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Does social/cultural learning increase human adaptability? Rogers's 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 [Am. Anthropol. 90 (1988) 819] 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's result implies that no special adaptive advantage accrues from social/cultural learning. We revisited this counterintuitive argument through use of an experiment with human subjects, and by a series of evolutionary computer simulations that extended Kameda and Nakanishi [Evol. Hum. Behav. 23 (2002) 373]. The simulation results indicated that, if agents can switch between 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 nonstationary 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.

Keywords: Social learning; Cultural transmission; Cultural capacities; Nonstationary uncertain environment; Mean fitness; Producer–scrounger dilemma

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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, including humans (e.g., Galef & Whiskin, 2001; Giraldeau & Caraco, 2000; Heyes & Galef, 1996; Laland, Odling-Smee, & Feldman, 2000; Rendall & 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 trial and error (Boyd & Richerson, 1985; Hernich & Boyd, 1998). However, as discussed below, the *temporally fluctuating* nature of adaptive environments, which is considered to be a core element of the human environment of evolutionary adaptedness (EEA; cf. 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 the use of an experiment with human subjects and by a series of evolutionary computer simulations, we revisit Rogers's question, examining the presumed uncertainty-reduction function of cultural transmission in a nonstationary uncertain environment.

1.1. Uncertainty reduction by social/cultural learning

To illustrate the uncertainty-reduction function of social/cultural learning, let us start with the "mushroom foraging 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). 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 mushrooms holds true across generations: If someone in your tribe died from a 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 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 submillennial time scales (cf. Potts 1996; Richerson & Boyd, 2000). 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 the "cultural knowledge pool," which is sustained by the fact that group members provide 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 updates of the cultural knowledge pool are frequently needed, we may have a totally different picture.

Kameda and Nakanishi (2002) argued that the free-rider problem about information provision is essential for understanding 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 potentially benefits everyone via the cultural knowledge pool. The cultural knowledge pool is similar to public goods in some respects, and thus a free-rider problem (Hardin, 1968) complicates the issue of information provision in a temporally fluctuating environment. More specifically, Kameda and Nakanishi argued that this situation constitutes a *producer–scrounger dilemma* like that found among social foragers (cf. Barnard & Sibly, 1981; Giraldeau & Caraco, 2000; Krebs & Inman, 1992; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991): 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. However, if too many others just rely on social information, it may be better to engage in individual learning. Theoretically, this situation 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 and Nakanishi formalized these ideas by a series of evolutionary computer simulations and confirmed them by an experiment with human subjects.

1.2.2. Rogers's question

These results imply that, because of the free-rider problem, the overall quality of a cultural knowledge pool that underlies the presumed adaptive advantage of social learning may not necessarily be guaranteed in a nonstationary 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 State 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 fitness of individual learners and imitators, as a function of the frequency of imitators in the population (cf. Boyd & Richerson, 1995).

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 their prevalence: When imitators are rare, the quality of the cultural knowledge pool is still high, allowing them to enjoy the benefit of culture without bearing the individual-learning cost, and imitators are therefore more fit than individual learners. If there are too many imitators, however, the flow of valid knowledge into the knowledge pool degrades, and imitators risk imitating other imitators making them less fit than individual learners. As discussed by Kameda and Nakanishi (2002), the situation leads to a mixed equilibrium eventually, where individual learners and imitators coexist at a stable ratio in the population.

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 the 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. Because 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, contrary to intuition, the Rogers model implies that social/cultural learning does not increase mean fitness of the population at all.

