

How Learning Can Guide Evolution of Communication

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Abstract

The Baldwin effect is known as a possible scenario of the genetic acquisition process of a learned trait without the Lamarckian mechanism. However, it is still controversial how learning can facilitate evolution in dynamically changing environments caused by internal factors. Our purpose is to clarify whether and how learning can facilitate evolution in dynamic environments which arise from communicative interactions among individuals. We constructed a simple computational model for the evolution of communication ability and its phenotypic plasticity. In the model, the levels of adaptive communication, which correspond to the expected fitness value when the communication results in success, of signalling and receiving processes are determined by different sets of traits under the assumption of the correlation between their fitness and the effects of epistatic interactions among traits. A communication is successful only when the levels of the signaller and the receiver are the same, and the individuals try to improve their communication levels through the learning process in which the values of plastic traits can be modified from their genetically determined values. The evolutionary experiments clearly showed that the Baldwin effect repeatedly occurred and facilitated the adaptive evolution of communication in this type of dynamic environments.

Introduction

The Baldwin effect (Baldwin, 1896, 1902) and the role of phenotypic plasticity in evolution have been drawing much attention in evolutionary studies (West-Eberhard, 2003; Crispo, 2007). The Baldwin effect is typically interpreted as a two-step evolution of the genetic acquisition of a learned trait without the Lamarckian mechanism: individuals that have successfully adapted their own trait to the environment through their lifetime learning processes occupy the population (1st step), and then the evolutionary path finds the innate trait that can replace the learned trait (2nd step) because of the cost of learning (Turney et al., 1996; Maynard-Smith, 1987). The second step is also known as genetic assimilation (Waddington, 1953), or a kind of genetic accommodation (West-Eberhard, 2003; Crispo, 2007).

Since the study by Hinton and Nowlan (Hinton and Nowlan, 1987), the computational approaches on this effect

have contributed to understanding of how learning can affect evolution. An important finding of these studies is that the balances between the benefit and cost of learning can smooth the fitness landscape, and as a result, can either facilitate or slow down the adaptive evolution. Especially, it has been reported that there can be situations in which learning is not always beneficial for genetic evolution (Mayley, 1997; Paenke et al., 2006). For example, if there is no cost for learning an adaptive trait, there is no difference in the fitness between the learned one and the genetically acquired one. In this case, the learning behavior can retard the genetic evolution of such a trait because the selection pressure cannot distinguish between these traits. Thus, it is an important issue how learning can become necessary or unnecessary for adaptive genetic evolution depending on various states of a population and its environment.

Recently, we discussed whether and how learning can facilitate the adaptive evolution of population on rugged fitness landscapes (Suzuki and Arita, 2007b). We constructed a simple fitness function that represents a multi-modal fitness landscape as typically illustrated in Fig. 1, in which there is a correlation between the adaptivity of individual and the effects of epistatic interactions among its traits. The evolutionary experiments of the individual traits and their phenotypic plasticity on this landscape clearly showed that the Baldwin effect repeatedly occurred through the evolutionary process of the population, and facilitated its adaptive evolution as a whole.

Also, the effects of learning on evolution have been discussed in the context of dynamically changing fitness landscapes. In such situations, we can expect that more complex scenarios of interactions between evolution and learning emerge because the balances between the benefit and cost of learning also change dynamically. While several studies focused on the effects of changes in the environmental conditions caused by the external factors (Sasaki and Tokoro, 1997; Ancel, 1999), we can also assume more complex situations in which the fitness landscapes can be changed by internal factors (Suzuki and Arita, 2004). The evolution and emergence of communication is one of the typical cases of

