Does Social/Cultural Learning Increase Human Adaptability? Rogers' Question Revisited

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Abstract

It is often taken for granted that social/cultural learning increases human adaptability, because it allows us to acquire useful information without costly individual learning by trial and error. Rogers (1988) challenged this common view by a simple analytic model. Assuming a “cultural” population composed of individual learners engaging in costly information search and imitators who just copy another member’s behavior, Rogers showed that mean fitness of such a mixed “cultural” population at the evolutionary equilibrium is exactly identical to the mean fitness of an “acultural” population consisting only of individual learners. Rogers’ result implies that no special adaptive advantage accrues from social/cultural learning. We revisited this counter-intuitive argument through use of an experiment with human subjects, and by a series of evolutionary computer simulations that extended Kameda & Nakanishi (2002). The simulation results indicated that, if agents can switch the individual learning and imitation selectively, a "cultural" population indeed outperforms an "acultural" population in mean fitness for a broad range of parameters. An experiment that implemented a non-stationary uncertain environment in a laboratory setting provided empirical support for this thesis. Implications of these findings for cultural capacities and some future directions are discussed.

Key Words: social learning, cultural transmission, non-stationary uncertain environment, mean fitness, producer-scrounger dilemma

1. Introduction

Social/cultural learning is fairly common in the animal kingdom at least in its elementary form. Accumulating evidence suggests that acquisition of food preferences, selection of foraging or nest sites, vocal and motor patterns, etc. are influenced by "cultural" transmission in some group-living species, let alone humans (e.g., Galef & Whiskin, 2001; Giraldeau & Caraco, 2000; Heys & Galef, 1996; Laland, Odling-Smee, & Feldman, 2000; Rendell & Whitehead, 2001). One major adaptive advantage usually ascribed to such cultural learning is its *uncertainty-reduction* function; Cultural learning allows us to acquire adaptive behaviors in an uncertain environment cheaply without costly individual learning by trail and error (Boyd & Richerson, 1985; Hernich & Boyd, 1998). However, as discussed below, *temporally-fluctuating* nature of adaptive environment, which is considered to be a core element of human EEA (Potts, 1996; Richerson & Boyd, 2000), poses a theoretical challenge to this view (Kameda & Nakanishi, 2002). Indeed, Rogers (1988) presented a theoretical model implying that cultural transmission may have no adaptive advantage in a temporally unstable environment. In this paper, through use of an experiment with human subjects and by a series of evolutionary computer simulations, we revisit the Rogers question, examining the presumed uncertainty-reduction function of cultural transmission in a non-stationary uncertain environment.

1.1. Uncertainty reduction by social/cultural learning

To illustrate the uncertainty-reduction function by social/cultural learning, let us start with the "mushroom problem" that we used before (Kameda & Nakanishi, 2002).

Suppose that you have found a clump of mushrooms in a forest but you are uncertain if they are edible. Individual learning by trial and error may be fatal in this case, so a cheap and reliable way to cope with this uncertainty is to ask experts' or elders' opinions, or simply observe their behaviors; Especially, if you refer to more than one "cultural parent" and follow their common view ("conformist transmission": Boyd & Richerson, 1985), your survival chance increases statistically. Indeed, the previous literature suggests that acquisition of food preferences among humans is heavily influenced by cultural transmission (Katz & Schall 1979; Rozin 1989; see also Galef & Whiskin 2001, for social acquisition of food preferences in rats).

Yet, the mushroom example may illuminate limitations of cultural learning as well. Notice that culturally transmitted knowledge about the mushroom holds true across generations: if someone in your tribe died from the mushroom centuries ago, the incident still conveys valuable information to the current generation. Social/cultural learning about such a *temporally stable* target should therefore function as a highly effective mechanism to reduce uncertainty, but a far more challenging case is provided by a *temporally unstable* environment where a behavior that was adaptive in previous generations may no longer be so (Henrich & Boyd, 1998). This sort of environmental instability was actually quite common in our evolutionary history; for example, recent studies on ice cores and ocean sediments suggest that the Pleistocene EEA was an environment with frequent climate fluctuations on sub-millennial time scales (cf. Richerson & Boyd, 2000; Potts 1996). Is social/cultural learning still adaptive in such a temporally unstable environment?

1.2. Provision of updated information about the adaptive environment

1.2.1. Free-rider problem

Usefulness of social/cultural learning depends on the overall quality of “cultural knowledge pool”, which is sustained through group members’ provisioning of adaptively appropriate information about the environment. In the mushroom example, the issue of information provision is relatively marginal; Given its stable nature, one “tragic accident” in the past should, in principle, be sufficient. However, in a temporally fluctuating environment where update of cultural knowledge pool is frequently needed, we may have a totally different picture.

Kameda & Nakanishi (2002) argued that *free-rider problem* about information provision is essential in cultural groups. In many actual situations, individual learning by trial and error is costlier than social learning in energy, time, or risk. The extra cost required for individual learning must be borne by the individual solely, whereas the acquired information benefits all members more or less via cultural knowledge pool. Cultural knowledge pool has a feature similar to public goods in some respects, and thus free-rider problem (Hardin, 1968) complicates the issue of information provision in a temporally fluctuating environment. More specifically, Kameda & Nakanishi (2002) argued that this situation constitutes a “producer-scrounger dilemma” often found in social foragers (cf. Barnard & Silby, 1981; Krebs & Inman, 1992; Giraldeau & Caraco, 2000; Vickery, Giraldeau, Templeton, & Chapman, 1991). That is, the asymmetry in learning cost creates the possibility that if many others engage in costly individual learning, it may be better for some to skip the individual information search completely and “free-ride” on others' efforts, whereas if too many others just rely on social information, it may be better to engage in individual learning. Theoretically, this relation should yield a mixed Nash equilibrium in the cultural population, where "information producers" who engage in costly individual information search and "information scroungers" who skip the search coexist at a stable ratio. Kameda & Nakanishi (2002) formalized these ideas by a series of evolutionary computer simulations, and confirmed them by an experiment with human subjects.

1.2.2. Rogers' question

These results imply that, because of the free-rider problem, overall quality of cultural knowledge pool that underlies the presumed adaptive advantage of social learning may not necessarily be guaranteed in a non-stationary environment. Rogers (1988) illustrated this possibility clearly using a simple but appealing model. The model assumes a population of hypothetical organisms living in a temporally fluctuating environment that can change between two states, A and B, with a small probability in any two consecutive generations; Behavior A is more fit if the environment is in state A, whereas behavior B is more fit in environment B. Rogers assumed two genotypes in the population – individual learners and imitators. Individual learners engage in costly information search, whereas imitators save this cost by picking a random individual from the population and copying its behavior. Fig. 1 illustrates the model's implication for the *mean fitness* of individual learners and imitators, as a function of the frequency of imitators in the population (cf. Boyd & Richerson, 1995).

Insert Fig. 1 about here.

As shown in the figure, the fitness of individual learners is constant regardless of the frequency of imitators in the population, because they are not affected by cultural information. However, the fitness of imitators depends on the frequency of other imitators critically. If imitators are rare in the population, the quality of cultural knowledge pool is still high, allowing them to enjoy the benefit of culture without bearing the individual-learning cost. This places imitators in a more fit position than individual learners. On the other hand, if there are too many imitators, the imitators are likely to end up imitating other imitators; thus they are less fit than individual learners. As discussed by Kameda & Nakanishi (2002), the population leads to a mixed equilibrium eventually, where individual learners and imitators coexist at a stable ratio.

Now, consider another population composed only of individual learners. Different from the mixed “cultural population” above, all agents in this population engage in individual information-search and are unaffected by social/cultural information at all. Then, what about mean fitness of this “acultural population” compared to the “cultural population”? Does the deprivation of social learning ability reduce mean fitness of the acultural population? Surprisingly, the answer is no. Since the fitness of individual learners is constant (see Fig. 1), it logically follows that the acultural population has exactly the same fitness (see the point marked Y in the figure) as the mixed cultural population (see the point marked X). In other words, quite contrary to our intuition, the Rogers model implies that social/cultural learning does <u>not</u> increase mean fitness of the population at all.

