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

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Running Head: Cultural transmission and human adaptability

Abstract

1
2 It is often taken for granted that social/cultural learning increases human adaptability, because
3 it allows us to acquire useful information without costly individual learning by trial and error.
4 Rogers (1988) challenged this common view by a simple analytic model. Assuming a
5 “cultural” population composed of individual learners engaging in costly information search
6 and imitators who just copy another member’s behavior, Rogers showed that mean fitness of
7 such a mixed “cultural” population at the evolutionary equilibrium is exactly identical to the
8 mean fitness of an “acultural” population consisting only of individual learners. Rogers’s
9 result implies that no special adaptive advantage accrues from social/cultural learning. We
10 revisited this counter-intuitive argument through use of an experiment with human subjects,
11 and by a series of evolutionary computer simulations that extended Kameda & Nakanishi
12 (2002). The simulation results indicated that, if agents can switch the individual learning and
13 imitation selectively, a “cultural” population indeed outperforms an “acultural” population in
14 mean fitness for a broad range of parameters. An experiment that implemented a
15 non-stationary uncertain environment in a laboratory setting provided empirical support for this
16 thesis. Implications of these findings for cultural capacities and some future directions are
17 discussed.

18

19

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

1 **1. Introduction**

2 Social/cultural learning is fairly common in the animal kingdom at least in its
3 elementary form. Accumulating evidence suggests that acquisition of food preferences,
4 selection of foraging or nest sites, vocal and motor patterns, etc. are influenced by “cultural”
5 transmission in some group-living species, including humans (e.g., Galef & Whiskin, 2001;
6 Giraldeau & Caraco, 2000; Heys & Galef, 1996; Laland, Odling-Smee, & Feldman, 2000;
7 Rendell & Whitehead, 2001). One major adaptive advantage usually ascribed to such cultural
8 learning is its *uncertainty-reduction* function; Cultural learning allows us to acquire adaptive
9 behaviors in an uncertain environment cheaply without costly individual learning by trial and
10 error (Boyd & Richerson, 1985; Hernich & Boyd, 1998). However, as discussed below, the
11 *temporally-fluctuating* nature of adaptive environments, which is considered to be a core
12 element of environment of evolutionary adaptedness (EEA: cf. Potts, 1996; Richerson & Boyd,
13 2000), poses a theoretical challenge to this view (Kameda & Nakanishi, 2002). Indeed,
14 Rogers (1988) presented a theoretical model implying that cultural transmission may have *no*
15 adaptive advantage in a temporally unstable environment. In this paper, through use of an
16 experiment with human subjects and by a series of evolutionary computer simulations, we
17 revisit Rogers’s question, examining the presumed uncertainty-reduction function of cultural
18 transmission in a non-stationary uncertain environment.

19 *1.1. Uncertainty reduction by social/cultural learning*

20 To illustrate the uncertainty-reduction function by social/cultural learning, let us start
21 with the “mushroom foraging problem” that we used before (Kameda & Nakanishi, 2002).
22 Suppose that you have found a clump of mushrooms in a forest but you are uncertain if they

1 are edible. Individual learning by trial and error may be fatal in this case, so a cheap and
2 reliable way to cope with this uncertainty is to ask experts' or elders' opinions, or simply
3 observe their behaviors; Especially, if you refer to more than one "cultural parent" and follow
4 their common view ("conformist transmission": Boyd & Richerson, 1985), your survival
5 chance increases significantly. Indeed, the previous literature suggests that acquisition of
6 food preferences among humans is heavily influenced by cultural transmission (Katz & Schall
7 1979; Rozin 1989; see also Galef & Whiskin 2001, for social acquisition of food preferences in
8 rats).

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

21 *1.2. Provision of updated information about the adaptive environment*

22 *1.2.1. Free-rider problem*

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

8 Kameda & Nakanishi (2002) argued that the free-rider problem about information
9 provision is essential in understanding cultural groups. In many actual situations, individual
10 learning by trial and error is costlier than social learning in energy, time, or risk. The extra
11 cost required for individual learning must be borne by the individual solely, whereas the
12 acquired information potentially benefits all members via the cultural knowledge pool. The
13 cultural knowledge pool is similar to public goods in some respects and thus a free-rider
14 problem (Hardin, 1968) complicates the issue of information provision in a temporally
15 fluctuating environment. More specifically, Kameda & Nakanishi (2002) argued that this
16 situation constitutes a *producer-scrounger dilemma* often found among social foragers (cf.
17 Barnard & Silby, 1981; Krebs & Inman, 1992; Giraldeau & Caraco, 2000; Vickery, Giraldeau,
18 Templeton, & Chapman, 1991). That is, the asymmetry in learning cost creates the possibility
19 that if many others engage in costly individual learning, it may be better for some to skip the
20 individual information search completely and “free-ride” on others’ efforts. However, if too
21 many others just rely on social information, it may be better to engage in individual learning.
22 Theoretically, this situation should yield a mixed Nash equilibrium in the cultural population,

1 However, the fitness of imitators depends critically on the frequency of other imitators. If
2 imitators are rare in the population, the quality of the cultural knowledge pool is still high,
3 allowing them to enjoy the benefit of culture without bearing the individual-learning cost.
4 This places imitators in a more fit position than individual learners. On the other hand, if
5 there are too many imitators, the imitators are likely to end up imitating other imitators; thus
6 they are less fit than individual learners. As discussed by Kameda & Nakanishi (2002), the
7 situation leads to a mixed equilibrium eventually, where individual learners and imitators
8 coexist at a stable ratio in the population.

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

19 Boyd & Richerson (1995) examined this “paradox” in detail, and concluded that the
20 Rogers thesis is logically correct as long as the only benefit of social/cultural learning is
21 cost-saving for imitators. In the following, we revisit Rogers’s question first empirically by
22 an experiment with human subjects, and then theoretically through a series of evolutionary

1 computer simulations. By linking an experiment to a theoretical model in an integrated
2 manner, this paper explores conditions under which social/cultural learning may increase
3 human adaptability via its uncertainty-reduction function.