Boyd and Richerson (1995) examined this "paradox" in detail, and they concluded that the Rogers thesis is logically correct as long as the only benefit of social/cultural learning is

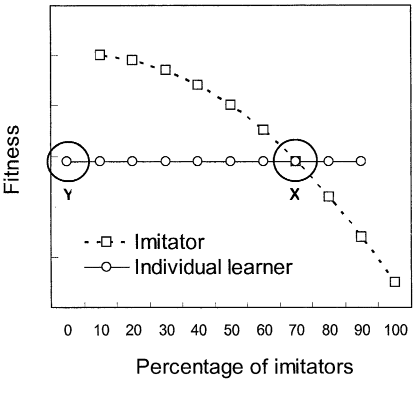

Fig. 1. Cultural learning provides no fitness advantage to the population in Rogers's (1988) model. When individual learners and imitators (cultural learners) are at equilibrium in a mixed population, their average fitness is the same as that of individual learners in a population without imitators.

cost-saving for imitators. In the following, we revisit Rogers's question 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 and Nakanishi (2002) 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 the same in the two populations. This feature was not tested by Kameda and Nakanishi. Thus, in the present experiment, we address Rogers's question directly in a laboratory setting that simulates a temporally fluctuating environment. In accord with 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 162 (98 male and 64 female) undergraduate students enrolled in introductory psychology classes at Hokkaido University, Japan.

2.2.2. Experimental task

The experimental task was identical to that used by Kameda and Nakanishi (2002), who 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 on 20% of the 60 experimental rounds.

2.2.3. Experimental design

There were two conditions, cultural vs. acultural. One hundred and twenty participants were assigned to the cultural condition, where they played the "Where is the rabbit?" game in six-person groups. Social referencing about other members' past behaviors was possible in the cultural condition, when each participant judged the current state of the fluctuating environment (the rabbit's location). In contrast, 42 participants assigned to the acultural condition played the game alone without the social referencing opportunity.

2.2.4. Procedure

For each hourly session, eight to ten participants came together to the laboratory. Upon their arrival, we randomly assigned six participants to the cultural condition and 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, a social learning opportunity was provided: Except for the first round, the preceding round judgments of three participants, 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 aggregated information that is cheap, but is possibly outdated because of environmental change (the rabbit's move). Besides the social/cultural information, these participants could also obtain updated information about the current environment for cost, via individual information search: In each round, participants could use a "rabbit-search-machine" by paying 15 yen (investing 50% of the potential reward). The rabbit-search-machine provided stochastic information about the rabbit's location. (In the first round only, when no social information was possible, these participants received this information for free.) In accordance with the "lens model" paradigm (Brunswik, 1956), three perceptual cues were presented on the computer screen that diagnosed the likelihood of the rabbit's presence in each nest. By a series of pilot tests, we set the overall accuracy of the cues 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 forms of feedback provided an opportunity for participants to assess 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; thus, direct learning of the rabbit's exact location was impossible.

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

2.3. Results

2.3.1. Producer–scrounger dilemma in the cultural condition

When individual learning is costly and cheap social/cultural learning is possible, the producer–scrounger dilemma would be expected to characterize interdependency in a group, affecting the average quality of the cultural knowledge pool (Kameda & Nakanishi, 2002). Fig. 2 displays the mean proportions of information producers (those who incurred the cost of individual information search) in the six-person cultural groups over 60 experimental rounds, as well as overall proportions of information producers in the acultural condition. As expected, the proportion of information producers was smaller in the cultural than in the acultural condition, and the discrepancy between the two conditions became larger over time. Dividing the 60 rounds into two blocks and composing six-person nominal groups in the acultural condition, a 2 (Learning: cultural vs. acultural) × 2 (Block) repeated-measures analysis of variance yielded a main effect for Learning [$F(1,25)=26.98$, $P<.0001$], a main effect for Block [$F(1,25)=32.5$, $P<.0001$], and a Learning × Block interaction effect [$F(1,25)=4.23$, $P=.05$].

To see if the proportion of information producers was approaching equilibrium over time in the cultural condition (as predicted for the producer–scrounger game; Kameda & Nakanishi, 2002), we examined changes in the variance of this proportion among groups.