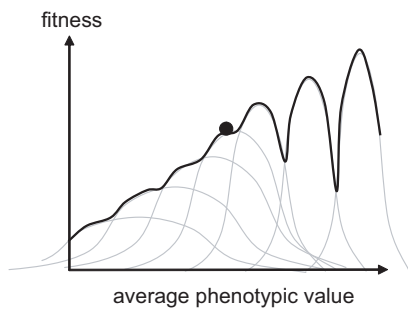


Figure 1: A rough image of the fitness landscape. The horizontal axis corresponds to the average phenotypic value among all phenotypes. Each peak (in gray) corresponds to the fitness which can be acquired when each trait group becomes adaptive. The black line is the actual fitness. As the fitness of the population increases, it tends to need to cross deeper valleys to reach the next optimum.

this situation because the fitness of the individuals are determined by the benefit of the successful communications among them. This topic has been discussed in ALife studies (Noble et al., 2001) from various viewpoints such as the emergence of lexicons through language games among agents (Steels, 1996), the adaptivity and diversity of the mating signals (Werner and Todd, 1997), the emergence of communication in embodied agents (Nolfi, 2005), the complexity of the birdsongs grammar (Sasahara and Ikegami, 2007) and so on. Also, several studies discussed the effects of learning on evolution in the context of language evolution (Arita and Koyama, 1998; Kirby, 2002; Munroe and Cangelosi, 2002; Yamauchi, 2007; Watanabe et al., 2008). For example, Watanabe et al. recently constructed a computational model into which both cultural learning of language and genetic evolution of language ability are incorporated (Watanabe et al., 2008). They found that the factors specific to language evolution (such as adaptive shift in language or overlearning to a variety of parents) are important for the occurrence of the second step in the Baldwin effect.

Among various roles and aspects of communication these previous studies have focused on, the frequency dependence of the individual fitness is one of the common key mechanisms in the evolution of communication. Here, we assume a communication as a process in which one individual generates and sends a kind of signals, then another individual receives and interprets that signal, which can potentially increase the fitness of both individuals. For example, if the individuals can correctly interpret the signals generated by conspecific ones, there is a positive frequency dependent selection on them in that the fitness of such individuals increases as they become more common. This selection pressure facilitates the increase in the number of them in the population, and thus increases the communicative coherence in

the population. Nowak discussed the evolution of language (grammar) by using a simple mathematical model in which the language of each individual can genetically or culturally evolve depending on the success in communication with other individuals (Nowak et al., 2001). The results showed that if the accuracy of the language acquisition through genetic or cultural evolution exceeds a certain threshold, the dominant language emerges as a result of positive frequency dependent selection on that language. However, it is expected that once the population is occupied by such individuals, new or different individuals are difficult to express their adaptivity and invade into the population even when their communication is more adaptive than the existing one because of the strong positive selection pressure on the existing individuals.

Furthermore, we focus on the difference in the processing mechanisms between signalling and receiving behaviors, which has often been overlooked in previous studies. The generation and interpretation of a signal are different ecological and cognitive behaviors and the individuals use the different set of traits for generating and sending a signal from that for receiving and interpreting it in general. In addition to the fact that animals have different phonatory and auditory organs, it is also known that the generation and interpretation ability of human language depend on different parts of the human brain such as Broca's and Wernicke's areas in the cortex although there are strong interactions between them (Deacon, 1997). It means that these mechanisms can evolve separately at least in part, and thus the individuals are not always able to correctly interpret the signal generated by the individual itself or conspecific ones. The frequency dependent selection works negatively on such communicatively incoherent individuals. However, how learning can affect evolution under the assumption of these dynamic factors has not been clearly discussed so far.

Our purpose is to clarify how learning can facilitate evolution in dynamically changing environments caused by internal factors. For this purpose, we constructed a simple computational model for the evolution of communication ability and its phenotypic plasticity by using the fitness function adopted in (Suzuki and Arita, 2007b). In the model, the levels of adaptive communication, which is the expected fitness value when the communication results in success, of signalling and receiving processes are determined by different sets of traits under the assumption of the correlation between their fitness and the effects of epistatic interactions among traits. The communication is successful only when the communication levels of the signaller and the receiver are the same, and the individuals try to improve their communication levels through the learning process in which the plastic traits can be modified from their genetically determined values. The evolutionary experiments clearly showed that the Baldwin effect repeatedly occurred and facilitated the adaptive evolution in this kind of dynamic environments.

