Replica symmetry breaking in an adiabatic spin-glass model of adaptive evolution

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Abstract – We study evolutionary canalization using a spin-glass model with replica theory, where spins and their interactions are dynamic variables whose configurations correspond to phenotypes and genotypes, respectively. The spins are updated under temperature $T_S$, and the genotypes evolve under temperature $T_J$, according to the evolutionary fitness. It is found that adaptation occurs at $T_S < T_{RS}^S$, and a replica symmetric phase emerges at $T_{RS}^S < T_S < T_{RS}^S$. The replica symmetric phase implies canalization, and replica symmetry breaking at lower temperatures indicates loss of robustness.

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Introduction. – Biological evolution occurs through changes in genotypes and phenotypes over generations, driven by random genetic variance and natural selection. Phenotypes, such as protein expression levels or the functional structures of proteins, are the result of dynamic processes governed by the genes. Genes are changed through evolutionary course, and such genotypes are preferentially selected which produce phenotypes that afford high evolutionary fitness [1,2]. Thus, the evolution shapes developmental dynamics to produce functional phenotypes. Indeed, much attention has been focused on the field “evo-devo” (evolution-development), where the connection between developmental and evolutionary time scales is explored.

In general, the dynamic processes that shape the phenotype involve stochasticity due to thermal noise, and thus phenotypes of isogenic individuals are not necessarily identical [3–5]. For a phenotype to conserve its function, however, it must be robust to this noise, at least to some degree. Besides this robustness to noise, the adapted phenotype should be robust to genetic change to acquire evolutionary stability. The possible relationship between these two types of robustness, as well as the positive role of noise, has been recently investigated both theoretically [6–11] and experimentally [12,13].

To achieve robustness to noise, it is favorable for the dynamic adaptation process that shapes phenotypes to exhibit global and smooth attraction. Indeed, such dynamics are observed in the folding dynamics of proteins [14,15], RNA [6], protein expression dynamics governed by gene regulatory networks [16], developmental dynamics [17], and so forth. Most biological dynamics involve global, complicated interactions, as in residue interactions in proteins and in protein expression networks, and such systems, if randomly chosen, show a rugged energy landscape, as seen in spin-glass models. Thus, selection of global attraction dynamics is expected to be a result of biological evolution. In fact, transitions in dynamic processes toward increased robustness to noise and genetic change were found to occur against an increase in the noise level (temperature), where the energy landscape for the dynamics changes from being rugged to having a funnel-like structure.

Considering the above change in the dynamical process, one may expect that loss of robustness could be viewed as a transition to the spin-glass phase in statistical physics. Indeed, we provided an example that suggests such transition from numerical simulation of an evolving spin system [11]. Thus far, however, no analytic theory to
support this view has been provided, and, from a theoretical standpoint, little is understood of this transition in the evolution of robustness against noise (temperature).

Here we introduce a simple statistical-mechanics model of adaptive evolution to explain the dynamical process that shapes phenotypes. We use an adiabatic two-temperature spin-glass model in which the spin configuration and interaction matrix correspond to the phenotype and genotype, respectively. The genotype evolves to increase fitness, which is defined by the spin configuration. This approach is similar to that employed in [11], but with a slightly modified fitness function, which enables us to explore phase-space structure analytically.

With an analysis based on replica theory, we demonstrate the emergence of a replica-symmetry-breaking (RSB) transition as the temperature decreases, and show that the transition corresponds to a loss of robustness in the phenotype. Adaptive evolution of robustness is shown to occur only in the replica symmetry phase, where the interactions between two spins are fully connected. We adopt a model with global interaction, as generally adopted in random spin models. We assume that fitness is determined by a specific configuration of given t spins, called target spins here. For example, protein function depends on the conformation of a set of residues, and is indeed modeled by the configurations of target spins in [7]. More specifically, we assume that a functional phenotype is generated when the configurations of target spins satisfy \( \sum_i S_i = t \mu \) with \( \mu \) being a constant value \((0 < \mu < 1)\). The remaining \( N - t \) spins, called non-target spins, have no direct influence on the selection of individuals. The fitness function is thus defined by

\[
\Psi(J) \equiv \log \left( \delta \left( \frac{1}{\beta} \sum_{i=1}^{t} S_i \right) \right) \equiv \log \langle \psi(S) \rangle, \tag{4}
\]