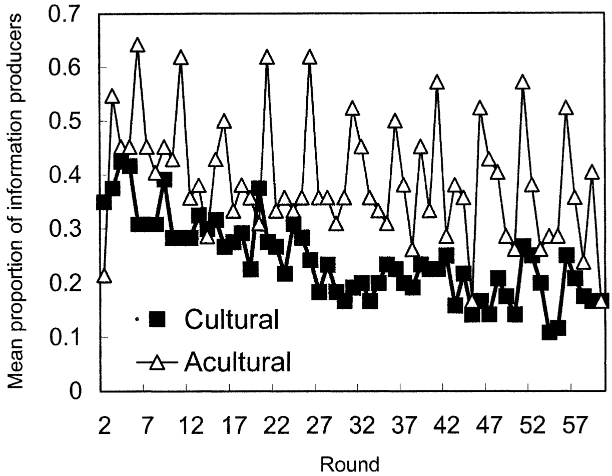

Fig. 2. Mean proportions of information producers (members who engage in costly individual information search) in the population over time (experiment).

If the proportion was indeed approaching equilibrium in the cultural condition, its between-groups variance should decrease over rounds. A multiple regression analysis of the between-groups variances, with experimental round as a predictor, revealed that the regression line had a negative slope ($\beta = -.35$, $P < .01$), confirming that variability in the proportion that were information producers decreased as play progressed. A similar analysis of within-groups variances that indexed fluctuations in the proportion within each group yielded the same pattern. Mean within-groups variances were 0.039 for the first block, and 0.027 for the second block [$t(19) = 4.84$, $P < .001$]. A further analysis revealed that the data were better described as a polymorphic equilibrium where "division of roles" about costly information search existed among members (producers vs. scroungers), than as a monomorphic equilibrium where all members played the identical mixed strategy, replicating Kameda and Nakanishi's (2002) observation about the equilibrium composition.

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 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. Fig. 3 displays mean monetary rewards in the cultural and acultural conditions for the first and second blocks. On average, participants earned more reward in the cultural condition ($M = 878$ yen) than in the acultural condition ($M = 794$ yen); a 2 (Learning) × 2 (Block) ANOVA yielded a significant main effect for Learning [$F(1,160) = 7.63$, $P < .01$]. No other effects were significant [Block: $F(1,160) = .53$, $P = .47$; Learning × Block interaction: $F(1,160) = .78$, $P = .38$].

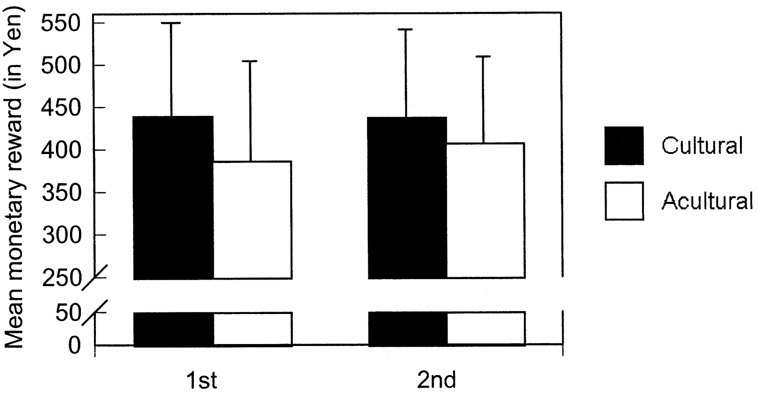

Fig. 3. Mean monetary rewards (with an S.D.) that participants earned in the cultural and acultural conditions (experiment).

We also examined participants' success rates in locating the rabbit correctly. Fig. 4 displays the mean number of rounds (out of 30 for each block) in which participants got the rabbit's location right. Interestingly, unlike the monetary reward measure, this "pure accuracy" measure showed no advantage of cultural transmission. In fact, although the two conditions yielded comparable accuracies in the first half of the experiment, the cultural condition became less accurate than the acultural condition in the second half of the experiment; a 2 (Learning) × 2 (Block) ANOVA yielded a marginal effect for Learning × Block interaction [$F(1,160)=3.69$, $P=.057$]. No other effects were significant [Learning: $F(1,160)=2.70$, $P=.103$; Block: $F(1,160)=1.99$, $P=.160$].