4

5 **2. Experiment**

6 *2.1. Overview*

7 Kameda & Nakanishi (2002) empirically demonstrated that, in a cultural population,
8 *information producers* who engage in costly information search and *information scroungers*,
9 who save the search cost, coexisted at a stable ratio as a result of individual-level fitness
10 maximization. The Rogers model implies that this “cultural” equilibrium is not
11 Pareto-efficient, compared to the “acultural” equilibrium; group-level fitness (mean fitness) is
12 the same in the two populations. This feature was not tested by Kameda & Nakanishi (2002).
13 Thus, in the present experiment, we address Rogers’s (1988) question directly in a laboratory
14 setting that simulates a temporally fluctuating environment. According to the Rogers
15 framework, we created two experimental “populations”, cultural or acultural, in the laboratory.
16 In the cultural population, participants could refer to other participants’ past behaviors when
17 deciding their own behaviors in the current environment, whereas such social referencing was
18 not possible in the acultural population. Opportunity for individual learning about the current
19 environment was equally available in both populations. We then compared mean “fitness” of
20 the two experimental populations to examine the Rogers thesis.

21 *2.2. Method*

22 *2.2.1. Participants*

1 Participants were 162 (98 male and 64 female) undergraduate students enrolled in
2 introductory psychology classes at Hokkaido University, Japan.

3 *2.2.2. Experimental task*

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

15 *2.2.3. Experimental design*

16 There were 2 conditions, cultural vs. acultural. One hundred and twenty participants
17 were assigned to the cultural condition, where they played the “Where is the rabbit game?” in
18 6-person groups. Social referencing about other members’ past behaviors was possible in the
19 cultural condition, when each participant judged the current state of the fluctuating
20 environment (the rabbit’s location). In contrast, 42 participants assigned to the acultural
21 condition played the game alone without the social referencing opportunity.

22 *2.1.4. Procedure*

1 For each hourly session, eight to ten participants came together to the laboratory.
2 Upon their arrival, we randomly assigned 6 participants to the cultural condition and assigned
3 the rest to the acultural condition. Each participant was seated in a private booth and received
4 further instructions individually via computer. “Where is the rabbit?” was explained, and the
5 participants were instructed that they would play this game for many rounds (unspecified) and
6 would gain 30 yen for each round in which they guessed the location of the rabbit correctly.

7 For the six participants assigned to the cultural condition, a social learning opportunity
8 was provided. Except for the first round, judgments of three participants in the preceding
9 round, who were randomly sampled from the five group members other than self, were
10 provided to each participant for free. As discussed earlier, social learning provides
11 statistically reliable (i.e., aggregated) information cheaply, but this information may be
12 outdated due to the possibility of environmental change (the rabbit’s move). Besides the
13 social/cultural information, these participants could also obtain updated information about the
14 current environment for cost, via individual information-search. In each round, participants
15 could use a “rabbit-search-machine” by paying 15 yen (investing 50% of the potential
16 reward).¹ The rabbit-search-machine provided stochastic information about the location of
17 the rabbit. According to the “lens model” paradigm (Brunswik, 1956), three perceptual cues
18 were presented on the computer screen that diagnosed the likelihood of the rabbit’s presence in
19 each nest. By a series of pilot tests, we set the overall accuracy of the cues so that using this
20 individual learning opportunity alone (i.e. without using social information) yielded 67%
21 correct judgments on average. In a practice session before the main experiment, participants
22 were given opportunities to familiarize themselves with the search machine and its accuracy.

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

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

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

16 *2.3. Results*

17 *2.3.1. Producer-scrounger dilemma in the cultural condition*

18 We have argued that, when individual information search was costly, whereas cheap
19 social/cultural learning was possible, the producer-scrounger dilemma (Kameda & Nakanishi,
20 2002) would characterize members’ interdependency in a group, consequently qualifying the
21 average quality of the cultural knowledge pool. Fig. 2 displays mean proportions of
22 information producers in the 6-person cultural groups, who incurred the extra cost for

1 individual information search, over 60 experimental rounds. We also display overall
2 proportions of information producers in the acultural condition. Consistent with the reasoning,
3 the proportion of information producers was smaller in the cultural than in the acultural
4 condition, and the discrepancy between the two conditions became more salient over time.
5 Dividing the 60 rounds into two blocks and composing 6-person nominal groups in the
6 acultural condition, a 2 (Learning: cultural vs. acultural) x 2 (Block) repeated measures
7 analysis of variance (ANOVA) yielded a main effect for Learning [$F(1,25)=26.98, p<.0001$], a
8 main effect for Block [$F(1, 25)=32.5, p<.0001$], and a Learning x Block interaction effect [$F(1,$
9 $25)= 4.23, p=.05$].

10 -----

11 Insert Fig. 2 about here.

12 -----

13 To see if the proportion of information producers was approaching equilibrium over
14 time in the cultural condition (as predicted for the producer-scronger game: Kameda &
15 Nakanishi, 2002), we examined temporal changes in variances associated with the proportion.
16 If the proportion was indeed approaching equilibrium in the cultural condition, between-groups
17 variances that indexed variability around the means in Fig. 2 should decrease over time. A
18 multiple regression analysis on the between-group variances, with experimental round as a
19 predictor, revealed that the regression line had a negative slope ($\beta=-.35, p<.01$), confirming
20 that variability among the groups in the information producer proportion decreased as play
21 progressed. A similar analysis on within-groups variances that indexed fluctuations in the
22 proportion within each group also yielded the same pattern. Mean within-group variances

1 were 0.039 for the first block, and 0.027 for the second block [$t(19)=4.84, p<.001$].²

2 2.3.2. *Does cultural transmission increase mean fitness?*

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

7 We examined the Rogers thesis by first focusing on monetary rewards that participants
8 earned in the experiment, as a laboratory counterpart of fitness. Fig. 3 displays mean
9 monetary rewards in the cultural and acultural conditions for the first and second blocks. On
10 average, participants earned more reward in the cultural condition ($M=878$ yen) than in the
11 acultural condition ($M=794$ yen); a 2 (Learning) x 2 (Block) ANOVA yielded a significant main
12 effect for Learning [$F(1,160)=7.63, p<.01$]. No other effects were significant [Block:
13 $F(1,160)=.53, p=.47$; Learning x Block interaction: $F(1,160)=.78, p=.38$].