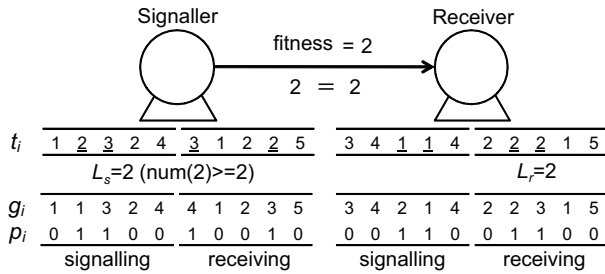


Figure 2: Example of genetic information and communication ($M=5$). The underlined values in t are plastic traits.

Model

The level of adaptive communication

There are N individuals in a population and each individual has $2M$ traits t_i ($i=0, \dots, 2M-1$) as shown in Fig. 2. Each gene g_i ($i=0, \dots, 2M-1$) in a $2M$ -length chromosome GI represents the initial value of the corresponding trait t_i which consists of an integer value within the range $[1, M]$. Also, each individual has another $2M$ -length chromosome GP which decides whether the corresponding trait is plastic ("1") or not ("0"). Each trait t_i whose corresponding bit p_i in GP equals to "1" can be changed through the communication process.

Among $2M$ traits, the former part of M traits determines the cognitive ability for generating and sending signals to others, and the latter part of M traits determines the cognitive ability for receiving and interpreting signals from others. Thus, this model can be regarded as a coevolutionary model of traits for sending and receiving signals. Here, we define the individual's level of adaptive communication of signalling (receiving) a signal L_s (L_r) as follows:

$$L_s(L_r) = \arg \max(f(n)), \quad (1)$$

$$f(n) = \begin{cases} n & \text{if } \text{num}(n) \geq n, \\ 0 & \text{otherwise,} \end{cases} \quad (2)$$

where $\text{num}(n)$ is the number of traits of which phenotypic value is n among the former (latter) half of M traits. $\arg \max(f(n))$ is the value of n which maximizes the function $f(n)$. This function is basically similar to the one adopted in (Suzuki and Arita, 2007b), and typically describes the following situation: The corresponding M traits of the individual are divided into several groups each in which the phenotypic values are identical. The trait group of n expresses its ability for sending (receiving) the signal of the level n if its group size ($\text{num}(n)$) is greater than or equals to n . The actual level of adaptive communication is defined as the highest value among adaptive trait groups. Fig. 2 shows an example of the levels of adaptive communication. Eq. (1) and (2) show that the higher the level of a trait group is, the larger its minimum size that is needed

Table 1: Example of the set of pairs ($N=8$). Each number represents the serial number of the individual.

Signaller	2	1	7	4	6	3	5	8
Receiver	8	7	3	1	2	5	6	4

for its ability to express becomes. The increase in the minimum size means that such a group becomes difficult to be acquired because it needs interactions with larger number of phenotypes. Thus, there is a positive correlation between the level of adaptive communication and the effects of epistatic interactions.

Communication and lifetime learning

In each generation, the N pairs of a signaller and a receiver are randomly arranged under the condition that each individual becomes a signaller once and also becomes a receiver once as shown in Table 1. The communication is successful only when the communication level of the signaller (L_s) and the receiver (L_r) are the same. Both individuals obtain the following fitness value:

$$\text{fitness} = \begin{cases} L & \text{if } L_r = L_s (= L), \\ 0 & \text{otherwise,} \end{cases} \quad (3)$$

where L is the shared level between the signaller and the receiver. Fig. 2 shows an example image of success in communication. The individuals obtain the fitness value 2 because both communication levels of signaller and receiver are 2.