Boyd & Richerson (1995) examined this "paradox" in detail, and concluded that the Rogers thesis is logically correct as long as the only benefit of social/cultural learning is cost-saving for imitators. In the following, we revisit the Rogers thesis first empirically by an experiment with human subjects, and then theoretically through a series of evolutionary computer simulations. By linking an experiment to a theoretical model in an integrated manner, this paper explores conditions under which social/cultural learning may increase human adaptability via its uncertainty-reduction function.

2. Experiment

2.1. Overview

Kameda & Nakanishi (2002) has empirically demonstrated that, in a cultural population, "information producers" who engage in costly information search and "information scroungers" who save the search cost coexisted at a stable ratio, as a result of individual-level fitness maximization. The Rogers model implies that this "cultural" equilibrium is not Pareto-efficient, compared to the "acultural" equilibrium; group-level fitness (mean fitness) is no different between the two populations. This feature was not tested by Kameda & Nakanishi (2002). Thus, in this experiment, we address Rogers' (1988) question directly in a laboratory setting that simulated a temporally fluctuating environment. According to the Rogers framework, we created two experimental "populations", cultural or acultural, in the laboratory. In the cultural population, participants could refer to other participants' past behaviors when deciding their own behaviors in the current environment, whereas such social referencing was not possible in the acultural population. Opportunity for individual learning about the current environment was equally available in both populations. We then compared mean "fitness" of the two experimental populations to examine the Rogers thesis.

2.2. Method

2.2.1. Participants

Participants were 300 (175 male and 125 female) undergraduate students enrolled in introductory psychology classes at Hokkaido University, Japan.

2.2.2. Experimental task

The experimental task was identical to the task used in Kameda & Nakanishi (2002). Kameda & Nakanishi (2002) developed a computer game called "Where is the rabbit?" that simulated a fluctuating uncertain environment in a laboratory setting. In this game, participants judged in which of two nests a rabbit was currently located based on stochastic information. Participants played the game for a total of 60 rounds. They were instructed that the rabbit (=environment) had a tendency to stay in the same nest over time, but this tendency was not perfect; the rabbit might change its location between any two consecutive rounds with a small probability. Thus, the location of the rabbit in a given round corresponds to the current state of the fluctuating environment. All participants experienced the same randomly determined fluctuation pattern where the rabbit moved in 20% of the 60 experimental rounds.

2.2.3. Experimental design

We used a 2 (Learning: cultural vs. acultural) x 2 (Cost for individual information-search: no cost vs. cost) factorial design. Both factors were between-subjects.

The first factor was concerned with a distinction whether *social information* about other members' past behaviors was available (cultural) or not (acultural) when each participant judging the current state of the fluctuating environment (=the rabbit's location). As explained below, participants played the "Where is the rabbit game?" in 6-person groups in the cultural condition, whereas alone in the acultural condition. The second factor varied cost required for individual information search about updated *environmental information*; the environmental information was provided as a default to all members in the no-cost condition, whereas it was available only to those incurring search cost in the cost condition (cf. Rogers, 1988). The number of participants in each condition was: 120 (cultural/cost), 96 (cultural/no-cost), 42 (acultural/cost), and 42 (acultural/ no-cost).

2.1.4. Procedure

For each hourly session, we ran either the cost or no-cost condition according to a usual randomization procedure. Eight to ten participants came together to the laboratory for each session.

Upon their arrival, we randomly assigned 6 participants to the cultural condition and assigned the rest to the acultural condition. Each participant was seated in a private booth and received further instructions individually via computer. "Where is the rabbit?" was explained, and the participants were instructed that they would play this game for many rounds (unspecified) and would gain 30 yen for each round in which they guessed the location of the rabbit correctly.

For the six participants assigned to the cultural condition, social learning opportunity was provided. Except for the first round, judgments of three participants in the *preceding* round, who were randomly sampled from the five group members other than self, were provided to each participant for *free*. As discussed earlier, social learning provides statistically reliable (i.e., aggregated) information cheaply, but this information may be *outdated* due to the possibility of environmental change (the rabbit's move). Besides the social/cultural information, these participants could also obtain updated information about the current environment via individual information-search. In each round, participants could use a "rabbit-search-machine" by paying 15 yen (defraying 50% of the potential reward) in the cost condition[1], or for free in the no-cost condition. The "rabbit-search-machine" provided stochastic information about the location of the rabbit. By a series of pilot tests, we set the accuracy of the search machine so that using this individual learning opportunity alone (i.e. without using social information) yielded 67% correct judgments on average. In a practice session before the main experiment, participants were given opportunities to familiarize themselves with the search machine and its accuracy.

In contrast, no social learning opportunity was provided to the participants assigned to the acultural condition. These participants worked alone throughout the experiment, and "cultural transmission" via social referencing was not possible. Opportunity for individual information-search via the "rabbit-search-machine" was available as in the cultural condition.

After every five rounds, participants received feedback about their performances. In the cultural condition, a summary table of all six members' cumulative rewards up to that point was displayed on the computer screen after every five rounds. Likewise, a summary table of one's own cumulative rewards up to the point was provided in the acultural condition after every five rounds. These feedbacks provided an opportunity for participants to learn the effectiveness of their learning strategies, permitting *adaptive learning of learning strategies*. It should also be noted that *no* direct feedback about the exact location of the rabbit was provided at any point in the experiment; direct learning of the rabbit's exact location was impossible throughout the experiment.

After completing 60 rounds, participants answered a brief post-session manipulation check questionnaire, and were then paid and dismissed.

2.3. Results

2.3.1. Producer-scrounger dilemma in the cultural/cost condition

We have argued that, when individual information search was costly whereas cheap social/cultural learning was possible, the producer-scrounger dilemma (Kameda & Nakanishi, 2002) would characterize members' interdependency in a group, consequently qualifying the average quality of cultural knowledge pool. Fig. 2 displays mean proportions of "information producers" in the 6-person cultural/cost groups, who actually incurred the extra cost for individual information search, over 60 experimental rounds. We also graphed overall proportions of information producers in the acultural condition. Consistent with the reasoning, the proportion of information producers was smaller in the cultural than in the acultural condition, and the discrepancy between the two conditions became more salient over time. Dividing the 60 rounds into three blocks and composing 6-person nominal groups in the acultural condition, a 2 (Learning: cultural vs. acultural) x 3

(Block) repeated measures analysis of variance (ANOVA) yielded a main effect for Learning [F(1,25)=6.59, p<.05], a main effect for Block [F(2,50)=35.92, p<.001], and a Learning x Block interaction effect [F(2,50)=5.47, p<.001].

Insert Fig. 2 about here.

To see if the proportion of information producers was approaching equilibrium over time in the cultural/cost condition (as predicted for the producer-scrounger game: cf. Kameda & Nakanishi, 2002), we examined temporal changes in variances associated with the proportion. If the proportion was indeed approaching equilibrium in the cultural condition, "between-groups variances" that indexed variability around the means in Fig. 2 should decrease over time. A multiple regression analysis on the between-group variances, with experimental round as a predictor, revealed that the regression line had a negative slope (β=-.35, p<.01), confirming that variability among the groups in the information producer proportion decreased as play progressed. A similar analysis on "within-groups variances" that indexed fluctuations in the proportion within each group also yielded the same pattern. Mean within-group variances were 0.038 for the first block, 0.031 for the second block, and 0.029 for the last block [F(2,38)=3.73, p<.05].[2]

2.3.2. Does cultural transmission increase mean fitness?

The above results clearly indicate that the producer-scrounger dilemma characterized members' interdependency in the cultural groups. As Rogers (1988) argued, such a game-theoretic structure may undermine the adaptive value of cultural transmission, especially in a temporally fluctuating environment as studied here.