14 -----
15 Insert Fig. 3 about here.
16 -----

17 We also examined participants' judgmental accuracies in the game. Fig. 4 displays
18 mean number of rounds (out of 30 for each block) in which participants identified the location
19 of the rabbit correctly. Interestingly, the advantage via cultural transmission as found with the
20 "reward measure" was not observed on this "pure accuracy" measure. Although the two
21 conditions yielded comparable accuracies in the first half of the experiment, the cultural
22 condition became less accurate than the acultural condition in the second half of the

1 experiment; a 2 (Learning) x 2 (Block) ANOVA yielded a marginal effect for Learning x Block
2 interaction [$F(1,160)=3.69, p=.057$]. No other effects were significant [Learning:
3 $F(1,160)=2.70, p=.103$; Block: $F(1,160)=1.99, p=.160$].

4 Taken together, these patterns imply the following. The producer-scrouter dilemma
5 in information provision (Kameda & Nakanishi, 2002) yielded a mixed Nash equilibrium in the
6 cultural population over time (Fig. 2). The proportion of information producers at the
7 equilibrium was smaller in the cultural condition than in the acultural condition, which
8 degraded quality of the cultural knowledge pool and members' mean judgmental accuracies
9 (Fig. 4). However, compensating such decrements in judgmental accuracies, the cultural
10 population was better off than the acultural population in terms of mean fitness (Fig. 3); higher
11 judgmental accuracy in the acultural condition did not result in fitness advantage, because of
12 the higher information-search cost to be borne by each individual. These results imply that
13 the net advantage of cultural transmission (e.g., aggregated information, saving of
14 information-search cost via social learning) may indeed outweigh its disadvantage accruing
15 from the free-rider problem in producer-scrouter dilemma.

16 -----
17 Insert Fig. 4 about here.
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19 *2.4. Discussion*

20 The experimental results confirmed that the producer-scrouter problem, as implied
21 by the Rogers (1988) model, is inherent in cultural groups where social learning opportunity is
22 readily available while individual information-acquisition is costly in terms of time, energy,

1 risk, and other resources (cf. Giraldeau & Caraco, 2000; Kameda & Nakanishi, 2002).
2 However, the thesis that social/cultural learning does not increase mean fitness of the cultural
3 population because of the producer-scrounger dilemma was not supported by the experiment.
4 Overall fitness, as indexed by mean monetary reward that participants earned in the experiment,
5 was higher in the cultural than the acultural condition. Then, why this difference between the
6 theory and empirical data?

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

15 However, this characterization may be unrealistic in human cases. The social
16 psychological literature has shown that humans are selective information-users, adjusting their
17 reliance on individually-acquired information dependent on its diagnosticity (e.g., Festinger,
18 1950; Sherif, 1936). For example, in a classical paper on attitude formation, Festinger (1954)
19 argued that humans turn to “social comparison” when “physical reality checks” do not provide
20 unambiguous information for assessing the validity of their beliefs. In other words, human
21 individual learners switch to social/cultural information contingent on the diagnosticity of
22 individually-acquired (via physical reality checks) information, rather than committing

1 themselves to the latter stringently. If Rogers’s organisms were “cognitively flexible” in this
2 sense, it might be the case that social/cultural learning not only benefits imitators in cost-saving
3 but also helps individual learners improve their judgmental accuracy, contributing to the
4 overall quality of the cultural knowledge pool (cf. Boyd & Richerson, 1995). Of course, this
5 reasoning could be wrong. Cognitive flexibility makes the individual learners more
6 vulnerable to the influence of imitators as well, which may reduce rather than enhance their
7 judgmental accuracy. In this sense, cognitive flexibility may work as a double-edged sword
8 in a temporally fluctuating environment.

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

17

18 **3. Evolutionary computer simulation**

19 The purpose of this simulation was to re-examine the Rogers question theoretically in
20 a wider parametric space. Although informative, the experimental test we conducted was
21 limited in that it could assess only a small subset of the space. Computer simulations are
22 particularly useful to see how robust the experimental results may be in other parametric

1 conditions. In this simulation, we use a theoretical model that we proposed earlier (Kameda
2 & Nakanishi, 2002). This model is an extension of theoretical work by Robert Boyd, Peter
3 Richerson and Joseph Henrich about cultural transmission (Boyd & Richerson, 1985, 1995;
4 Henrich & Boyd, 1998), and has been demonstrated to predict actual human learning well in a
5 temporally-fluctuating laboratory setting (see Kameda & Nakanishi, 2002, for details). Using
6 this model, we compare mean fitness of cultural and acultural populations while varying key
7 parameters of the model systematically.

8 *3.1. Model and algorithm*

9 Fig. 5 shows a simulation algorithm of our model (see Kameda & Nakanishi, 2002, for
10 more details). Like Rogers (1988), let us assume that the environment can change between
11 two states, A and B, with a small probability in any two consecutive generations. Behavior A
12 is more fit if the environment is in state A, whereas behavior B is more fit in state B. Natural
13 selection favors learning mechanisms that make individuals more likely to adopt the behavior
14 that is adaptive in the current environment (see Fig. 5, bottom). As in the behavioral
15 experiment, we assumed cultural and acultural populations, and continued simulation runs until
16 an equilibrium state emerged in each population.

