p_D = 0 \), and thus from \((18)\)

\[
w_3 = w_4 = \frac{1}{N}.
\]

Because \( H \) is independent of \( c \), the rates \( w_1 \) and \( w_2 \) can be taken as

\[
w_1 = \frac{1}{N}(1 - \delta) - p_R, \quad w_2 = \frac{1}{N}(1 + \delta) - p_L, \quad (c = p_L - p_R - \frac{2}{N}).
\]

These rates satisfy \((18)\) and \((19)\). The corresponding stochastic matrix is

\[
H_{ASEP} = \frac{1}{N} \sum_{j=1}^{N} \begin{bmatrix}
1 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 \\
0 & 0 & (1 - \delta) - \eta_R & \eta_L \\
0 & 0 & \eta_R & (1 + \delta) - \eta_L
\end{bmatrix}_{jj+1},
\]

\[
\Delta H_{ASEP} = \frac{2}{N} \sum_{j=1}^{N} \left[ \frac{1}{2}(\eta_R s_j^- s_{j+1}^+ + \eta_L s_j^+ s_{j+1}^-) + \frac{1}{2}(\eta_R + \eta_L)s_j^z s_{j+1}^z \right. \\
\left. - \frac{1}{8}(\eta_R + \eta_L)I + \frac{1}{4}(\eta_R - \eta_L - 2\delta)(s_j^z - s_{j+1}^z) \right].
\]

This is the ASEP with discretized time step. Because of the periodic boundary condition, the last term vanishes and the operator is independent of \( \delta \). The rates \( \delta \) and \(-\delta \) always appear pairwise in the summation \( \sum_{j=1}^{N} \), and finally give no contribution to the probability. When one set \( \eta_R = 1 - \delta \) and \( \eta_L = 1 + \delta \), the system is reduced to \((24)\) and \((25)\). In this case, the ASEP is a simple random walk process with hard-core interactions.

As a model of the movement of ribosomes, the rates are asymmetric and the open boundary condition should be introduced. With these restrictions, the expression of \( H_{ASEP} \) by spin operators have already been written by Sandow (1994, see also Alcaraz 1994). The condition
is satisfied provided $\delta = 0$. The attachment at the site $j = 1$ and the displacement at the site $j = N + 1$ are introduced by the terms $\alpha_1[s_1^+ - (1 - n_1)]$ and $\beta_{N+1}[s_{N+1}^- - n_{N+1}]$. Then with the use of the transformation $V = \exp[(\log q)\sum_{j=1}^{N+1}j\eta_j]$, which is slightly modified from (26), one obtains

$$V\Delta H_{\text{ASEP}}V^{-1} = \frac{2}{N}\sqrt{\eta_L\eta_R}\sum_{j=1}^{N}[s_j^x s_{j+1}^x + s_j^y s_{j+1}^y + \frac{1}{2}(q + q^{-1})s_j^z s_{j+1}^z - \frac{1}{8}(q + q^{-1})I]$$

$$+ \frac{1}{N}\sqrt{\eta_L\eta_R}\frac{1}{2}(q - q^{-1})(s_1^z - s_{N+1}^z)$$

$$+ \alpha_1[qs_1^+ - (1 - n_1)] + \beta_{N+1}[q^{-(N+1)}s_{N+1}^- - n_{N+1}].$$

Therefore the ASEP with asymmetric rates and with the open boundary condition is nothing but the XXZ spin chain with $\Delta = (q + q^{-1})/2$ with boundary magnetic fields. Here we find that $q$ is the parameter in the quantum group symmetry of the XXZ spin chain (Pasquier and Saleur 1990; Jimbo and Miwa 1993).

Other generalizations of the ASEP reviewed above can be handled as generalizations of spin Hamiltonians. The biochemical states can be introduced using spin operators with the spin magnitude $S$, in which the number of the eigenstates is $n = 2S + 1$, and the bottleneck or the non-uniform hopping rates correspond to non-uniform coupling constants of spin chains. The ASEP with continuous time variation is also governed by the same operator (27): its time dependence is

$$\frac{d}{dt}P(t) = (\Delta H_{\text{ASEP}})P(t),$$

where each element of $P(t)$ is equal to $P(x_1, x_2, \ldots, x_m; t)$, the probability that the system is in the configuration $\{x_1, x_2, \ldots, x_m\}$ at time $t$.