We examined the Rogers thesis by first focusing on monetary rewards that participants earned in the experiment, as a laboratory counterpart of fitness in a fluctuating uncertain environment. Fig. 3 displays mean *monetary rewards* in the cultural and acultural conditions as a function of information-search cost. On average, participants earned more reward in the cultural than in the acultual condition. A 2 (Learning) x 2 (Cost) ANOVA yielded significant main effects for Learning [*F*(1,296)=4.37, *p*<.05] and for Cost [*F*(1,296)=314.15, *p*<.001]. Learning x Cost interaction effect was not significant [*F*(1,296)=0.16, *ns*].

Insert Fig. 3 about here.

We also examined participants' *judgmental accuracy* in the game. Fig. 4 displays mean number of rounds (out of 60) in which participants identified the location of the rabbit correctly. Interestingly, the advantage via cultural transmission as found with the "reward measure" was not evident on this "pure accuracy" measure. A 2 (Learning) x 2 (Cost) ANOVA yielded a significant main effect for Cost [*F*(1,296)=67.13, *p*<.001] and a marginal Learning x Cost interaction effect [*F*(1,296)=3.51, *p*=.062], but no effect for Learning [*F*(1,296)=0.07, *ns*]. As can be seen from the figure, the marginal interaction effect was mainly due to the benefit of cultural transmission when the individual information search required no cost. To recapitulate, when all members have a *free* access to environmental information, collective knowledge pool is constantly updated and thus cultural learning can enjoy statistically reliable (i.e., aggregated) information, outperforming acultural learning in terms of judgmental accuracy (cf. Henrich & Boyd, 1998; Kameda & Nakanishi, 2002). However, when individual information search is costly, such an advantage of cultural learning is not necessarily guaranteed because of the producer-scrounger problem -- as actually shown in the nearly comparable judgmental accuracy between the cultural and acultural conditions in Fig. 4. Taken together, the overall fitness advantage of the cultural condition (Fig. 3) seems to have accrued from collective saving of information-search cost while not much sacrificing judgmental accuracy through statistical aggregation (Fig. 4), compared to the acultural condition where such a collective cost-saving was impossible.

Insert Fig. 4 about here.

2.4. Discussion

The experimental results confirmed that the producer-scrounger problem, as implied by the Rogers (1988) model, is essential in cultural groups where social learning opportunity is readily available while individual information-acquisition is costly in terms of time, energy, risk, and so on (cf. Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002). However, his thesis that social/cultural learning does not increase mean fitness of the cultural population because of the producer-scrounger dilemma was not supported by the experiment; Overall “fitness”, as indexed by mean monetary reward that participants earned in the experiment, was generally higher in the cultural than the acultural condition. Then, why this difference between the theory and empirical data?

Let us revisit the Rogers model. Although the experimental setting could be different from the model in several ways, one of the most conceptually important differences may be with cognitive characteristics assumed for “individual learners.” Rogers (1988) defined “individual learners” as those who engage in costly individual information search and always disregard social information completely; these agents are not only information producers but also blind to social/cultural information even when it is readily available. For this reason, their fitness is unaffected by the number of imitators (“information scroungers”: Kameda & Nakanishi, 2002) in the population (see Fig. 1).

However, this characterization may be unrealistic in human cases. The social psychological literature has shown that humans are selective information-users, adjusting their reliance on individually-acquired information dependent on its diagnosticity (e.g., Festinger, 1950; Sherif, 1936). For example, in a classical paper on attitude formation, Festinger (1954) argued that humans turn to “social comparison” when “physical reality checks” do not provide unambiguous information for assessing the validity of their beliefs. In other words, human “individual learners” switch to social/cultural information in an if-then manner contingent on the diagnositicity of individually-acquired (via physical reality checks) information, rather than commit themselves to the latter stringently. If the Rogers organisms were “cognitively flexible” in this sense, it might be the case that social/cultural learning not only benefits imitators in cost-saving but also help individual learners improve their judgmental accuracy, contributing to the overall quality of cultural knowledge pool (cf. Boyd & Richerson, 1995). Of course, this reasoning could be wrong;

Cognitive flexibility makes the individual learners more vulnerable to influence of imitators as well, which may reduce, rather than enhance, their judgmental accuracy. In this sense, the cognitive flexibility may work as a double-edged sword in a temporally fluctuating environment.

To test if the above reasoning is correct, it is necessary to distinguish conceptually information search strategy (produce or scrounge) from information use strategy (relative weighting for individual and social/cultural information) at least for human "individual learners." The Rogers model did not make this distinction, assuming that information producers do not use social/cultural information at all even if it is readily available. We thus revisit the Rogers question in the next section by a theoretical model that incorporates the above features. We report a series of evolutionary computer simulations exploring fitness advantage of cultural transmission in a temporally fluctuating environment.

3. Evolutionary computer simulation

The purpose of this simulation was to re-examine the Rogers question theoretically in a wider parametric space. Although informative, the experimental test we conducted was limited by nature in that it could assess only a small subset of the space. Computer simulations are particularly useful to see how robust the experimental results may be in other parametric conditions. In this simulation, we use a theoretical model that we proposed earlier (Kameda & Nakanishi, 2002). This model is an extension of theoretical work by Robert Boyd, Peter Richerson and Joseph Henrich about cultural transmission (Boyd & Richerson, 1985, 1995; Henrich & Boyd, 1998), and has been demonstrated to predict actual human learning-behaviors well in a temporally-fluctuating laboratory setting (see Kameda & Nakanishi, 2002, for details). Using this model, we compare mean fitness of cultural and acultural populations while varying key parameters of the model systematically.

3.1. Model and algorithm

Fig. 5 shows a simulation algorithm of our model. Like Rogers (1988), let us assume that the environment can change between two states, A and B, with a small probability in any two consecutive generations. Behavior A is more fit if the environment is in state A, whereas behavior B is more fit in environment B. Natural selection favors learning mechanisms that make individuals more likely to adopt the behavior that is adaptive in the current environment (see Fig. 5, bottom). As in the experiment, we assumed two independent populations (cultural or acultural), and continued simulation runs until an equilibrium state emerges in each population.

In the cultural population, two information sources are available for agents, viz., opportunities for *individual learning* and *social learning*. The individual learning opportunity is optional and its usage requires extra cost. It provides updated information about the *current* environment, yet because of random noise in environmental information, as a single observation, individual learning is statistically less reliable. The social learning opportunity is default, providing information about the choices of several cultural parents in the *preceding* generation for free. Learning from several predecessors leads to a statistically reliable estimate about the environment in many cases (law of large numbers), but the information is outdated if an environmental change has occurred.

Insert Fig. 5 about here.

Each cultural agent combines the two kinds of information to decide how to behave in the current environment. Three "genes" are pertinent to this combination. A first gene represents each agent's *information-search* strategy, which is central to the Rogers (1988) argument. Haploid agents with the "on" allele at this locus are "information producers" (cf. Fig. 2) who pay the extra cost for updated information about the current environment; those with the "off" allele are "information scroungers" who skip the search.

The other two genes represent the cultural agent's *information-use* strategy (Boyd & Richerson, 1995; Henrich & Boyd, 1998). One gene controls variations in *propensity to use social information over individually-acquired information*, representing the "cognitive flexibility" that we discussed above. Environmental information, if acquired via costly search, contains random noise, so that even though the signal suggests that the current environment is in state A, it may actually be in state B. As in signal detection theory (Green & Swets 1966), the model assumed that each cultural agent has a decision threshold and if the signal value exceeds it, he or she makes a choice based on the individually-acquired information (e.g., adopting behavior A). However, if the signal is insufficiently diagnostic, the agent disregards the individual information and relies solely on social information (cf. Festinger, 1950, 1954). Individual variations about the threshold were represented as effects of a gene in the simulation (the higher one's threshold, the more likely one is to use social information).[3]

Another information-use gene regulates individual variations in *conformity bias when using social information* (Boyd & Richerson, 1985, 1995; Henrich & Boyd, 1998). If the environmental signal is insufficiently diagnostic (or if the agent behaves as information scroungers: cf. footnote 3), the individual must rely on social information. Suppose that 2 of 3 cultural parents sampled from the previous generation chose behavior A, while 1 chose behavior B. The model conceptualizes the degree of "conformity bias" when using social information as a likelihood of preferentially adopting the most frequent behavior among the cultural parents (behavior A in the above example). That is, agents with *no* conformity bias adopt behavior A only proportionally (with a 67% chance in this case), having no tendency to focus preferentially on the most common behavior among the cultural parents. Agents with a *full* conformity bias adopt behavior A with a 100% chance, *always* following the majority view.