For each pair, the $C + 1$ steps of a learning and a communication are conducted. In the initial step, the fitness is evaluated by using the initial communication levels of the signaller and the receiver, which are determined by the initial phenotypic values g_i . Then, during the C steps, both individuals try to communicate by using their corresponding traits t_i all of which phenotypic values are determined by the following equation:

$$t_i = \begin{cases} g_i + \text{rand}() & \text{if } p_i = 1, \\ g_i & \text{otherwise,} \end{cases} \quad (4)$$

where $\text{rand}()$ is the function that returns a randomly selected value from $\{-1, 0, 1\}$. Note that, if a generated phenotypic value exceeds its domain, another randomly selected value is added to the initial value. This equation shows that the values of plastic traits can slightly deviate from their genetically specified values at each step.

The actual fitness of the individual at each step c ($c = 1, \dots, C + 1$) is defined as the highest value among all c fitness values which are previously measured during the communications in each pair. It means that, in each step, the pairs first try to communicate by using the sets of generated traits, and then adopt the most adaptive trait sets so far.

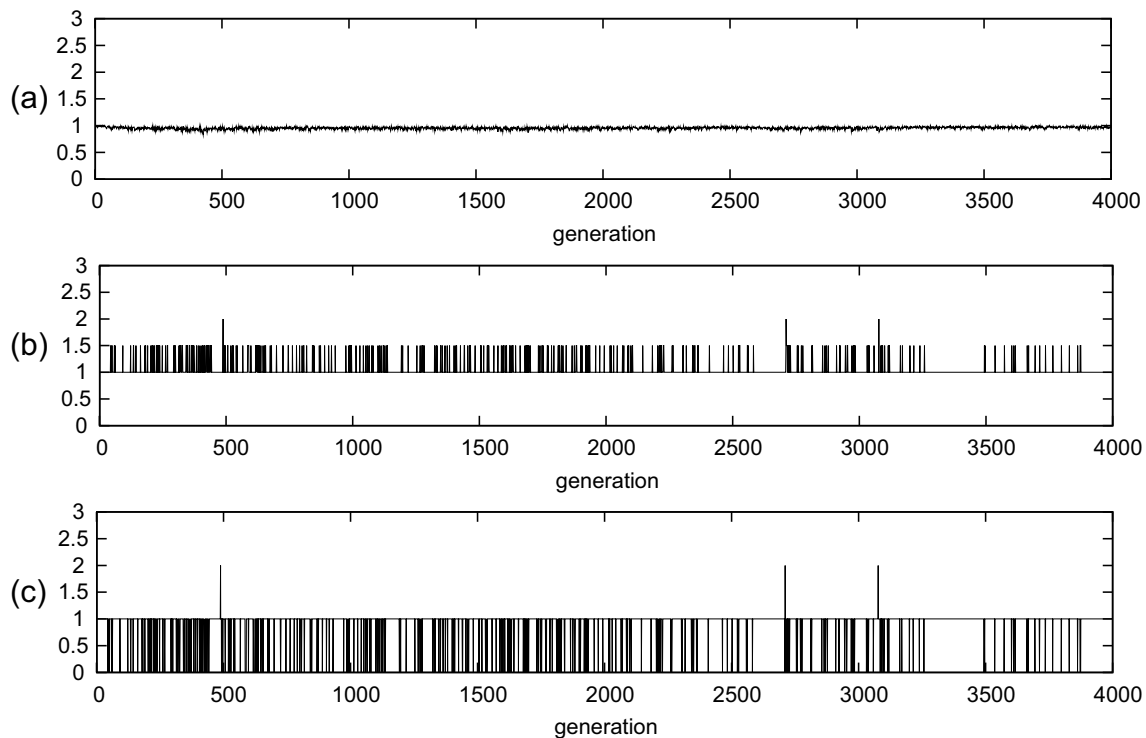


Figure 3: Evolutionary dynamics without learning ($C=0$). (a) Average lifetime (innate) fitness. (b) Lifetime (innate) fitness of the best individual. (c) Potential fitness of the best individual.