17 -----
18 Insert Fig. 5 about here.
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20 In the cultural population, two information sources are available for agents, namely,
21 opportunities for individual learning and social learning. The individual learning opportunity
22 is optional and its usage requires extra cost. The social learning opportunity is default,

1 providing information about the choices of several cultural parents in the preceding generation
2 for free.

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

9 The other two genes represent the cultural agent’s information-use strategy (Boyd &
10 Richerson, 1995; Henrich & Boyd, 1998). One gene controls variations in propensity to use
11 social information over individually-acquired information, representing the “cognitive
12 flexibility” that we discussed above. Environmental information, if acquired via costly search,
13 contains random noise, so that even though the signal suggests that the current environment is
14 in state A, it may actually be in state B. As in signal detection theory (Green & Swets 1966),
15 the model assumed that each cultural agent has a decision threshold and if the signal value
16 exceeds it, the agent makes a choice based on the individually-acquired information (e.g.,
17 adopting behavior A). However, if the signal is insufficiently diagnostic, the agent disregards
18 the individual information and relies solely on social information (see Festinger, 1950, 1954 for
19 related arguments in social psychology). Individual variations about the threshold were
20 represented as effects of a gene in the simulation (the higher one’s threshold, the more likely
21 one is to use social information).³

22 Another information-use gene regulates individual variations in conformity bias when

1 using social information (Boyd & Richerson, 1985, 1995; Henrich & Boyd, 1998). If the
2 environmental signal is insufficiently diagnostic (or if the agent behaves as an information
3 scrounger, footnote 3), the individual must rely on social information. Suppose that 2 of 3
4 cultural parents chose behavior A, while 1 chose behavior B. The model conceptualizes the
5 degree of “conformity bias” as a likelihood of preferentially adopting the most frequent
6 behavior among the cultural parents (behavior A in the above example). Agents with no
7 conformity bias adopt behavior A only proportionally (with a 67% chance in this case), having
8 no tendency to focus preferentially on the most common behavior. Agents with a full
9 conformity bias adopt behavior A with a 100% chance, always following the majority view.
10 Combining individual and social information as determined by these three genes, each agent in
11 the cultural population [“cultural(Festinger) population” hereafter to be distinguished from the
12 following “cultural(Rogers) population”] makes a behavioral choice.

13 As a benchmark, we also created another cultural population where agents behaved as
14 assumed by Rogers (1988). In this population [“cultural(Rogers) population”, hereafter],
15 information producers (individual learners in Rogers, 1988) always rely on the
16 individually-acquired information, discarding the social information completely. Technically,
17 throughout the simulation runs, their propensity to use social information over
18 individually-acquired information (controlled by the 2nd gene) was fixed at 0, and their 3rd
19 gene (conformity bias) was also inactivated; these individual learners are cognitively inflexible,
20 always committing themselves to the individually-acquired information. Information
21 scroungers (imitators in Rogers, 1988) behave in the same manner as in the cultural(Festinger)
22 population.

1 In contrast to the two cultural populations, opportunity for social learning is
2 unavailable to agents in the acultural population from the outset. The only gene pertinent to
3 these acultural agents is the 1st gene, controlling variations in the costly individual information
4 search. Agents with the “on” allele at this locus acquire updated environmental information
5 for cost and choose a behavior suggested by the information; agents with the “off” allele
6 choose one of the two behaviors randomly.

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

14 *3.2. Results & Discussion*

15 Three simulation parameters are critical to re-examine the Rogers question
16 theoretically: extra cost required for individual information search (Rogers, 1988; Kameda &
17 Nakanishi, 2002), accuracy of the environmental information, and rate of environmental
18 fluctuation (Henrich & Boyd, 1998; Richerson & Boyd, 2000). For a same set of parameter
19 values, we conducted 10 simulation runs over 100,000 generations for the cultural (Festinger,
20 Rogers) and acultural populations respectively, and averaged the results.

21 Fig. 6 displays mean fitness of the cultural and acultural populations at the respective
22 equilibrium as a function of individual information-search cost, which was varied

1 systematically while keeping the other simulation parameters unchanged (see footnote 4).
2 First, notice that mean fitness of the cultural(Rogers) population was exactly identical to that of
3 the acultural population for the range of information search-cost shown in Fig. 6. This
4 verifies Rogers's analysis. However, mean fitness of the cultural(Festinger) population was
5 higher than that of the acultural population. Fig. 7 displays equilibrium proportions of
6 information producers in each population again as a function of the search cost. The figure
7 shows that the producer proportion decreased rapidly in the cultural(Festinger) population with
8 an increase in the search cost; for example, when the search cost was 0.0054 (5.4% of the
9 benefit from choosing an adaptive behavior: cf. footnote 4), the equilibrium proportion of
10 information producers was about 13% in the cultural population, while it was 100% in the
11 acultural population. Still, even with such a small proportion of information producers, the
12 cultural(Festinger) population outperformed the acultural population in mean fitness (Fig. 6).
13 This pattern is consistent with the behavioral experiment finding.

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15 Insert Figs. 6 & 7 about here.
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17 How robustly does this result hold for other parameter values? We conducted a
18 sensitivity analysis by varying two of the key parameters (information-search cost and rate of
19 environmental fluctuation) simultaneously, while keeping the third parameter unchanged
20 (accuracy of environmental information=0.66). Fig. 8 shows mean fitness of the cultural and
21 acultural populations at the respective equilibrium. As can be seen, mean fitness of the
22 cultural population was again higher than that of the acultural population for the entire

1 parameter space examined. [The cultural population hereafter refers to the cultural(Festinger)
2 population. Mean fitness of the cultural(Rogers) population was identical to that of the
3 acultural population.]