Combining individual and social information as determined by these three genes, each agent in the cultural population makes a behavioral choice.

In contrast, opportunity of social learning is unavailable to agents in the <u>acultural</u> population. The only gene pertinent to these acultural agents is the information-search gene controlling variations in individual propensity to engage in costly information search. Agents with the "on" allele at this locus acquire updated environmental information for cost and choose a behavior suggested by the information; agents with the "off" allele choose one of the two behaviors randomly.

Then, natural selection operates respectively in the cultural and acultural populations: those who behave adaptively gain a slight survival advantage, and with the relevant genes transmitted in a haploid, asexual fashion, the genes and resultant learning mechanisms that generate adaptive behavior in the current environment increase in each population gradually. The simulation repeats this process for many generations until an equilibrium state emerges in each population. We then compare mean fitness of the cultural and acultural populations at the respective equilibrium.

3.2. Results & Discussion

Three simulation parameters are critical to re-examine the Rogers question theoretically: extra cost required for individual information search (Rogers, 1988; Kameda & Nakanishi, 2002), accuracy of the environmental information, and rate of environmental fluctuation (Henrich & Boyd, 1998; Richerson & Boyd, 2000). For a same set of parameter values, we conducted 10 simulation runs over 100,000 generations for the cultural and acultural populations respectively, and averaged the results. Fig. 6 displays mean fitness of the cultural and acultural populations at the respective equilibrium as a function of individual information-search cost, which was varied systematically while keeping the other simulation parameters unchanged (see Footnote 4). The results showed that mean fitness of the cultural population was higher than that of the acultural population for the range of individual search-cost shown in Fig. 6. Fig. 7 displays equilibrium proportions of information producers in each population again as a function of the search cost. The figure shows that the producer proportion decreased rapidly in the cultural population with an increase in the search cost; for example, when the search cost was

0.0054 (5.4% of the benefit from choosing an adaptive behavior: cf. footnote 4), the equilibrium proportion of information producers was less than 5% in the cultural population, while it was 100% in the acultural population. Still, even with such a small proportion of information producers, the cultural population outperformed the acultural population in terms of mean fitness (Fig. 6). This pattern is consistent with the experimental finding.

Insert Figs. 6 & 7 about here.

How robustly does this result hold for other parameter values? We conducted a sensitivity analysis by varying two of the key parameters (information-search cost and rate of environmental fluctuation) simultaneously, while keeping the third parameter unchanged (accuracy of environmental information=0.66). Fig. 8 shows mean fitness of the cultural and acultural populations at the respective equilibrium. As can be seen, mean fitness of the cultural population was again higher than that of the acultural population for the entire parameter space examined. A simple thought experiment may further help to see what happens outside the parameter space shown in Fig. 8.

Insert Fig. 8 about here.

Let us start with the rate of environmental fluctuation; what if the environment becomes more variable? The most extreme case in the focal two-state environment is the one with a 0.5 fluctuation rate. All else being equal, all agents in the cultural population should become information producers, and their "propensity to use social information over individually-acquired information" (Festinger, 1950, 1954; see Section 3.1) should also become minimal, since cultural information has absolutely no value with the 0.5 fluctuation rate. This means that those agents in the cultural population will behave in exactly the same manner as the acultural agents. Thus, there should be no difference in mean fitness between the two populations in the most extreme case; Given the monotonically-decreasing pattern in Fig. 8, this implies that the cultural population is more fit than the acultural population even when the environment is highly variable (i.e., even if it is close to but less than 0.5).

Then, what if the individual information-search cost gets larger? As shown in Fig. 7, the number of information producers decreases monotonically with an increase in the search cost. The most extreme case is the one where cost required for the search exceeds net advantage accruing from it, with no information producers in the population. In this most extreme case, agents in both cultural and acultural populations are vulnerable to the environmental variability completely, being no different from each other in terms of mean fitness; Again, given the monotonically-decreasing pattern in Fig. 8, this implies that the cultural population is more fit than the acultural population as far as the search cost is bearable for some of its members to acquire updated environmental information.[5]

4. General discussion

In this paper, we revisited the Rogers question, examining the uncertainty-reduction function of cultural transmission in a non-stationary uncertain environment. Although the producer-scrounger dilemma about information provision (Kameda & Nakanishi, 2002) clearly characterized members' interdependency in the cultural population as implied by the Rogers (1988) model, his thesis per se was not supported; in both the experiment and simulations, the cultural population was more fit than the acultual population on average, for a broad range of parameters. In other words, the mixed "cultural" equilibrium as a result of individual-level fitness maximization is also Pareto-efficient at the group level, compared to the "acultural" equilibrium."

4.1. Discrepancies between the Rogers model and our experiment/simulation setting?

Before discussing the implications of these results, it may be useful to check once again the relation between the Rogers model and the setting we used in this paper. Besides the "cognitive flexibility" of agents, there may be other features that could be responsible for the differential results between the two studies. For example, our agents could refer to several "cultural parents" under a conformity bias to focus preferentially on the most common behavior among them (Boyd & Richerson, 1985; Henrich & Boyd, 1998; see also Kameda, Tindale, & Davis, in press, for related findings in social psychology), but these features were absent in the Rogers agents referring to just one cultural parent. Are these additional features responsible for the differential results? The answer is negative. To see why, let us suppose that as in our model, the imitators in the Rogers model refer to more than one cultural parent under a conformity bias. As can be seen in Fig. 1, these changes certainly affect steepness of the fitness curve for imitators, but they should have no impact on the fitness of individual learners; it remains flat. Thus, as far as the individual learners remain completely “asocial”, making the imitators more social would not affect the Rogers model’s key conclusion: Cultural transmission does not increase mean fitness of the cultural population.

Another criticism to our approach may be that we isolated the cultural agents from the acultural agents in two separate populations from the outset, focusing only on their population-level fitness at the respective equilibrium. What if we have two types of agents in the same population and place them under the evolutionary control? Is cultural learning an evolutionarily stable strategy (ESS) that outperforms acultural learning in such a mixed population? We addressed this question in additional computer simulations that extended our model reported in this paper. In the extended simulation, we introduced a fourth gene controlling cultural or acultural learning, such that haploid agents with the “on” allele at this locus were cultural agents engaging in social-information search *for cost*, while those with the “off” allele were acultural agents skipping the social-information search. The only difference from the original simulation was that social information was not given as a default, but provided only to the cultural agents who paid extra cost for it; the other features were identical to the original simulation. Although space does not allow us to report the results in detail, the overall conclusion is unchanged from the original simulation. As far as social information search is cheaper than individual information search and if the environment is not too unstable (both are basic assumptions of standard models of cultural transmission: cf. Boyd & Richerson, 1985; Cavalli-Sforza, & Feldman, 1981; Rogers, 1988), all agents in the population become cultural agents at the equilibrium. Some of these cultural agents are information producers who also engage in individual information search for extra cost, but others are information scroungers, constituting a mixed Nash equilibrium as in the original simulation. Taken together, these results provide a further support to our argument that cultural agents are more fit than acultural agents for a broad range of parameters, at both the individual and population levels.