Evolution

This learning and communication process of $C + 1$ steps is conducted in all pairs. The lifetime fitness of each individual, which is used for reproductive process, is defined as the average among the fitness values in its all participating steps. Also, so as to measure the innate adaptivity of each individual, we pick up the (genetically determined) fitness values at the initial step in its all participating processes, and defined the average among them as the innate fitness.

The offsprings in the next generation are selected by the “roulette wheel selection” (in which the probability that an individual will be chosen as an offspring is proportional to its lifetime fitness) from the current population. Then, every gene of all offsprings is mutated with a probability p_{mi} for GI and p_{mp} for GP respectively. A mutation in GI adds a randomly selected value from $\{-1, 1\}$ to the current value. If a generated value exceeds its domain, another mutation is operated on the original value again. A mutation in GP flips the current binary value.

Results

We conducted evolutionary experiments using the following parameters: $N=200$, $M=10$, $p_{mi}=0.002$ and $p_{mp}=0.005$. The initial population was generated on condition that initial values in GI were 1 and the genetic values in GP were

randomly decided. We adopted this initial condition so as to observe the adaptive evolution from the state in which the individuals have established a successful communication but their level is the lowest.

Experiments without learning

First, we conducted experiments without learning process ($C=0$). Fig. 3 (a) shows a typical example of the evolution of the lifetime fitness over 4000 generations. The horizontal axis represents the generation, and the line shows the average lifetime fitness at each generation. In this case, the lifetime fitness is the same as the innate fitness. We see that the average lifetime fitness did not increase from the initial value 1.0, thus the population was never able to improve its shared communication level.

We also depicted the lifetime fitness of the best individual (who has the best lifetime fitness among individuals in each generation) in Fig. 3 (b), and its potential fitness in Fig. 3 (c). The potential fitness is the expected value of the fitness when the individual tries to communicate with the focal individual itself. In Fig. 3 (b), we see that the lifetime fitness was basically 1.0 but often increased to 1.5. It means that there appeared several adaptive individuals who succeeded in establishing higher communication level of 2 once during their lifetime, but they could not invade into the population. There are supposed to be two factors for this phenomenon.