where \( \delta \) is Kronecker’s delta and \( \langle \cdots \rangle \) is the thermal average with respect to the bare distribution \( \langle \psi(S) \rangle \). The latter corresponds to a quench limit in random spin models. We assume that fitness is determined by a specific configuration of given \( t \) spins, called target spins here. For example, protein function depends on the conformation of a set of residues, and is indeed modeled by the configurations of target spins in [7]. More specifically, we assume that a functional phenotype is generated when the configurations of target spins satisfy \( \sum_i S_i = t \mu \) with \( \mu \) being a constant value \((0 < \mu < 1)\). The remaining \( N - t \) spins, called non-target spins, have no direct influence on the selection of individuals. The fitness function is thus defined by

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\]
where \( \psi_\alpha = \psi(S^\alpha) \) (\( \alpha = 1, \ldots, \beta_j \)), and \( H_\alpha = H(S^\alpha|J) \) (\( \alpha = 1, \ldots, n \)), respectively. The right-hand side of eq. (6) is originally calculated for a positive integer \( n \) and \( \beta_j \) while keeping \( \beta_j \) smaller than \( n \), and then the partition function \( Z_J \) is analytically continued to non-integer \( \beta_j \) and \( n = 0 \), where \( \beta_j \) is larger than \( n \). The \( n \to 0 \) limit in our analysis does not follow the quench limit in a conventional manner of spin-glass theory, but is given as a mathematical procedure to obtain the expectation value of \( \psi(J) \). After some calculations, the total free energy can be derived as a function of replicated order parameters \{\( q_{\alpha\beta} \)\}, their conjugate parameters \{\( \bar{q}_{\alpha\beta} \)\}, and parameters \{\( \bar{S}_\alpha \)\] conjugated with \{\( \mu_\alpha \)\], where \( \mu_\alpha = \mu \) for every \( \alpha \), and the parameters are determined by self-consistent equations. The order parameter \( q_{\alpha\beta} \) corresponds to the physical quantity

\[
q_{\alpha\beta} = \frac{1}{N} \sum_{i=1}^{N} [(S^\alpha_i S^\beta_i)^2]_{\beta_j},
\]

where \([ \cdots ]_{\beta_j} \) indicate the average over the spins in the two-replicated system with \( H(S^\alpha|J) \) and \( H(S^\beta|J) \) and that over \( J \) according to the distribution equation (5) at \( \beta_j \), respectively. In the second line of eq. (7), summation over the spins is decomposed into that over the target and that over the non-target spins. It is noted that the replica number \( n \) is introduced for calculating a random average of \( \beta_j \)-th moment of \( \langle \psi(S) \rangle \) in the present study. This is in contrast to the early studies [18,19] where the replica number is given by \( T_J/T_S \).

The first to \( \beta_j \)-th replicas are subjected to the external field \( \psi_\alpha \), and the others are not. Taking the differences among the replicas into account, we introduce replica symmetric (RS) assumptions within the first \( \beta_j \) replicas and within the latter \( n-\beta_j \) replicas, and hence \( q_{\alpha\beta} \) are classified into three types depending on \( \alpha \) and \( \beta \), as

\[
q_{\alpha\beta} = \begin{cases} 
q_1, & \alpha \leq \beta_j, \beta \leq \beta_j \\
q_2, & \alpha \leq \beta_j, \beta > \beta_j \text{ or } \alpha > \beta_j, \beta \leq \beta_j \\
q_3, & \alpha > \beta_j, \beta > \beta_j.
\end{cases}
\]

The block dependence of \( q_{\alpha\beta} \) is because of the existence of the fitness function. This formula of eq. (8) is similar to that of 1-step RSB, but the block size corresponding to Parisi’s breaking parameter is given by an external parameter \( \beta_j \). For the conjugate parameters \{\( \bar{\mu}_\alpha \)\], it is assumed that \( \bar{\mu}_\alpha = \bar{\mu} \) for any \( \alpha \leq \beta_j \). With these assumptions, the RS total free energy density \( f_{RS} \) is given by

\[
f_{RS}(T_S,T_J,\mu) = -p\mu_\beta \bar{\mu} - \beta_j \beta_3^2 (q_1 - q_3) / 2 - \beta_j \beta_3^2 (q_1 - q_3) / 2 - \beta_j \beta_3^2 (q_1 - q_3) / 2
\] + (1 - p) \log \Xi(0) + p \log \Xi(\bar{\mu}),
\]