4.2. Implications and future directions

The empirical and theoretical development in this paper implies that the "cognitive flexibility" of agents is likely to be a key for cultural transmission to be beneficial in a non-stationary uncertain environment. If agents are "Festingerian" who can switch to social information contingent on the diagnosticity of individually-acquired information (Festinger, 1950, 1954), cultural learning not only benefits the information scroungers in cost-saving but also the information producers in increasing their judgmental accuracy on average (Boyd & Richerson, 1995; Laland, Richerson, & Boyd, 1996). In other words, cultural transmission functions as an effective collective uncertainty-reduction device, even though the producer-scrounger problem qualifies provision of updated information about the current environment severely.

Festinger (1950, 1954) only argued that humans possess such a cognitive flexibility, and was silent about non-human animals. However, this type of cognitive ability may indeed be found among non-human animals as well, which may explain the existence of social learning in many group-living species. "Culture" at this level (i.e., behavioral variations acquired and maintained by social learning) is widely observed in the animal kingdom (e.g., Galef & Whiskin, 2001; Giraldeau & Caraco, 2000; Heys & Galef, 1996;

Laland et al., 2000; Lefebvre, 2000; Rendell & Whitehead, 2001).

On the other hand, most of such “proto-cultures” are non-cumulative. As argued by various theorists, human culture is uniquely cumulative (e.g., Boyd & Richerson, 1996; Duhram, 1991; Richerson & Boyd, 2000); No single individual ever could invent human subsistence systems, artistic productions, ideologies, religions, etc. that have existed over extended periods of time. The evidence so far suggests that cumulative cultural evolution is limited to humans, song birds, and perhaps chimpanzees. Why so? How could the human cognitive capacities evolve that have enabled us to accumulate complex knowledge or sophisticated skills in the population over so many generations? These bigger issues were beyond the scope of this paper. However, future work on adaptive value of cultural transmission should be directed to such issues, because the core merits of human cultures (e.g., technologies) hinge on our very ability of “true imitation” fundamentally (Boyd & Richerson, 1996; Tomassello, 1996).

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Footnotes

[1] In the first round only, when no social information was possible, these participants received information via the search machine for free.

[2] A further analysis revealed that this equilibrium was closer to a polymorphic equilibrium where “division of roles” about costly information search existed among members (producers vs. scroungers), than to a monomorphic equilibrium where all members played the identical mixed strategy. This pattern replicated Kameda & Nakanishi’s (2002) observation about the equilibrium composition.

[3] In the simulation, this gene was inactivated for “information scroungers” who had no individually-acquired information; those agents always used social information.

[4] The simulation parameters in Fig. 6 were set as follows: rate of environmental fluctuation=0.01, average accuracy of environmental information=0.66. The fitness value of choosing an adaptive behavior in the current environment was fixed at 0.1, and the number of “cultural parents” for cultural agents was fixed at 3 for all simulation runs reported in this paper.

[5] We also conducted a sensitivity analysis varying the accuracy of environmental information systematically. The general conclusion is unchanged: Cultural population is more fit than acultural population for a broad range of parameter values. The advantage of cultural population over acultural population takes an inverted-U shape of information accuracy, being maximized when the environmental information is moderately accurate (cf. Henrich & Boyd, 1998). When the environmental information is perfectly accurate (i.e., noise free), there is no fitness difference between the cultural and acultural populations.

Figure Captions

Figure 1. Illustration of the Rogers (1988) model.

Figure 2. Mean proportions of information producers (members who engage in costly individual information search) in the population over time (Experiment).

Figure 3. Mean monetary rewards that participants earned as a function of cultural/acultural learning and individual information-search cost (Experiment).

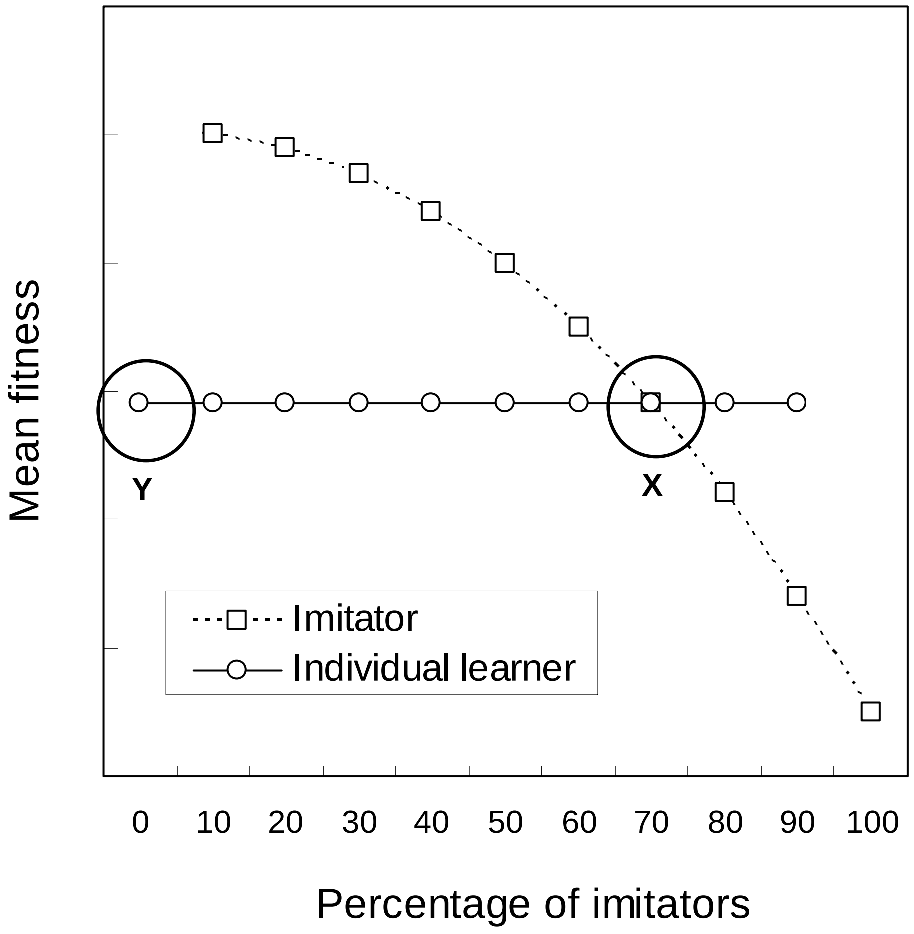
Figure 4. Mean judgmental accuracies as a function of cultural/acultural learning and individual information-search cost (Experiment).

Figure 5. An outline of Kameda & Nakanishi’s (2002) simulation algorithm.