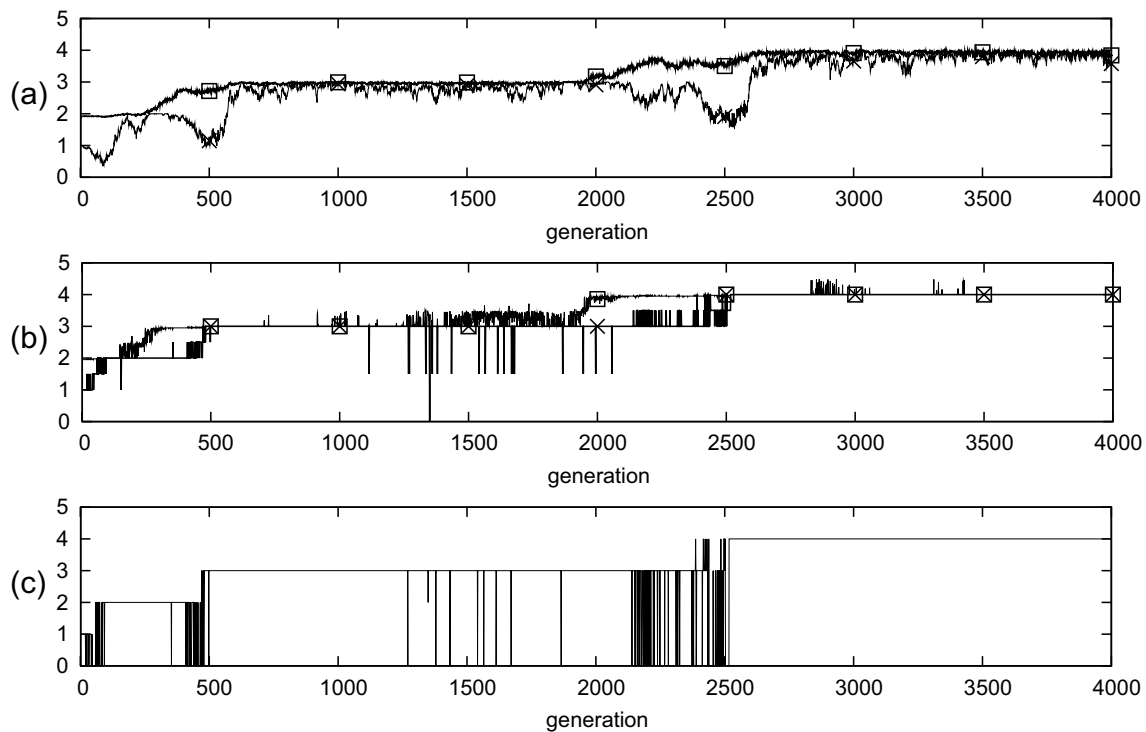


Figure 4: Evolutionary dynamics with learning ($C=20$). (a) Average lifetime (upper) and innate (lower) fitness. (b) Lifetime (upper) and innate (lower) fitness of the best individual. (c) Potential fitness of the best individual.

The first is the strong positive frequency dependent selection on majority individuals. The appeared individuals mostly fail in communication and disappear at the next generation because they rarely have another chance to meet a similar partner again because they are minority. The second is the negative selection pressure on them caused by the incoherence of their communication levels between signalling and receiving processes. As we see in Fig. 3 (c), their potential fitness was 0. It means that the increase in their proportion rather decreases their own fitness. In addition, we also observe that both best lifetime and potential fitness sometimes reached 2; but such individuals also failed to invade. This is supposed to be due to the fact that the effect of the first factor was quite strong even when the second factor was resolved by chance.

We can say that the population is never be able to improve its shared communication level due to these strong frequency dependent selection pressures if the individuals do not learn.

Experiments with learning

Next, we conducted experiments with learning. Figure 4 shows the typical transitions of the lifetime, innate and potential fitness in case of $C=20$.

Fig. 4 (a) clearly shows that the average lifetime fitness gradually increased to 4.0. How could the population suc-

cessfully increase its shared level of adaptive communication despite the fact that the population was never able to increase in the case without learning? This adaptive evolution was due to the repeated occurrences of the Baldwin effect. In Fig. 4 (a), we see the several transitions of the average fitness through which the lifetime fitness increased while the innate fitness decreased, and then the innate fitness subsequently caught up with the lifetime fitness. Each transition can be regarded as a single occurrence of the Baldwin effect.

Here, take the evolution of the population from around 1800th to 2700th generation for example. Around the 1800th generation, both the average lifetime and innate fitness is almost 3.0; all individuals innately established the adaptive communication level of 3. From around 1900th to 2500th generation, the lifetime fitness slowly increased to about 3.5, and the innate fitness gradually decreased. This phenomenon can roughly be regarded as the first step of the Baldwin effect in that the adaptive property of the whole population became dependent on learning process.

The transitions of the lifetime, innate and potential fitness of the best individual in Fig. 4 (b) and (c) give us more detailed information about the evolutionary dynamics of the population during this period. From the 1900th generation, the best lifetime fitness increased to almost 4.0 while the best innate fitness basically remained 3.0 but sometimes

fluctuated. It shows that these best individuals could improve their communication level through learning without discarding successful communications with the majority individuals. It is because that they start to communicate with the level 3 at the initial step, which is coherent with the communication level of the majority individuals, and then try to establish higher level of adaptive communication through learning depending on the level of the partner. Thus, their fitness are basically larger than those of majority individuals 3.0. This benefit of learning enabled these individuals to gradually invade into the population. This can be regarded as the typical first step of the Baldwin effect in that the individuals which could obtain higher level of communication through learning process occupied the population.