Taken together, these patterns imply the following. The producer–scrounger dilemma in information provision (Kameda & Nakanishi, 2002) yielded a mixed Nash equilibrium in the cultural population over time (Fig. 2). The proportion of information producers at equilibrium was smaller in the cultural condition than in the acultural condition, which degraded the quality of the cultural knowledge pool and hence judgmental accuracy (Fig. 4). However, lower search costs compensated for this loss of accuracy, and the cultural population was better off than the acultural population in terms of mean fitness (Fig. 3). These results imply that the net advantage of cultural transmission (e.g., aggregated information, saving of information-search cost via social learning) may indeed outweigh its disadvantage accruing from the free-rider problem in producer–scrounger dilemma.

2.4. Discussion

The experimental results confirmed that the producer–scrounger problem is inherent in cultural groups where social learning opportunity is readily available and individual information acquisition is costly in terms of time, energy, risk, and other resources (cf. Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002). However, the notion that social/cultural learning cannot increase mean fitness of the cultural population because of the

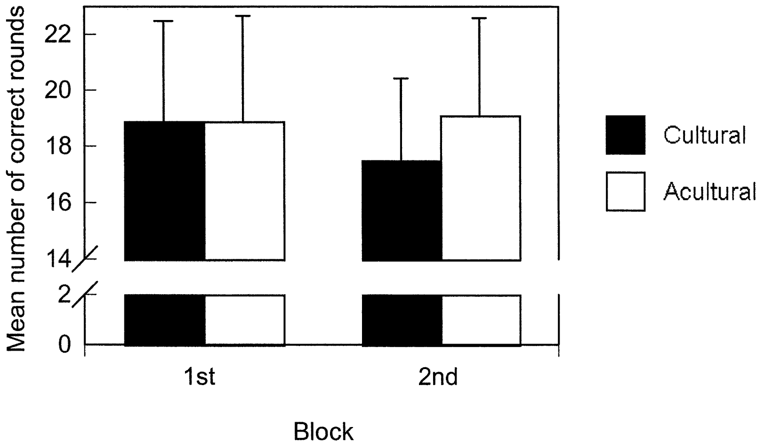

Fig. 4. Mean judgmental accuracies (with an SD) in the cultural and acultural conditions (experiment).

producer–scrounger dilemma was not supported by the experiment. Overall fitness, as indexed by mean monetary reward that participants earned in the experiment, was higher in the cultural than the acultural condition.

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 in 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. These agents are not only information producers, but are 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. If Rogers's organisms were "cognitively flexible" in this sense, it might be the case that social/cultural learning not only benefits imitators by saving costs, but also helps individual learners improve their judgmental accuracy, contributing to the overall quality of the cultural knowledge pool (cf. Boyd & Richerson, 1995). Of course, this reasoning could be wrong. Cognitive flexibility makes the individual learners more vulnerable to the influence of imitators as well, which may reduce rather than enhance their accuracy. In this sense, 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 between an information-search strategy (produce or scrounge) and an 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 Rogers's question in the next section by a theoretical model that incorporates the above features. We report a series of evolutionary computer simulations exploring the fitness advantage of cultural transmission in a temporally fluctuating environment.

3. Evolutionary computer simulation

The purpose of this simulation was to reexamine the Rogers question in a wider parametric space. Although informative, the experimental test above was limited in that it could assess only a small subset of the space. Computer simulations are useful for seeing how robust such experimental results may be in other parametric conditions. In this simulation, we use a theoretical model proposed earlier (Kameda & Nakanishi, 2002), which is an extension of theoretical work on cultural transmission by Boyd and Richerson (1985, 1995) and Henrich and Boyd (1998), and which has been demonstrated to predict actual human learning 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), we 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, and Behavior B when in State B. Natural selection favors learning mechanisms that make