4 -----
5 Insert Fig. 8 about here.
6 -----

7 A simple thought experiment may further help to see what happens outside the
8 parameter space shown in Fig. 8. Let us start with the rate of environmental fluctuation; what
9 if the environment becomes more variable? The most extreme case in the focal two-state
10 environment is the one with a 0.5 fluctuation rate. All else being equal, all agents in the
11 cultural population should become information producers, and their “propensity to use social
12 information over individually-acquired information” (Festinger, 1950, 1954; see Section 3.1)
13 should also become minimal, since cultural information has absolutely no value with the 0.5
14 fluctuation rate. This means that those agents in the cultural population will behave in exactly
15 the same manner as the acultural agents. Thus, there should be no difference in mean fitness
16 between the two populations in the most extreme case; Given the monotonically-decreasing
17 pattern in Fig. 8, this implies that the cultural population is more fit than the acultural
18 population even when the environment is highly variable (i.e., even if it is close to but less than
19 0.5).

20 Then, what if the individual information-search cost gets larger? As shown in Fig. 7,
21 the number of information producers decreases monotonically with an increase in the search
22 cost. The most extreme case is the one where cost required for the search exceeds the net

1 advantage accruing from it, with no information producers in the population. In this most
2 extreme case, agents in both cultural and acultural populations are vulnerable to the
3 environmental variability completely, being no different from each other in mean fitness.
4 Again, given the monotonically-decreasing pattern in Fig. 8, this implies that the cultural
5 population is more fit than the acultural population when the search cost is bearable so that
6 some of its members acquire updated environmental information.⁵

7

8 **4. General discussion**

9 In this paper, we revisited the Rogers question, examining the uncertainty-reduction
10 function of cultural transmission in a non-stationary uncertain environment. Although the
11 producer-scrounger dilemma about information provision (Kameda & Nakanishi, 2002) clearly
12 characterized members' interdependency in the cultural population, the cultural population was
13 found to be more fit than the acultural population in both the behavioral experiment and
14 simulations. In other words, the mixed cultural equilibrium as a result of individual-level
15 fitness maximization is also Pareto-efficient at the group level, compared to the acultural
16 equilibrium.

17 *4.1. Discrepancies between the Rogers model and our experiment/simulation setting?*

18 Before discussing the implications of these results, it may be useful to check once
19 again the relation between the Rogers model and the setting we used in this paper. Besides
20 the “cognitive flexibility” of agents, there may be other factors that could be responsible for the
21 differential results between the two studies. For example, our agents could refer to several
22 “cultural parents” under a conformity bias to focus preferentially on the most common

1 behavior among them (Boyd & Richerson, 1985; Henrich & Boyd, 1998; see also Kameda,
2 Tindale, & Davis, in press, for related empirical findings in social psychology), but these
3 features were absent, as Rogers's agents received social information from only one cultural
4 parent. Are these additional features responsible for the differential results? The answer is
5 negative. To see why, let us suppose that as in our model, the imitators in Rogers's (1988)
6 model refer to more than one cultural parent under a conformity bias. As can be seen in Fig.
7 1, these changes certainly affect steepness of the fitness curve for imitators, but they should
8 have no impact on the fitness of individual learners. Thus, as long as the individual learners
9 remain completely asocial, making the imitators more social would not affect the Rogers
10 model's key conclusion: Cultural transmission does not increase mean fitness of the cultural
11 population.

12 Another criticism of our approach may be that we isolated the cultural agents from the
13 acultural agents in separate populations from the outset, focusing only on their population-level
14 fitness at the respective equilibrium. What if we have two types of agents in the same
15 population and place them under the evolutionary control? Is cultural learning an
16 evolutionarily stable strategy (ESS) that outperforms acultural learning in such a mixed
17 population? We addressed this question in additional computer simulations that extended our
18 model reported in this paper. In the extended simulation, we introduced a fourth gene
19 controlling cultural or acultural learning, such that haploid agents with the "on" allele at this
20 locus were cultural agents engaging in social-information search for cost, while those with the
21 "off" allele were acultural agents skipping the social-information search. The only difference
22 from the original simulation was that social information was not given as a default, but

1 provided only to the cultural agents who paid extra cost for it; the other features were identical
2 to the original simulation. Although space does not allow us to report the results in detail, the
3 overall conclusion is unchanged from the original simulation. As long as social information
4 search is cheaper than individual information search and if the environment is not too unstable
5 (both are basic assumptions of standard models of cultural transmission: cf. Boyd & Richerson,
6 1985; Cavalli-Sforza, & Feldman, 1981; Rogers, 1988), all agents in the population become
7 cultural agents at the equilibrium. Some of these cultural agents are information producers
8 who also engage in individual information search for extra cost, but others are information
9 scroungers, constituting a mixed Nash equilibrium as in the original simulation. Taken
10 together, these results provide further support to our argument that cultural agents are more fit
11 than acultural agents for a broad range of parameters, at both the individual and population
12 levels.

13 *4.2. Implications and future directions*

14 The empirical and theoretical development in this paper implies that the “cognitive
15 flexibility” of agents is likely to be a key for cultural transmission to be beneficial in a
16 non-stationary uncertain environment. If agents are “Festingerian” and can switch to social
17 information contingent on the diagnosticity of individually-acquired information (Festinger,
18 1950, 1954), cultural learning not only benefits the information scroungers in cost-saving but
19 also the information producers in increasing their judgmental accuracy on average (Boyd &
20 Richerson, 1995; Laland, Richerson, & Boyd, 1996). In other words, cultural transmission
21 functions as an effective collective uncertainty-reduction device, even though the
22 producer-scrounger problem severely qualifies provision of updated information about the

1 current environment. Festinger (1950, 1954) argued that humans possess such a cognitive
2 flexibility, but he was silent about non-human animals. However, this type of cognitive
3 ability may indeed be found among non-human animals as well, which may explain the
4 existence of social learning in many group-living species. “Culture” at this level (i.e.,
5 behavioral variations acquired and maintained by social learning) is widely observed in the
6 animal kingdom (e.g., Galef & Whiskin, 2001; Giraldeau & Caraco, 2000; Heys & Galef,
7 1996; Laland et al., 2000; Lefebvre, 2000; Rendell & Whitehead, 2001).