Kinesins moving on a microtubule: Kinesin is a single molecular motor observed in vitro to move along a linear microtubule template. It moves stochastically and stepwise along a one-dimensional track (for example, a review by Yildiz and Selvin 2005).

Experimental methods to measure the biochemical and biomechanical properties of a single-molecule enable us to observe the movement of a single kinesin. It was shown that kinesin moves stepwise along microtubules occasionally moving both forwards and backwards (Kojima et al. 1997). It was observed that kinesin is released spontaneously from the microtubule (Block et al. 1990), and that the increase of the load results in an increasing rate of dissociation (Coppin et al. 1997). It was suggested that two or more sequential processes dominate the biochemical cycle (Svoboda et al. 1994), and the time to force generation after release of ATP was measured (Higuchi et al.
1997). Force-velocity curves was obtained for single kinesin molecules (Svoboda and Block 1994).

Pioneering theoretical models related to the dynamics of kinesin are already known. An elementary “barometric” relation was introduced for the driving force (Fisher and Kolomeisky 1999a; b). Nearest-neighbor kinetic hopping models with arbitrary forward and backward periodic rate constants with three generalizations was introduced (Kolomeisky and Fisher 2000a). The one-dimensional random walk process with general waiting-time distributions, finite side branches, and annihilation was also considered (Kolomeisky and Fisher 2000b).

The observed movement of kinesin can be described adequately by simple discrete-state stochastic models (Fisher and Kolomeisky 2001). The model has also been applied to analyze the dynamics of myosin-V (Kolomeisky and Fisher 2003). Brownian particles moving in two or more periodic but spatially asymmetric and stochastically switched potentials have also been considered (Jülicher et al. 1997) The models have been summarized in review articles (Reimann 2002; Kolomeisky and Fisher 2007).

Let us consider a model for kinesin on a microtubel (Kolomeisky and Fisher 2000a). A kinesin is assumed to locate on a site \( j \) of a one-dimensional lattice, where \( j = 1, 2, \ldots, N + 1 \). Let us introduce an index \( k \) (\( k = 0, 1, 2, \ldots, K - 1 \)) which distinguishes the internal states of kinesin. A kinesin changes its internal state from \( k \) to \( k + 1 \) with the rate \( u_k \), and from \( k \) to \( k - 1 \) with the rate \( w_k \). A kinesin at site \( j \) in the maximum internal state \( k = K - 1 \) can move to the next site \( j + 1 \) and initialize its state as \( k = 0 \) with the rate \( u_{K-1} \). A kinesin at site \( j + 1 \) in the minimum state \( k = 0 \) can move to the previous site \( j \) and have the maximum state \( k = K - 1 \) with the rate \( w_0 \).

Let us consider the case with two internal states: the case \( K = 2 \). Each site takes one of the three possible states: \( k = 0, 1, \) and "empty". Thus let us introduce the spin operator with the spin magnitude \( S = 1 \), in which there are \( 2S + 1 = 3 \) possible eigenstates with the eigenvalues \( S^z = -1, +1, \) and \( 0 \). Let us assume that the states with \( S^z = -1, +1, \) and \( 0 \) correspond to the states \( k = 0, 1, \) and "empty", respectively. Let the generating matrix be \( H_{KF} = I + \Delta H_{KF} \), and consider \( \Delta H_{KF} \).