where \( p = t/N \). Here \( \Xi(w) \) is defined as the normalization constant of the distribution

\[
P(u,v;w) = e^{-u^2/2} / (\cosh(w + \sqrt{w} u) \cosh(w - \sqrt{w} u)),
\]

where \( W(u,v) = \sqrt{\beta_j^2 / \bar{q}_1 u + \sqrt{(\bar{q}_1 \bar{q}_2 - \bar{q}_1^2) / \bar{q}_1 v} \bar{q}_1 v \text{ and } \bar{q}_1, \bar{q}_2, \text{ and } \bar{q}_3 \text{ are the conjugate parameters of } q_1, q_2, \text{ and } q_3 \text{, respectively. At } \mu = 0, \text{ the free energy is identical to that of the SK model under the RS ansatz. The self-consistent equations for the order parameters } q_1, q_2, \text{ and } q_3 \text{ are given by}
\]

\[
q_1 = (1 - p)(\tanh^2(\sqrt{q_1} u) + p(\tanh^2(\mu + \sqrt{q_1} u) \bar{\mu},
\]

\[
q_2 = (1 - p)(\tanh^2(\sqrt{q_1} u) \tanh W(u,v)) + p(\tanh(\mu + \sqrt{q_1} u) \tanh W(u,v)),
\]

\[
q_3 = (1 - p)(\tanh^2 W(u,v)) + p(\tanh^2 W(u,v)),
\]

where \((\cdots)_x \) denotes the average according to the distribution (10) at \( x = w \). The conjugate parameters \( \bar{q}_i \) are given by \( \bar{q}_i = \beta_i^2 q_i \) \( i = 1, 2, 3 \). By comparing eq. (7) and eqs. (11)–(13), it is found that first and second terms of eqs. (11)–(13) come from the non-target spins and the target spins, respectively, and so \( q_i \)'s can be rewritten as the summation of the non-target and the target parts, \( q_i = (1 - p) q_i^\alpha + p q_i^\beta \) \( i = 1, 2, 3 \). The conjugate parameter \( \bar{\mu} \) is implicitly determined by the equation

\[
\mu = (\tanh(\bar{\mu} + \sqrt{q_1} u)) \bar{\mu},
\]

where \( \mu \) is a given parameter in the fitness function and the right-hand side depends on \( \bar{\mu} \). The stability analysis for the RS solutions presented by de Almeida and Thouless (AT) [22] affords three conditions [23]:

\[
AT_1 \equiv 1 - \beta_3^2 (1 - 2q_1 + r_{11}) > 0,
\]

\[
AT_2 \equiv \left\{ 1 - \beta_3^2 \left( 1 - (\beta_j + 4) q_3 + (\beta_j + 3) r_{33} \right) \right\}
\times \left[ \beta_j + 1 - \beta_3^2 \left( (\beta_j + 1)(1 - q_3) + (\beta_j - 1)(q_1 - r_{22}) \right) \right]
+ 2 \beta_j (\beta_j + 2) \beta_3^2 (q_2 - r_{23})^2 > 0,
\]

\[
AT_3 \equiv 1 - \beta_3^2 (2q_3 + r_{33}) > 0,
\]

where

\[
r_{11} = (1 - p)(\tanh^4(\sqrt{q_1} u)) + p(\tanh^4(\mu + \sqrt{q_1} u)) \bar{\mu},
\]

\[
r_{22} = (1 - p)(\tanh^2(\sqrt{q_1} u) \tanh^2 W(u,v)) + p(\tanh^2(\mu + \sqrt{q_1} u) \tanh^2 W(u,v)) \bar{\mu},
\]

\[
r_{23} = (1 - p)(\tanh(\sqrt{q_1} u) \tanh^3 W(u,v)) + p(\tanh(\mu + \sqrt{q_1} u) \tanh^3 W(u,v)) \bar{\mu},
\]

We introduce an expectation value for the target magnetization \( m_t = \langle \sum_{i=1}^N S_i \rangle / t_{\beta_j} \). When \( m_t = 0 \), the averaged
fitness function \( \Psi(J) \) is also equal to 0. Hence, the adaptation phase is the region satisfying \( m_t > 0 \). Following the replica method, the target magnetization is given by

\[
m_t = \langle \tanh W(u, v) \rangle_\mu, \tag{18}\]

which indicates that when \( q_2 = 0 \) and hence \( W(u, v) = \sqrt{q_3}v \), the target magnetization is also equal to 0. Thus, the parameter region with \( q_2 > 0 \) and \( q_3 = 0 \) corresponds to the adaptation and non-adaptation phase, respectively.