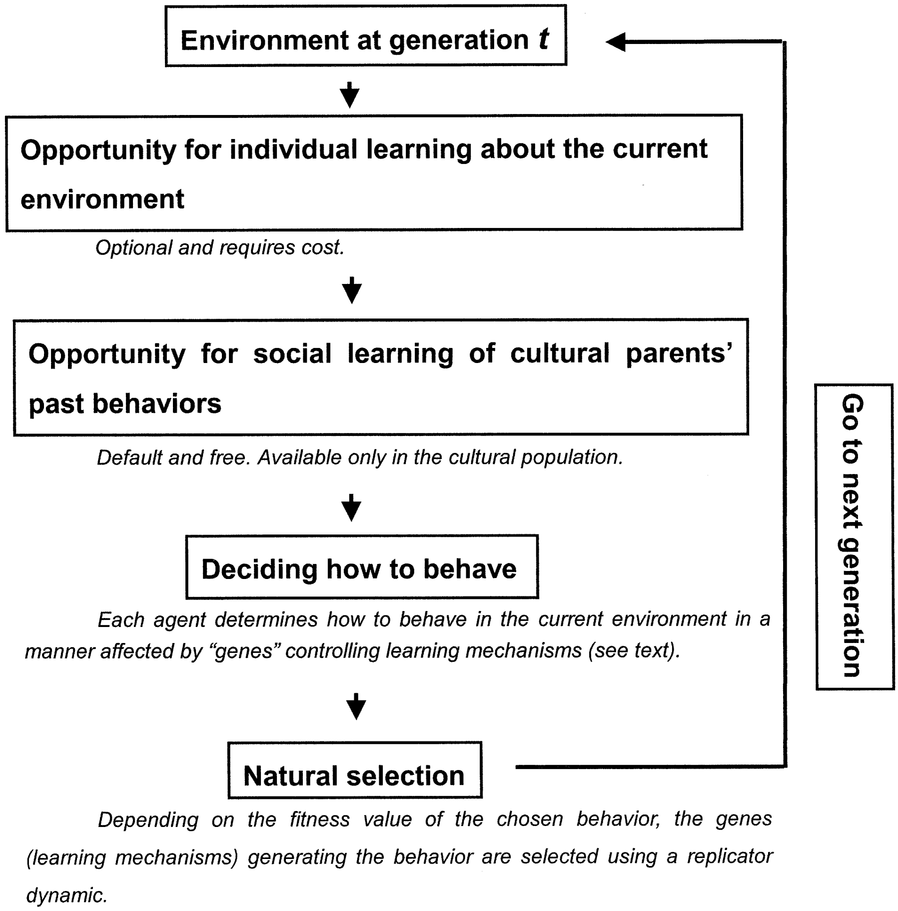

Fig. 5. An outline of Kameda and Nakanishi's (2002) simulation algorithm about evolvability of cultural learning capacities.

individuals more likely to adopt the behavior that is adaptive in the current environment (see Fig. 5, bottom). As in the experiment, we created cultural and acultural populations and continued simulation runs until an equilibrium state emerged in each population.

In the cultural population, two information sources are available for agents: opportunities for individual learning and social learning. The individual learning opportunity is optional and its usage requires paying a cost. The social learning opportunity is default, providing information about the choices of several cultural parents in the preceding generation for free.

Each cultural agent combines the two kinds of information to decide how to behave. 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 who pay the extra cost for updated environmental information; those with the "off" allele are information scroungers.

The other two genes represent the cultural agent's information-use strategy. One gene controls variations in propensity to use social information over individually acquired information, representing the "cognitive flexibility" discussed above (Boyd & Richerson, 1995). 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 the signal detection theory (Green & Swets 1966), the model assumed that each cultural agent has a decision threshold and if the signal value exceeds it, the agent makes a choice suggested by 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 (Festinger, 1954). Individual variations about the threshold were represented as effects of a gene in the simulation. (This gene was inactivated for information scroungers who had no individually acquired information and always used social information.)