The hopping from the state \( k = 0 \) to \( k = 1 \) at site \( j \) is expressed as

\[
H^+_j = u_0 \left( \begin{bmatrix} 0 & 0 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}_j - \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix}_j \right) 
= u_0 \left( \frac{1}{\sqrt{2}} s^+_j \right)^2 - \left( I_j - \frac{1}{\sqrt{2}} s^+_j \frac{1}{\sqrt{2}} s^-_j \right) = u_0 (s^+_j s^-_j - I_j).
\]

The backward hopping from the state \( k = 1 \) to \( 0 \) is, in the same way, expressed as \( H^-_j = w_1 (s^-_j s^+_j - I_j) \). The hopping from the state \( k = 1 \)
at site \( j \) to the state \( k = 0 \) at site \( j + 1 \) is expressed as

\[
H_{jj+1}^+ = u_1 \left( \begin{bmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}_j \otimes \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}_{j+1} - \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}_j \otimes \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{bmatrix}_{j+1} \right)
\]

\[
= u_1 \left[ \left( \frac{1}{\sqrt{2}} s^+_j s^-_j \right)(s^z_{j+1} - \frac{1}{\sqrt{2}} s^-_{j+1}) - (I_j - \frac{1}{\sqrt{2}} s^-_j \frac{1}{\sqrt{2}} s^+_j)(I_{j+1} - (s^z_{j+1})^2) \right]
\]

\[
= -u_1 \left[ (s^-_j s^+_j)(s^z_{j+1}s^-_{j+1}) + ((s^z_j)^2 + s^z_j)(I_{j+1} - (s^z_{j+1})^2) \right],
\]

where we made use of the relations \((s^z_j)^2 + (s^y_j)^2 + (s^x_j)^2 = S(S+1) = 2\) and

\[
I_j - \frac{1}{\sqrt{2}} s^+_j \frac{1}{\sqrt{2}} s^-_j = \frac{1}{2}[((s^z_j)^2 + s^z_j].
\]

The backward hopping from the state \( k = 0 \) at site \( j + 1 \) to the state \( k = 1 \) at site \( j \) is, in the same way, expressed as

\[
H_{jj+1}^- = -u_0 \left[ (s^+_j s^-_j)(s^z_{j+1}s^-_{j+1}) + (I_j - (s^z_j)^2)((s^z_{j+1})^2 - s^z_{j+1}) \right].
\]

These operators constitute \( \Delta H_{KF} \). The operator \( H_{KF} \) is then obtained as

\[
H_{KF} = I + \sum_{j=1}^{N+1} (H^+_{jj} + H^-_{jj}) + \sum_{j=1}^{N} (H^+_{jj+1} + H^-_{jj+1}).
\]

The operator should be normalized by the maximum eigenvalue \( \lambda_0 \).

**General correspondence:** In these three examples the generation of the biological stochastic systems are written in terms of the spin Hamiltonians. The correspondence between stochastic systems and spin models are more general. Let us consider a system with \( n \) discrete internal states. The law governing changes from one state to another is written as a matrix of order \( n \). Let us derive the fact that this matrix can always be expressed by the spin operators with spin \( S \), where \( n = 2S + 1 \).

Let us consider the unit matrix \( I \) and the matrices \((s^z)^k\) \((k \in \mathbb{N})\). They are diagonal and the diagonal elements of \((s^z)^k\) are \( S^k, (S-1)^k, \ldots, (-S-1)^k \) and \((-S)^k\). The set of the matrices \( I, s^z, (s^z)^2, \ldots, (s^z)^{2S}, (s^z)^{2S+1} \) are not independent because they satisfy the eigenequation of \( s^z \), which is a polynomial of order \( 2S + 1 \). For the purpose to show the independence of \( I, s^z, (s^z)^2, \ldots, (s^z)^{2S} \), let us consider the following determi-
nant
\[
\begin{vmatrix}
1 & S & S^2 & \cdots & S^{2S} \\
1 & S - 1 & (S - 1)^2 & \cdots & (S - 1)^{2S} \\
1 & \vdots \\
1 & -(S - 1) & (-S - 1)^2 & \cdots & (-S)^{2S} \\
1 & -S & (-S)^2 & \cdots & (-S)^{2S}
\end{vmatrix}
= (-1)^{\frac{1}{2} n(n-1)} \prod_{1 \leq i < j \leq n} (z_i - z_j),
\]
where \( n = 2S + 1 \) and
\[
z_1 = S, \quad z_2 = S - 1, \ldots, \quad z_{2S+1} = -S.
\]
This is the Vandermonde’s determinant and, in our case, clearly non-zero. Hence all the diagonal matrices can be expressed as a linear combination of \( I \) and \( (s^\pm)^k \) \((k = 1, 2, \ldots, 2S + 1)\).