Furthermore, if we look at the fluctuation of the best innate fitness in detail, we see that it gradually tended to increase to 3.5 especially after the 2150th generation. This means that as the individual of which the innate levels of signalling and receiving were 3.0 and 4.0 (or 4.0 and 3.0) became more adaptive and invaded into the population. In this model, the more quickly an adaptive communication level is established, the larger the lifetime fitness becomes because it is defined as the average values over all steps. Thus, when the most of individuals can express the communication levels of 4 through learning process, it becomes beneficial for the individuals to genetically acquire the communication level of 4 because they can establish adaptive communications more quickly. In this sense, there is the implicit cost of learning in this model.

We also see the gradual decrease in the average innate fitness and it became about 1.5 at around the 2500th generation as shown in Fig. 4 (a). This is due to the decrease in the potential fitness of the best individuals as shown in Fig. 4 (c). The increase in their number brought about the decrease in the expected innate fitness because they cannot establish the communication with each other without the help of learning. In this sense, the population became more strongly dependent on learning process during the latter generations of this step despite that the genetic assimilation of either level of communication occurred as explained above.

Finally, when such individuals occupied the population, the individuals of which both communication levels of signalling or receiving were 4.0 appeared at around the 2500th generation and then rapidly occupied the population until about the 2700th generation. Both the innate and potential fitness caught up with the lifetime fitness. This is also due to the cost of learning explained above. We can say that the typical second step of the Baldwin effect occurred during this period in that the established communication level of 4 through learning in the first step became genetically acquired in this step completely.

We observed the similar scenarios of the Baldwin effect around the 1-200th and the 250-650th generations, and each process brought about the increase in the communication

level of the whole population. In other words, the result of the Baldwin effect became the scaffold for the next Baldwin effect to occur. We also observed that each scenario took longer generations as the lifetime fitness increased because of the increase in the epistasis of adaptive trait group. It also should be noted that when we conducted the experiments with the condition in which all traits were always plastic, it tended to take longer generations for the Baldwin effect to occur (not shown). This means that the evolution of the phenotypic plasticity has an important role for the occurrence of these scenarios although we did not observe significant increase and subsequent decrease in the proportion of plastic traits in our model.

As a whole, we can say that the Baldwin effect repeatedly occur and facilitate the adaptive evolution in this kind of a dynamic environment.

Conclusion

Hinton and Nowlan's pioneering work (Hinton and Nowlan, 1987) clarified that learning can facilitate the evolution on a "needle in a haystack" fitness landscape, and our previous work (Suzuki and Arita, 2007b) also showed that the Baldwin effect also facilitate evolution on a static but rugged fitness landscape as in Fig. 1. In this paper, we further discussed whether and how leaning can facilitate evolution on dynamically changing fitness landscapes which arise from communicative interactions among individuals. We have constructed a simple evolutionary model of the adaptive communication levels and their phenotypic plasticity in which the levels of signalling and receiving processes are determined by different sets of traits under the assumption of the correlation between their adaptivity and the effects of epistatic interactions among traits.

The evolutionary experiments showed that the population with learning successfully increased its shared level of adaptive communication while the population was never able to increase in the case without learning. Here we summarize the observed scenario of evolution by using an image of transition of the population on the dynamic fitness landscape in Fig. 5. The innate communication levels of each individual is represented as a connected set of a circle (signalling) and a square (receiving) filled in dark gray, and the x-axis corresponds to the value of their levels (L or $L + 1$). The learned level of the individual is also represented as an open circle or square, which is connected with the innate one. Each arrow represents the communication between two individuals. The vertical axis roughly represents the fitness of the individuals which has corresponding level of adaptive communication.