Another information-use gene regulates individual variations in conformity bias when using social information (Boyd & Richerson, 1985). If the environmental signal is insufficiently diagnostic (or if the agent behaves as an information scrounger), the individual relies on social information. Suppose that two of three cultural parents chose Behavior A, while one chose Behavior B. The model conceptualizes the degree of "conformity bias" as a likelihood of preferentially adopting the most frequent behavior among the cultural parents. In this example, agents with no conformity bias adopt Behavior A proportionally (with a 67% chance), having no tendency to focus preferentially on the most common behavior. 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 — the "cultural-Festinger population," hereafter to be distinguished from the following "cultural-Rogers population" — makes a behavioral choice.

As a benchmark, we also created another cultural population where agents behaved as assumed by Rogers (1988). In this "cultural-Rogers population," information producers (Rogers's individual learners) always rely on the individually acquired information, discarding the social information completely. Technically, throughout the simulation runs, their propensity to use social information over individually acquired information (controlled by the

2nd gene) was fixed at 0, and their 3rd gene (conformity bias) was also inactivated; these individual learners are cognitively inflexible, always committing themselves to the individually acquired information. Information scroungers (Rogers's imitators) behave in the same manner as in the cultural-Festinger population.

In the acultural population, opportunity for social learning is unavailable to agents from the outset. The only gene pertinent to the acultural agents is the 1st gene, controlling variations in the costly individual 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, in all populations, natural selection operates: 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 their respective equilibria.

3.2. Results and discussion

Three simulation parameters are critical to reexamine the Rogers question theoretically: extra cost required for individual information search (Kameda & Nakanishi, 2002; Rogers, 1988), accuracy of the environmental information, and rate of environmental fluctuation (Henrich & Boyd, 1998; Richerson & Boyd, 2000). For each set of parameter values, we

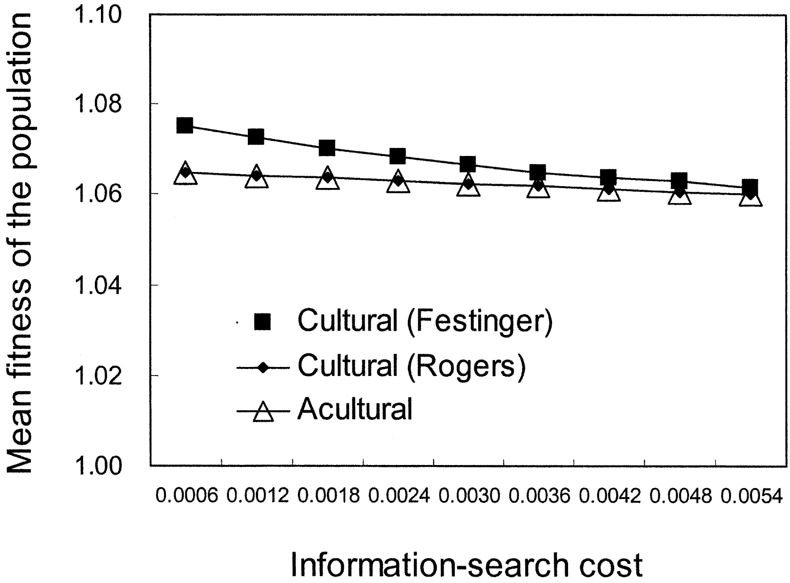

Fig. 6. Mean fitness of the cultural and acultural populations at the respective equilibria as a function of individual information-search cost (simulation: see text for the parametric setting). Mean fitness could range from 1.0 to 1.1.

conducted 10 simulation runs over 100,000 generations for the cultural (Festinger, Rogers) and acultural populations, respectively, and we averaged the results.