**Results.** – The phase diagram on the \( T_S-T_J \) plane at \( p = 0.2 \) is shown in fig. 1. Here we focus on the case with \( \mu = 1 \), in which the interactions that make the target spins completely aligned are preferred, and set \( \mu \) to be sufficiently large to satisfy the self-consistent equation (14) with \( \mu = 1 \). We define the transition temperatures \( T_S^{q_2} \) and \( T_S^{q_3} \) such that \( q_2 \) and \( q_3 \) are positive or zero, respectively, whereas \( q_1 \) takes a non-zero value at any finite \( T_S \) because the function \( \Phi_\alpha \) for \( \alpha < \beta \) plays a role of a symmetry-breaking field. At \( T_J > 1 \), the transition temperature \( T_S^{q_2} \) is equal to 1 and the temperature \( T_S^{q_2} \) is smaller than \( T_S^{q_3} \) in a larger region.

A preliminary Monte Carlo simulation indicates that the transition for \( q_2 > 0 \) and RSB occurs at \( T < T_S^{q_3} = 1 \) [23]. At \( T_J \leq 1 \), \( T_S^{q_3} \) coincides with \( T_S^{q_2} \), whereas RSB occurs at a lower temperature at which \( AT_3 = 0 \). Thus, the adaptation phase \( T_S < T_S^{q_2} \) consists of RS and RSB phases, separated by the line \( AT_3 = 0 \). The RS adaptation phase is thermodynamically stable at \( T < T_S^{RS} \), whereas \( T_S^{RS} \), given by \( AT_3 = 0 \), is the boundary between the RSB and RS phases, and \( T_S^{RS} \) is the transition temperature for \( q_2 \) and \( q_3 \). \( T_S^{RS} \) merges at \( T_S = T_J \) for any \( T_J \) at \( p = 0 \). In this limit, the present model is identical to the SK model whose spin-glass transition with RSB occurs at \( T_S = T_J \) independent of \( T_J \).

To distinguish the interactions evolved in the RS phase from those in the RSB phase, we calculate the equilibrium frustration parameters. Indeed, the frustration characterizes the interactions in spin glasses and related random spin models. It is defined as the product of \( J_{ij} \)’s along a minimal loop whose length is equal to three in the fully connected model studied in this work. When the interactions among the three spins satisfy \( J_{ij}J_{jk}J_{ki} < 0 \), their local energy cannot be lowered simultaneously, and such interactions are said to be frustrated [20,24]. In the present model, the target spins play a distinct role because their configuration determines the fitness function. Hence, by distinguishing the target spins from others, we introduce the frustration parameters as

\[
\Phi_1 = \frac{1}{C_2^t} \sum_{1 < j \leq t} [J_{ij}]_{\beta_j}, \tag{19}\]

\[
\Phi_2 = \frac{1}{C_2^t(N-t)} \sum_{1 < j \leq t} \sum_{k=1}^N [J_{ik}J_{jk}]_{\beta_j}, \tag{20}\]

where \( C_2^t \) is the number of interactions between the target spins. When \( \Phi_1 = 0 \), the interactions between the target spins are randomly distributed; however, when \( \Phi_1 > 0 \), ferromagnetic interactions are dominant. The ferromagnetic interactions between the target spins energetically favor the spin configuration with \( m_t = 1 \). The frustration parameter \( \Phi_2 \) is the average correlation of the interactions between the target and non-target spins. When the interactions that couple a non-target spin \( S_t \) to the target spins \( S_t \) and \( S_j \) satisfy the condition \( J_{ik}J_{jk} > 0 \), the target configuration \( S_t = S_j = 1 \) is stable irrespective of \( S_t \). Therefore, the finite frustration parameter \( \Phi_2 > 0 \) implies that the configuration with \( m_t > 0 \) is energetically supported by the interactions between target and non-target interactions. Under the RS ansatz, the frustration parameters are calculated as

\[
\Phi_1 = \frac{\beta_S \beta_J}{\sqrt{N}} (\mu^2 - m_t^2), \tag{21}\]

\[
\Phi_2 = \frac{\beta_S \beta_J}{N} \left\{ (\beta_J - 1)q_{i}^n \mu^2 - 2\beta_J q_{i}^n \mu m_t + (\beta_J + 1)q_{i}^n m_t^2 + (\mu^2 - m_t^2) \right\}. \tag{22}\]