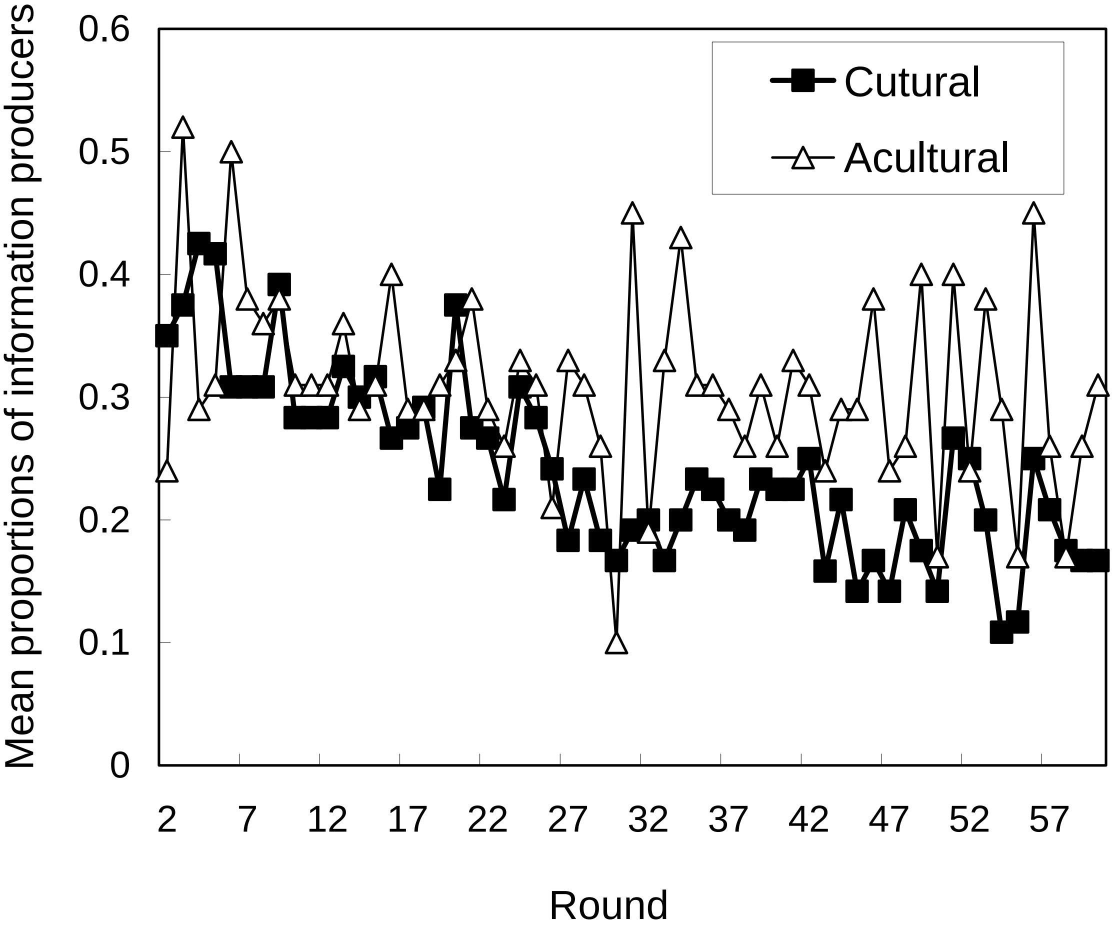
Figure 6. Mean fitness of the cultural and acultural populations at the respective equilibrium as a function of individual information-search cost (Simulation: see footnote 4 for the parametric setting).

Figure 7. Mean equilibrium proportions of information producers in the cultural and acultural populations as a function of individual information-search cost (Simulation: see footnote 4 for the parametric setting).

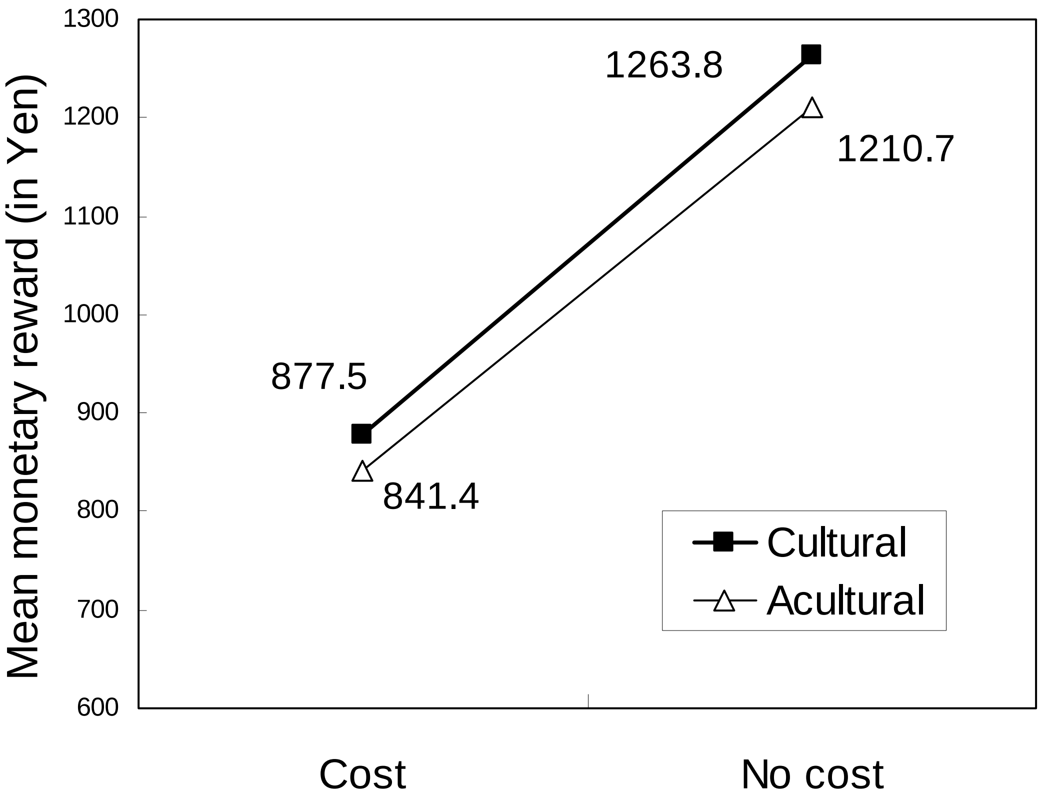
Figure 8. Mean fitness of the cultural and acultural populations at the respective equilibrium as a function of individual information-search cost and rate of environmental fluctuation (Simulation: see text for the parametric setting).


Mean fitness
Y
X
Imitator
Individual learner
0
10
20
30
40
50
60
70
80
90
100
Percentage of imitators

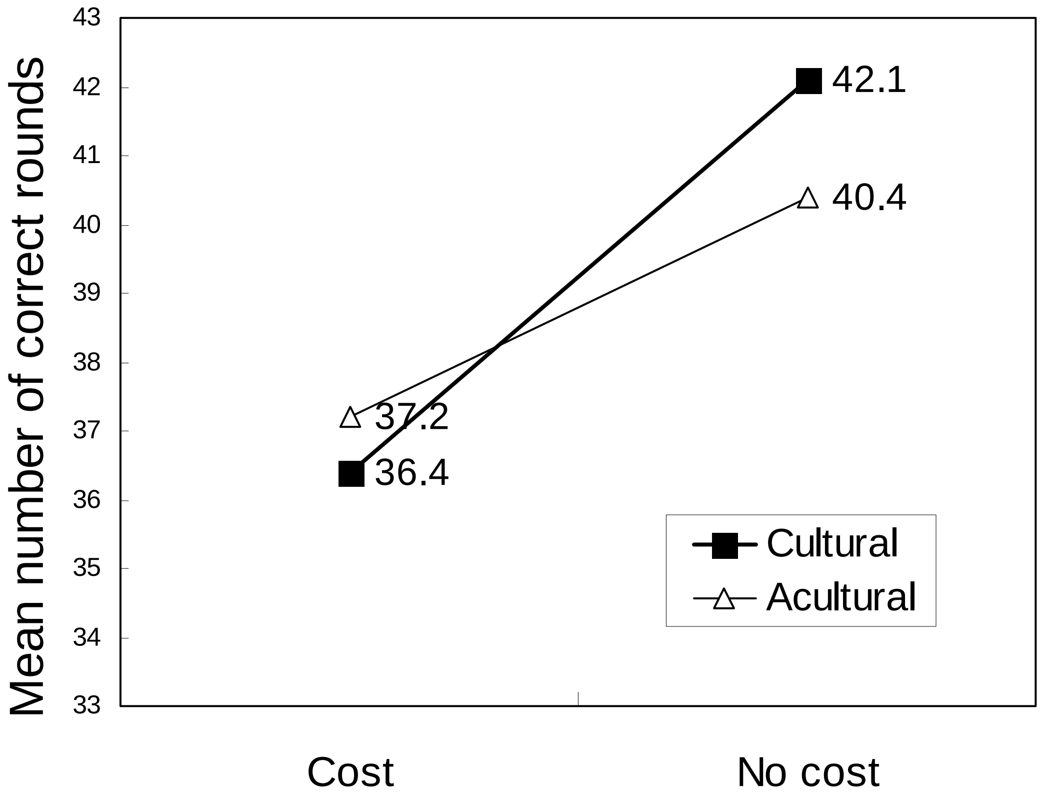
< *Fig. 1* >


Mean proportions of information producers
0.6
0.5
0.4
0.3
0.2
0.1
0
2
7
12
17
22
27
32
37
42
47
52
57
Round
Cutural
Acultural