Fig. 6 displays mean fitness of the cultural and acultural populations at their respective equilibria as a function of individual information-search cost, which was varied systematically while keeping the other simulation parameters unchanged. The simulation parameters in Fig. 6 were set as follows: rate of environmental fluctuation = 0.04, 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 baseline fitness was 1.0. Thus, mean fitness shown in Fig. 6 (and in Fig. 8) could range from 1.0 to 1.1. The number of cultural parents was 3 for all simulation runs reported in this paper.

First, notice that mean fitness of the cultural-Rogers population was exactly identical to that of the acultural population for the range of information-search cost shown in Fig. 6. This verifies Rogers's analysis. However, mean fitness of the cultural-Festinger population was higher than that of the acultural population. 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-Festinger 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), the equilibrium proportion of information producers was about 13% in the cultural population, while it was 100% in the acultural population. Still, even with such a small proportion of information producers, the cultural-

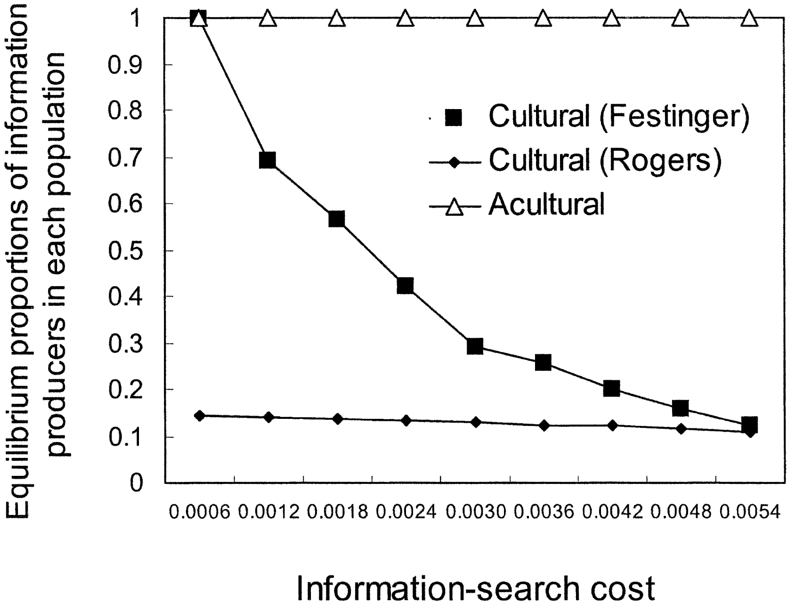

Fig. 7. Mean equilibrium proportions of information producers in the cultural and acultural populations as a function of individual information-search cost (simulation: see text for the parametric setting).

Festinger population outperformed the acultural population in mean fitness (Fig. 6). This pattern is consistent with the results of the behavioral experiment.

How robust is this result across 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 equilibria. 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. The "cultural population" hereafter refers to the cultural-Festinger population. Mean fitness of the cultural-Rogers population was identical to that of the acultural population.

A simple thought experiment may further help to see what happens outside the parameter space shown in Fig. 8. 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, because cultural information has no value with the 0.5 fluctuation rate. This means that agents in the cultural population will behave exactly as the acultural agents, and 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,