Here, the coefficients \( N^{-1/2} \) and \( N^{-1} \) reflect the change in the order of the interactions into \( O(N^{-1/2}) \) terms through evolution [25].

As seen in fig. 2, for any \( p \), the frustration parameters \( \Phi_1 \) and \( \Phi_2 \) increase with a decrease in \( T_S \) down to \( T_S = T_S^{RS} \). However, with a further decrease in \( T_S < T_S^{RS} \), \( \Phi_1 \) and \( \Phi_2 \) decrease. Thus, frustration is minimal at
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![Graph](image)

**Fig. 2**: (Color online) $T_S$-dependence of the frustration parameters $\Phi_1$ (a) and $\Phi_2$ (b) at $T_J = 0.2$. The vertical axes in (a) and (b) are rescaled with $\sqrt{N}$ and $N$, respectively. The RS transition temperature of each $p$ coincides with the cusp point of the frustration parameters. The RSB transition temperature, which weakly depends on the value of $p$ shown here, is indicated by the dashed lines.

around the transition temperature $T_S^{RS}$. The configurations of the interactions evolved in the intermediate temperature range $T_S^{RS} < T_S < T_S^{RSB}$ have smaller frustration in the interactions between target spins and those between target and non-target spins. This result is consistent with the behavior of the energy, which takes a minimum value in the less frustrated region, $T_S^{RSB} < T_S < T_S^{RS}$ [23].

The behavior of the frustration parameters is consistent with the result shown in [11]. The transition to reduce frustration at an intermediate temperature $T_S$ can be understood as the transition from RS to RSB phase by the statistical-mechanical analysis.

**Summary and discussion.** – In summary, we employed a spin-glass model of adaptive evolution to discuss evolutionary robustness in terms of statistical physics. Our analysis showed the existence of two kinds of adaptation phases, an RS adaptation phase at $T_S^{RSB} < T_S < T_S^{RS}$ and an RSB adaptation phase at $T_S < T_S^{RS}$. The equilibrium properties of the interactions were characterized by the frustration parameters, which showed that the RS adaptation phase energetically supports the target configurations by suppressing frustration in the evolved interactions.

Next we discuss the biological relevance of our results. An evolved system in the RS phase is robust to noise in the dynamic processes and to genetic change. The relaxation dynamics of spins to the equilibrium state is generally supposed to progress smoothly without becoming stuck at any metastable states. In the RS phase, the adapted phenotype, that is, the target spin configuration, is a unique stable state that is reachable from any initial condition after a short time of relaxation. This dynamical process agrees well with that of the funnel-shaped energy landscape in protein folding [14,15], as is also observed in evolution dynamics in biology [16,17]. Furthermore, the self-averaging property in the RS phase guarantees an identical equilibrium distribution of the phenotype even if the genotype $J$ is distributed around the evolved point. An identical phenotype is generated irrespective of genotypic variance, which is known as genetic canalization [26]. However, phenotypic robustness is lost at lower temperatures by RSB, as represented by the appearance of a continuous overlap function. Here, the relevance of the RS phase corresponds to the robustness to shape the phenotype and the robustness to genetic change for mutation. As for evolution to gain novelty or speciation, some instability to bifurcate the phenotype will be necessary, for which the transition to the RSB phase may be also important. To summarize, we showed the relevance of thermal noise in creating funnel-like dynamics and canalization in evolution, which provide robustness to noise and mutation, respectively. This transition toward increased robustness with an increase in temperature is represented as a statistical-mechanical transition from the RSB to the RS state.

Finally, despite the use of a simple statistical-physics model of interacting spins, we expect our findings to hold true in other problems involving evolutionary and developmental dynamics. In addition, the proposed replica formalism could function as a theoretical basis for understanding the evolution of robustness in general.

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