Let us start from the state in which all individuals have innately established the adaptive communication level of L as shown in Fig. 5 (i). In this state, the population have converged to a single peak of the level L . The individuals which can improve their level from L to $L+1$ through learning process invade into the population as in Fig. 5 (ii). It is because

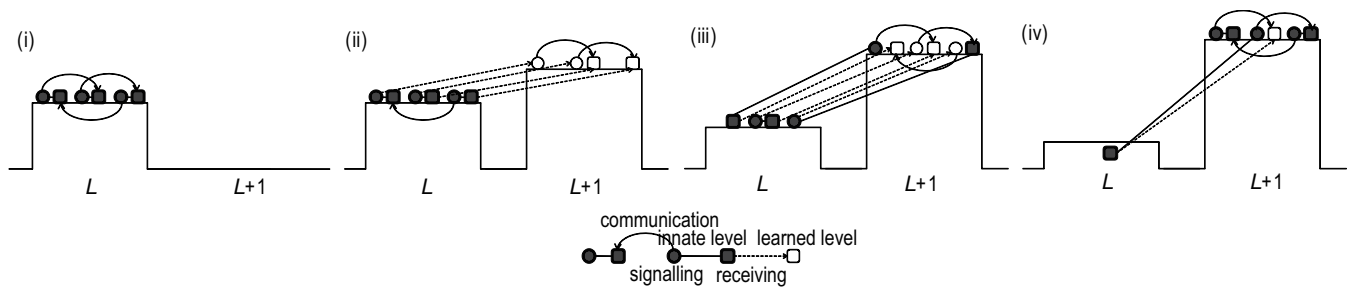


Figure 5: An image of transition of the population on the dynamic fitness landscape.

that such individuals can improve their communication level without discarding successful communications with the majority individuals. This corresponds to the phenomenon that the individuals reach out one of their communication levels to another peak of the level $L+1$ by using their phenotypic plasticity.

When the most of individuals come to establish the communication levels of $L+1$ through learning process, the individuals which innately acquired either level of $L+1$ gradually invade into the population due to the implicit cost of learning as in Fig. 5 (iii). During this process, the peak of the level $L+1$ gradually becomes higher and that of the level L becomes lower because the individuals have begun to innately use the communication level of $L+1$. At the same time, the innate fitness decreases because they are communicatively incoherent.

Finally, as in Fig. 5 (iv), the individuals of which both innate levels are $L+1$ occupy the population. The genetic assimilation of learned traits completely occurs and the peak of the level L disappears at last. This scenario can repeatedly occur and an occurrence of the Baldwin effect can become the scaffold for the next Baldwin effect to occur. This implies that the repeated occurrences of the Baldwin effect might be a general phenomenon which can emerge in both static and dynamic environments.

As explained before, the Baldwin effect has sometimes been discussed in the context of language evolution (Pinker and Bloom, 1990; Nowak et al., 2002; Kirby, 2002). Languages are composed of several levels of syntactic representations as Chomsky clarified (Chomsky, 1957). The level of communication in this model corresponds to a kind of finely classified ones of such syntactic representations. Pinker and Bloom pointed out that comprehension abilities do not have to be in perfect synchrony with production abilities because comprehension can use cognitive heuristics to decode word sequences even in the absence of grammatical knowledge, and a selection pressure on such an adaptive decoding process bring about a kind of innate grammatical module through the Baldwin effect (Pinker and Bloom, 1990). The process in which the learned level for receiving becomes innate one can be regarded as an example of such scenario.

Dennett points out that the Baldwin effect is essential to explain the genetic acquisition process of a complex trait such as the innate ability for language acquisition, which is impossible to acquire by evolution alone (Dennett, 2003). He regards Hinton and Nowlan's experimental result (Hinton and Nowlan, 1987) as a typical case of such a scenario. Our results further supports in part his claim in that the Baldwin effect can occur in the context of the evolution of communication among individuals. On the other hand, Deacon also points out that the genetic evolution that can support symbolic communication and the cultural evolution of language can mutually facilitate their evolution, although learning becomes more and more important in his scenario (Deacon, 2003). Although the cultural evolution of the learned traits is not introduced into our model, the repeated occurrences of the Baldwin effect supports his claim in that the acquired adaptive communication through learning process brings about the genetic evolution of the innate communication ability, which results in a further acquisition of more adaptive communication through learning process.

We believe the observed scenarios reflect the general dynamics of interactions between evolution and learning in dynamically changing environments caused by internal factors.

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