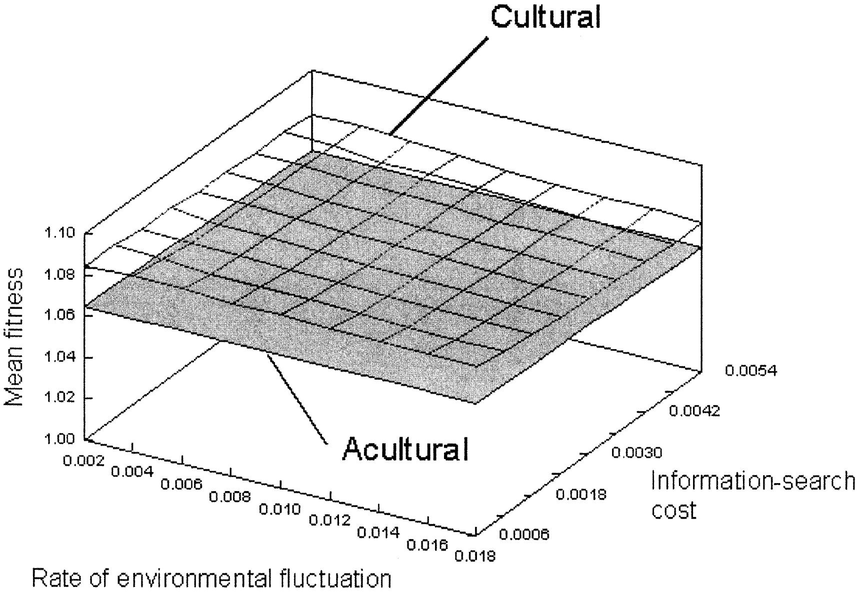

Fig. 8. Mean fitness of the cultural and acultural populations at the respective equilibria as a function of individual information-search cost and rate of environmental fluctuation (simulation: see text for the parametric setting).

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).

What, then, 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 the 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 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 long as the search cost is bearable so that some of its members acquire updated environmental information.

We also conducted a sensitivity analysis varying the accuracy of environmental information systematically. The general conclusion is unchanged: The cultural population is more fit than the acultural population for a broad range of parameter values. The advantage of the cultural population over the 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.

4. General discussion

In this paper, we revisited the Rogers question, examining the uncertainty-reduction function of cultural transmission in a nonstationary uncertain environment. Although the producer–scrounger dilemma about information provision (Kameda & Nakanishi, 2002) clearly characterized the members' interdependency in the cultural population, the cultural population was found to be more fit than the acultural population in both the behavioral experiment and the simulations. 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 relationship between the Rogers model and the setting we used in this paper. Besides the "cognitive flexibility" of agents, there may be other factors that could be responsible for the differential results between the two studies. For example, our agents could refer to several "cultural parents," with 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 empirical findings in social psychology), but these features were absent, as Rogers's agents received social information from only 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 Rogers's (1988) model refer to more than one cultural parent under a conformity bias. These changes would certainly affect the steepness of Fig. 1's fitness curve for imitators, but they should have no impact on the fitness of individual learners. Thus, as long as the individual learners remain completely asocial, making the imitators more social would not affect the Rogers model's key conclusion that cultural transmission does not increase mean fitness of the cultural population.

Another criticism of our approach may be that we isolated the cultural agents from the acultural agents in separate populations from the outset, focusing only on their population-level fitness at the respective equilibria. 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 the 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 for free, but was provided only to the cultural agents who paid extra cost for it. Although space does not allow us to report the results in detail, the overall conclusion is unchanged from the original simulation. As long as social information search is cheaper than individual information search and if the environment is not too unstable (both of which 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 further support for 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 developments in this paper imply that the "cognitive flexibility" of agents is likely to be a key for cultural transmission to be beneficial in a nonstationary uncertain environment. If agents are "Festingerian" and can switch to social information contingent on the diagnosticity of individually acquired information (Festinger, 1950, 1954), cultural learning not only benefits the information scroungers, by cost-saving, but also benefits the information producers by increasing their average accuracy (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 severely qualifies provision of updated information about the current environment. Festinger (1950, 1954) argued that humans possess such a cognitive flexibility, but he was silent about nonhuman animals. However, this type of cognitive ability may indeed be found among nonhuman 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; Heyes & Galef, 1996; Laland et al., 2000; Lefebvre, 2000; Rendall & Whitehead, 2001).

However, most of such "proto-cultures" are noncumulative. As argued by various theorists, human culture is uniquely cumulative (e.g., Boyd & Richerson, 1996; Durham, 1991; Richerson & Boyd, 2000). No single individual could ever invent the 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 that have enabled us to accumulate complex knowledge or sophisticated skills in the population over so many generations evolve? These bigger issues are 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) depend fundamentally on our capacity for "true imitation" (Boyd & Richerson, 1996; Tomassello, 1996).

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