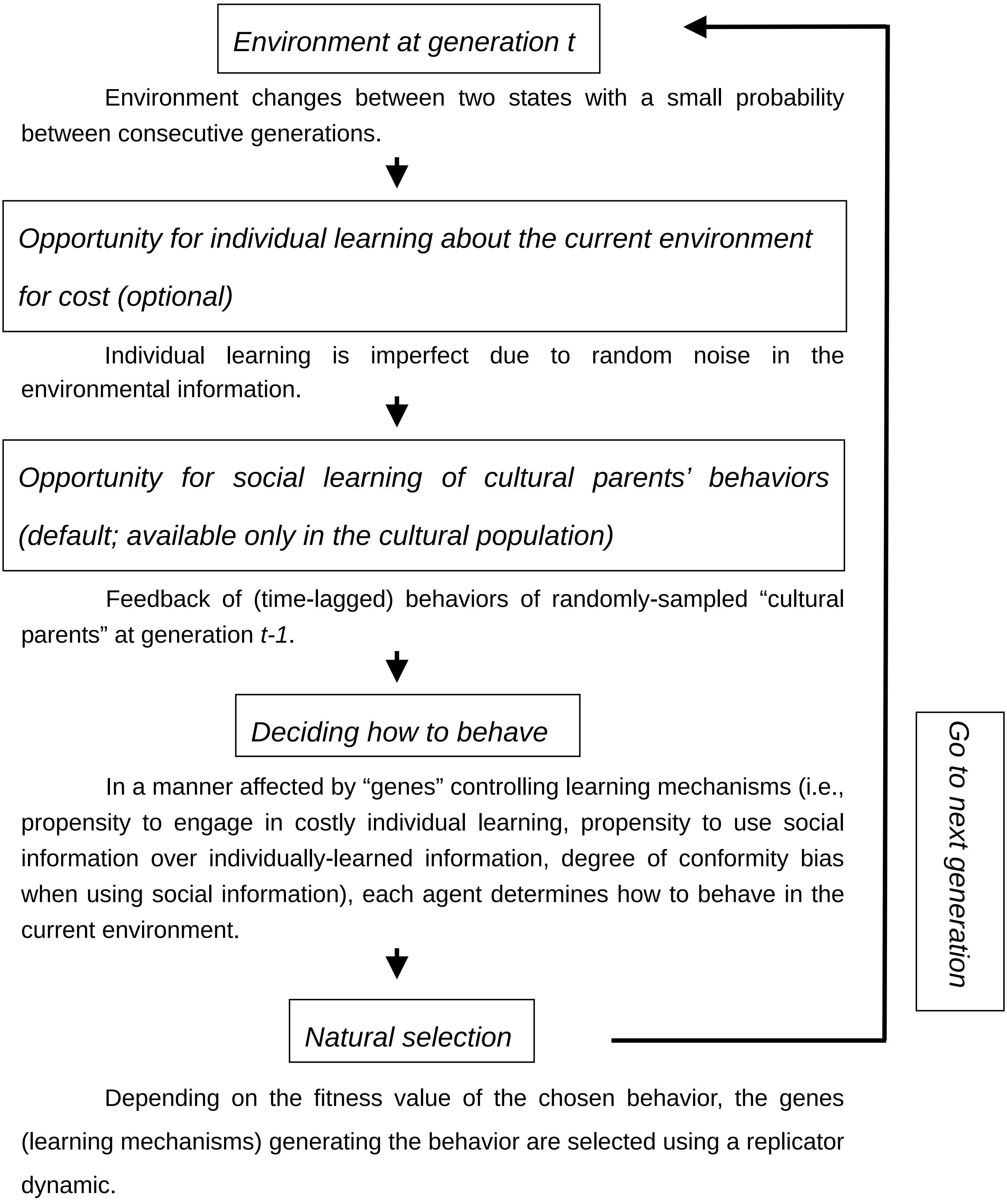
< ***Fig. 2*** >


Mean monetary reward (in Yen)
1300
1200
1100
1000
900
800
700
600
1263.8
1210.7
877.5
841.4
Cultural
Acultural
Cost
No cost

< Fig. 3 >


Mean number of correct rounds
43
42
41
40
39
38
37
36
35
34
33
42.1
40.4
37.2
36.4
Cultural
Acultural
Cost
No cost

< ***Fig. 4*** >



Environment at generation t

Environment changes between two states with a small probability between consecutive generations.

Opportunity for individual learning about the current environment for cost (optional)

Individual learning is imperfect due to random noise in the environmental information.

Opportunity for social learning of cultural parents' behaviors (default; available only in the cultural population)

Feedback of (time-lagged) behaviors of randomly-sampled "cultural parents" at generation *t-1*.

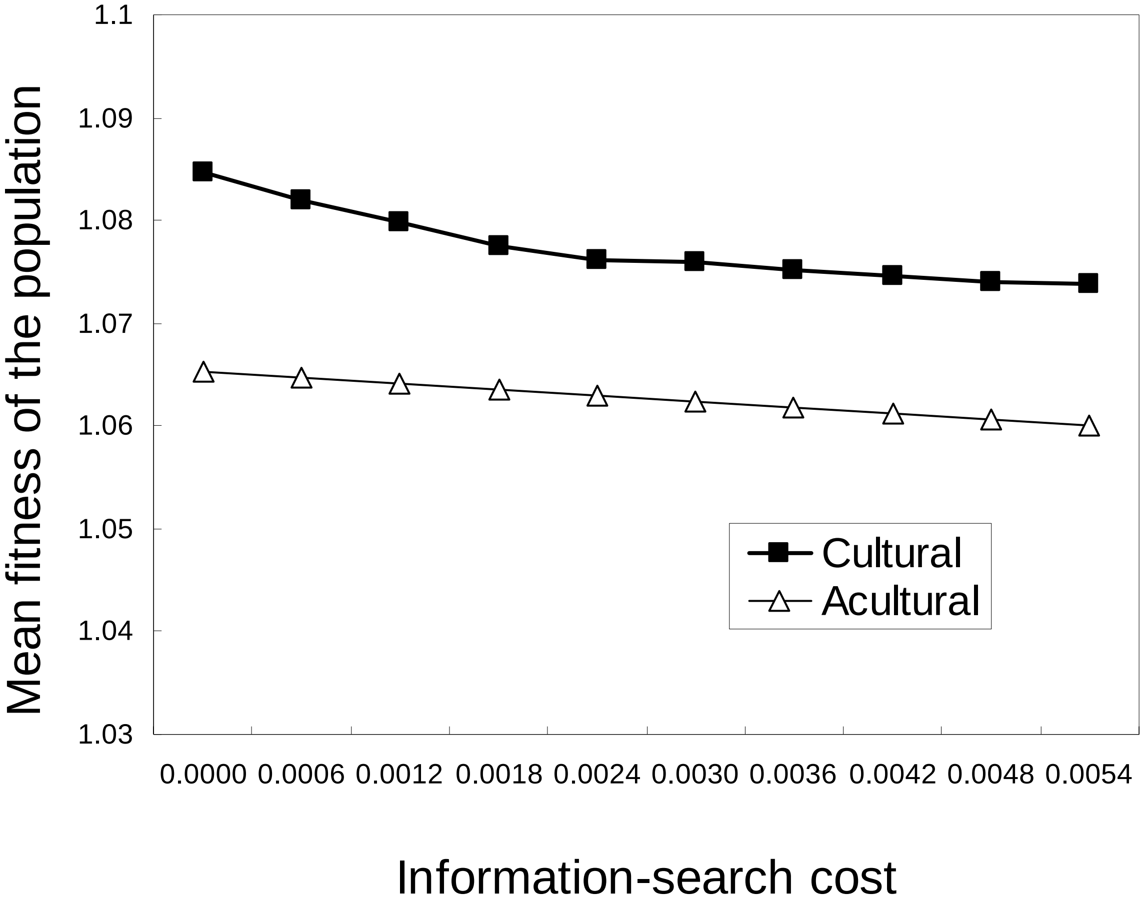
Deciding how to behave

In a manner affected by "genes" controlling learning mechanisms (i.e., propensity to engage in costly individual learning, propensity to use social information over individually-learned information, degree of conformity bias when using social information), each agent determines how to behave in the current environment.