In the case of spin operators with the spin magnitude \( S \), it is derived from the commutation relations that the eigenstate of \( s^z \) corresponding to the eigenvalue \( M \) satisfies \( s^\pm |M\rangle = [S(S+1) - M(M+1)]^{1/2}|M\rangle \). Thus the matrix elements of \( s^\pm \) satisfy \((s^\pm)_{ij} \neq 0 \) if and only if \( j = i \pm 1 \), and \((s^\pm)_{ij} \neq 0 \) if and only if \( j = i \pm l \). Let us introduce a diagonal matrix \( P_k \) by \((P_k)_{ij} = \delta_{ki}\delta_{kj} \), i.e. \((P_k)_{kk} = 1 \) and \((P_k)_{ij} = 0 \) when \( i \neq k \) or \( j \neq k \). It is easy to convince that
\[
(P_k(s^+)_{ij} \neq 0 \quad i = k, \quad j = k + l,
(P_k(s^-)_{ij} \neq 0 \quad i = k, \quad j = k - l,
\]
and all the other matrix elements are equal to 0. Therefore arbitrary \( n \times n \) matrices can be expressed in terms of the spin operators with spin \( S \), where \( n = 2S + 1 \).

The Hamiltonian generally has the form
\[
H = \sum_{i,j} \sum_{\alpha\alpha'} J^{(\alpha\alpha')}_{mn}(s^\alpha_i)^m(s^{\alpha'}_j)^n,
\]
where \( \alpha \) and \( \alpha' \) denotes \( z, +, \) or \( - \). An external field can be introduced through the terms with the powers \((m, n) = (0, 1) \) or \((1, 0) \). Therefore all the biological systems with finite number of states and discrete law of change can find its equivalent spin model.

6 Summary and discussions

In this study, it was derived that the adhesion probabilities in a two-dimensional cell-sorting model are analytically expressed by the expectation values in the one-dimensional random walk model with pair
creations and annihilations. I believe that this is the first example in which completely different biological systems show mathematical equivalence to each other. It was also derived that the equivalencies with spin systems are general, i.e. the generation rules of stochastic movements in biological systems can always be written in terms of the lattice spin Hamiltonians. This provides a path to study biological systems using the techniques and results already obtained in the area of spin systems.

It should be noted that general correspondences between $d$-dimensional quantum spin systems and $(d+1)$-dimensional Ising-type spin systems are known to exist (Suzuki 1976). This implies that for each stochastic system in $d$-dimension with hopping, creation and annihilation of particles, there exist equivalent $(d+1)$-dimensional model with an adhesion-type structure.

Although the stochastic models can be expressed in terms of spin operators, the corresponding Hamiltonians are usually not simple. In such situations, numerical calculation techniques might be powerful, and many sophisticated techniques have been developed for the lattice spin models (see for example the series by Domb and Green 1972). Exact results also exist, for example, in the case of $\alpha = \alpha' = z$ in the one-dimensional case of (28), that are $n$-state Ising-type systems with independent one-particle creations and annihilations (Minami 1998).

The dynamics of the Ising model have been studied through the system proposed by Glauber (Glauber 1963) or Kawasaki (Kawasaki 1966). The cell-sorting model considered in this study with pair exchange probability corresponds to the Kawasaki dynamics. The dynamics of $n$-spin flip models were considered, in which the two-spin flip-model is equivalent to the XY chain apart from the boundary terms (Felderhof and Suzuki 1971). It is interesting to consider the equivalencies of dynamical properties.

The XXZ model is related to the random walk model, and therefore related to the Brownian motion. The one-dimensional XXZ model is equivalent to the six-vertex model, and it is known to demonstrate fractal structure in its configuration space (Minami 2010). The XY model with periodically varying interactions also becomes interesting from biological viewpoints.

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