8 On the other hand, most of such “proto-cultures” are non-cumulative. As argued by
9 various theorists, human culture is uniquely cumulative (e.g., Boyd & Richerson, 1996;
10 Duhram, 1991; Richerson & Boyd, 2000). No single individual could ever invent the human
11 subsistence systems, artistic productions, ideologies, religions, etc. that have existed over
12 extended periods of time. The evidence so far suggests that cumulative cultural evolution is
13 limited to humans, song birds, and perhaps chimpanzees. Why so? How could the human
14 cognitive capacities evolve that have enabled us to accumulate complex knowledge or
15 sophisticated skills in the population over so many generations? These bigger issues were
16 beyond the scope of this paper. However, future work on adaptive value of cultural
17 transmission should be directed to such issues, because the core merits of human cultures (e.g.,
18 technologies) depend fundamentally on our capacity for “true imitation” (Boyd & Richerson,
19 1996; Tomassello, 1996).

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1 **Footnotes**

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

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

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

11 ⁴ The simulation parameters in Fig. 6 were set as follows: rate of environmental
12 fluctuation=0.04, average accuracy of environmental information=0.66. The fitness value of
13 choosing an adaptive behavior in the current environment was fixed at 0.1, and the baseline
14 fitness was 1.0. Thus, mean fitness shown in Figs. 6 & 8 could range from 1.0 to 1.1. The
15 number of cultural parents was 3 for all simulation runs reported in this paper.

16 ⁵ We also conducted a sensitivity analysis varying the accuracy of environmental information
17 systematically. The general conclusion is unchanged: Cultural population is more fit than
18 acultural population for a broad range of parameter values. The advantage of cultural
19 population over acultural population takes an inverted-U shape of information accuracy, being
20 maximized when the environmental information is moderately accurate (cf. Henrich & Boyd,
21 1998). When the environmental information is perfectly accurate (i.e., noise free), there is no
22 fitness difference between the cultural and acultural populations.

1 **Figure Captions**

2 Figure 1. Cultural learning provides no fitness advantage to the population: Rogers's (1988)
3 model.

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

6 Figure 3. Mean monetary rewards (with an SD) that participants earned in the cultural and
7 acultural conditions (Experiment).

8 Figure 4. Mean judgmental accuracies (with an SD) in the cultural and acultural conditions
9 (Experiment).

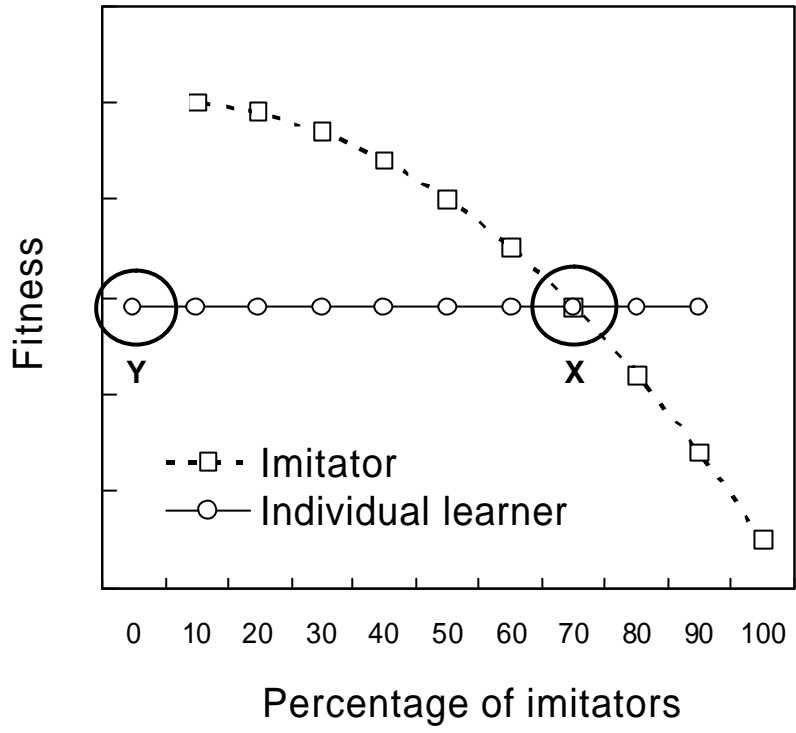
10 Figure 5. An outline of Kameda & Nakanishi's (2002) simulation algorithm about evolvability
11 of cultural learning capacities.

12 Figure 6. Mean fitness of the cultural and acultural populations at the respective equilibrium as
13 a function of individual information-search cost (Simulation: see footnote 4 for the parametric
14 setting). Mean fitness could range from 1.0 to 1.1.