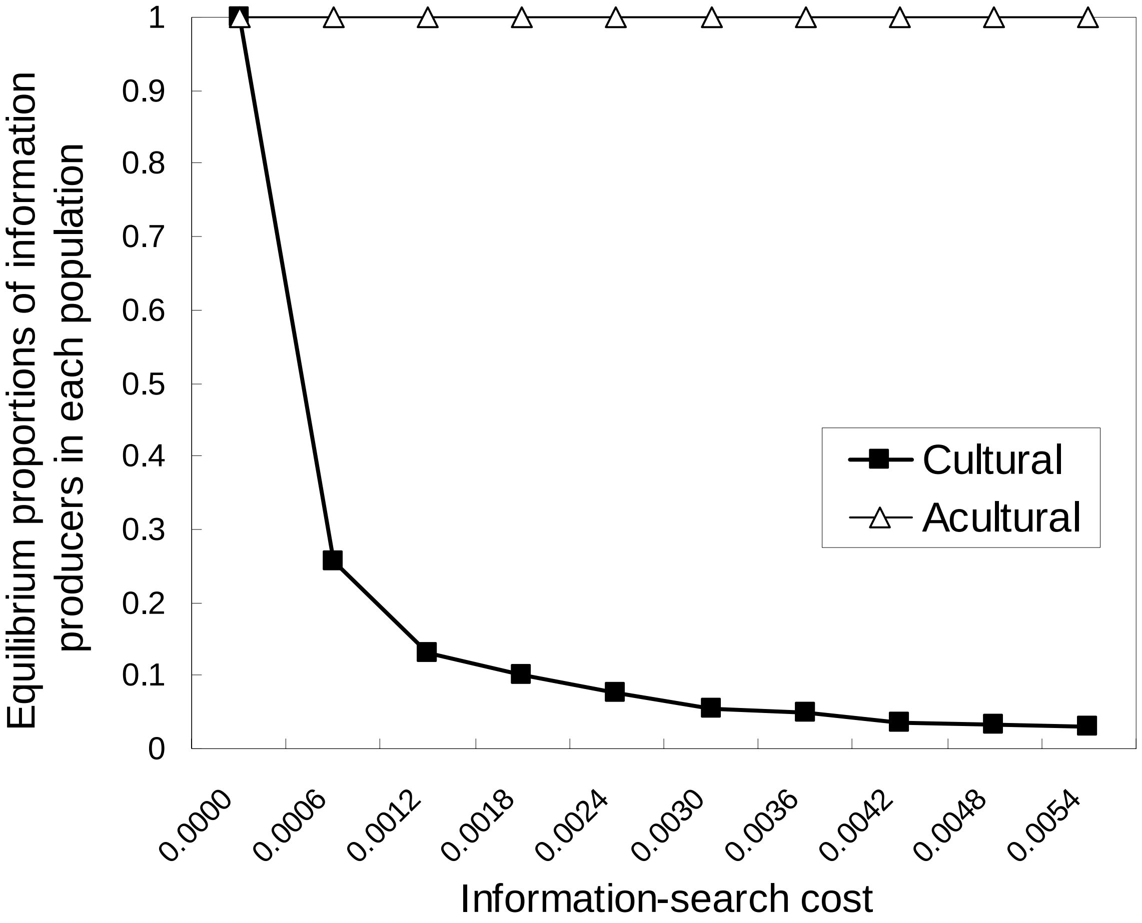
Natural selection

Depending on the fitness value of the chosen behavior, the genes (learning mechanisms) generating the behavior are selected using a replicator dynamic.

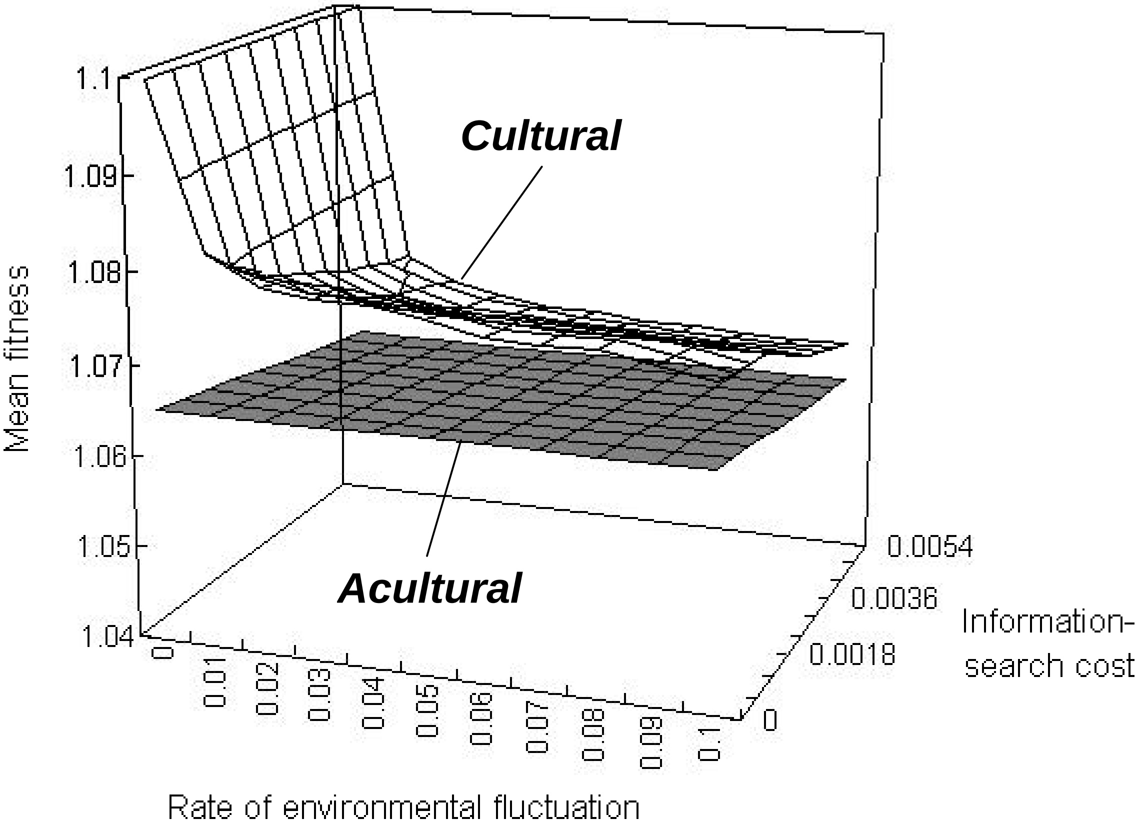
< ***Fig. 5*** >


1.1
1.09
1.08
1.07
1.06
1.05
1.04
1.03
Mean fitness of the population
0.0000
0.0006
0.0012
0.0018
0.0024
0.0030
0.0036
0.0042
0.0048
0.0054
Information-search cost
Cultural
Acultural

< Fig. 6 >


1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Equilibrium proportions of information producers in each population
0.0000
0.0006
0.0012
0.0018
0.0024
0.0030
0.0036
0.0042
0.0048
0.0054
Information-search cost
Cultural
Acultural

< ***Fig. 7*** >


Cultural
Acultural
Mean fitness
1.1
1.09
1.08
1.07
1.06
1.05
1.04
0
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.1
Rate of environmental fluctuation
0
0.0018
0.0036
0.0054
Information-search cost

< Fig. 8 >