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

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

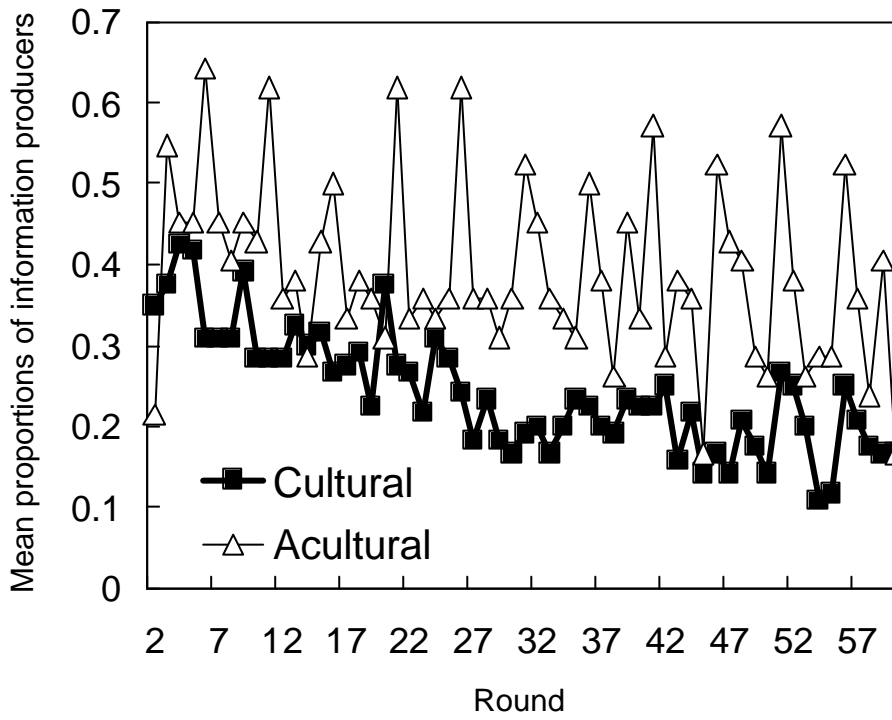
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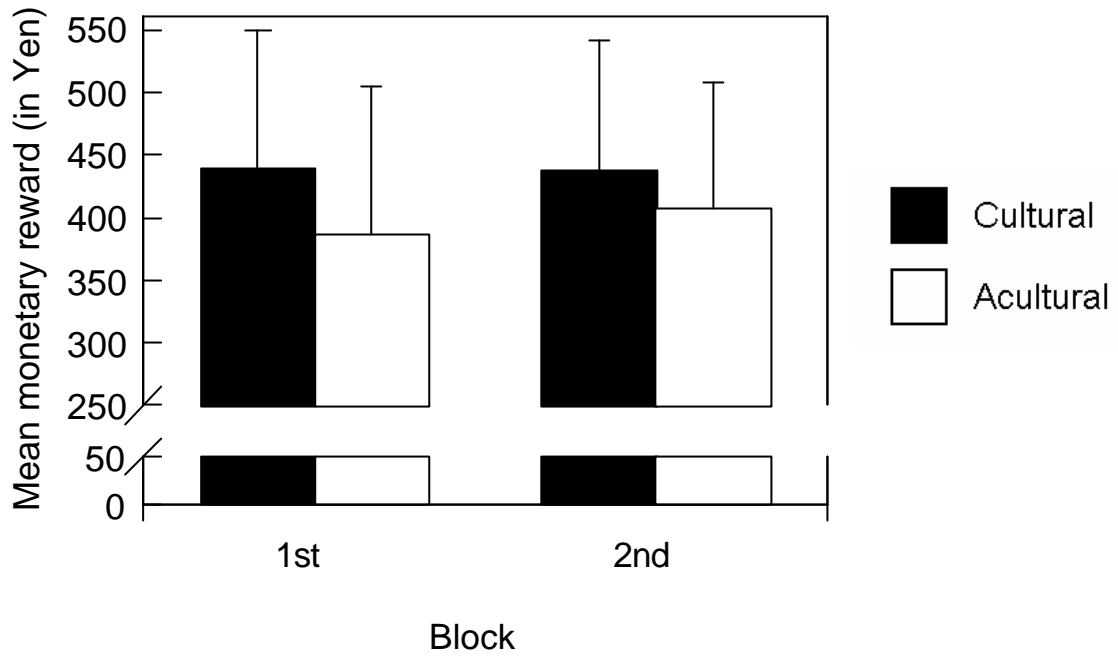
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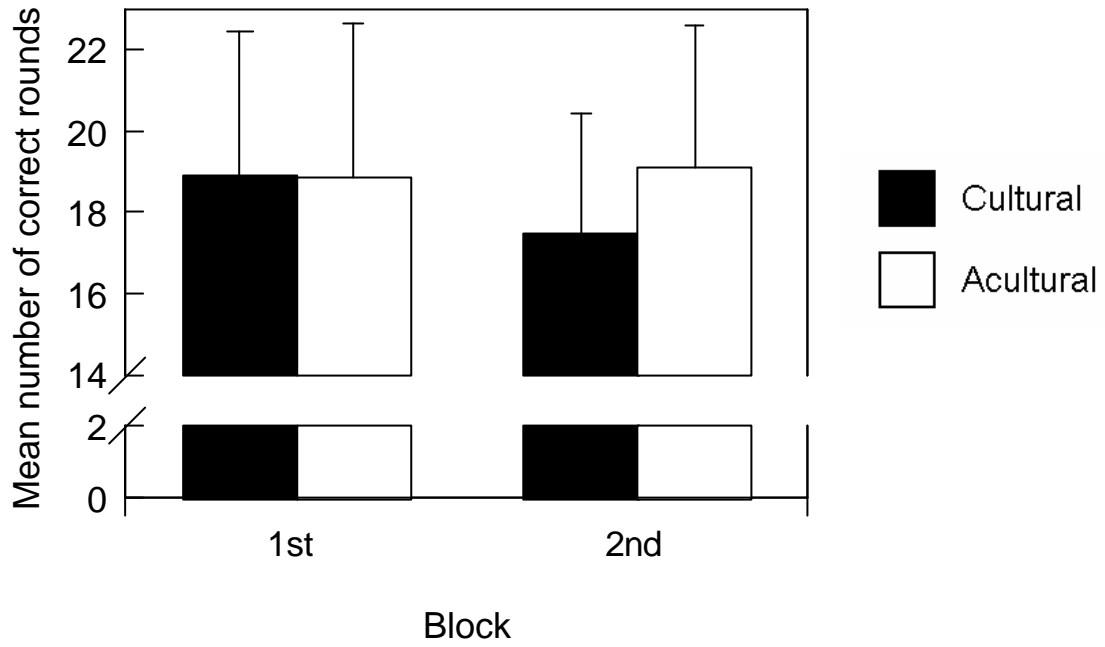
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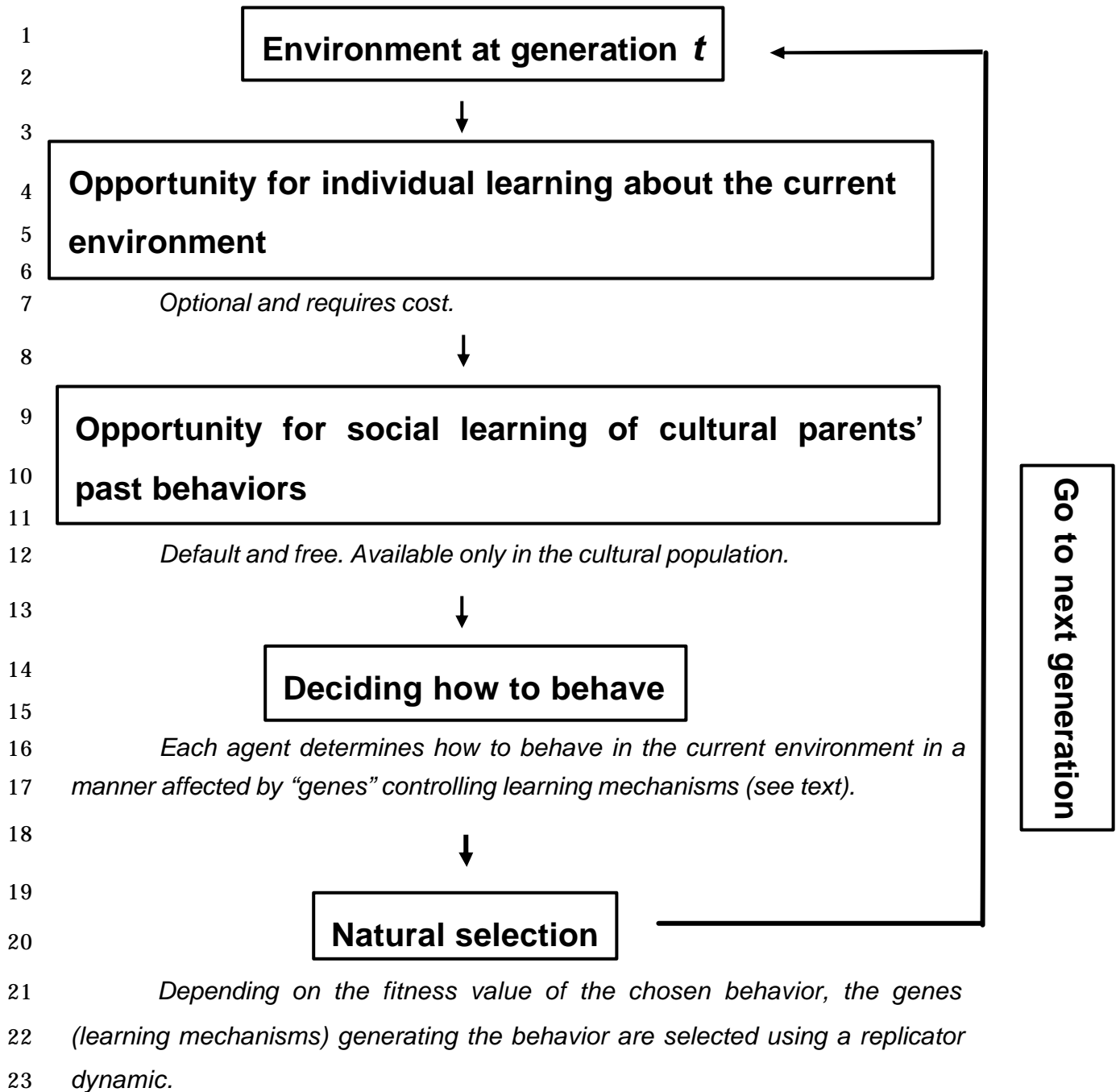
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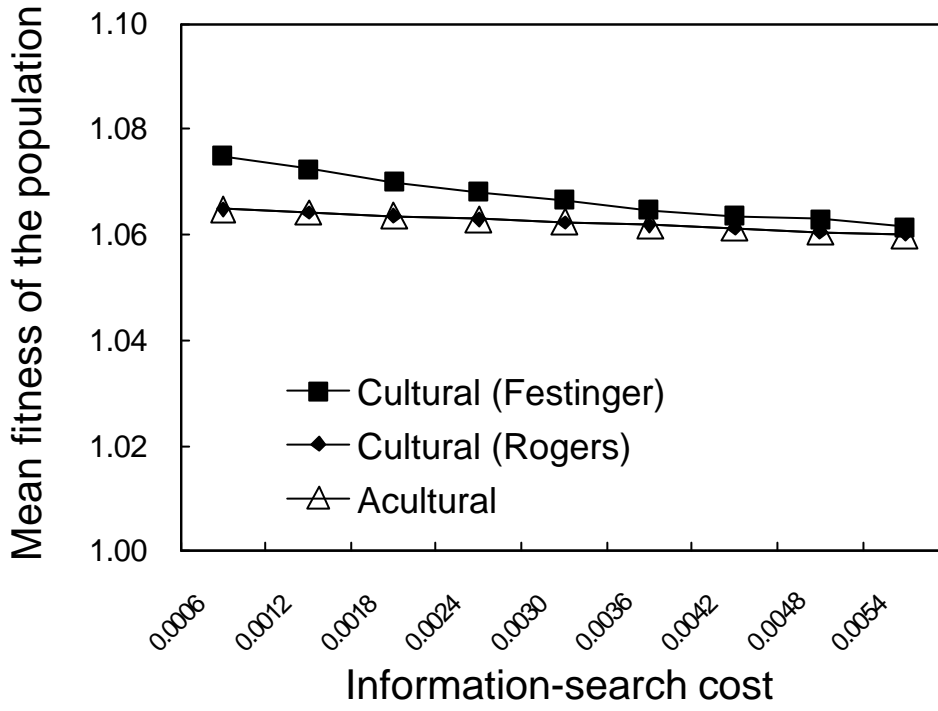


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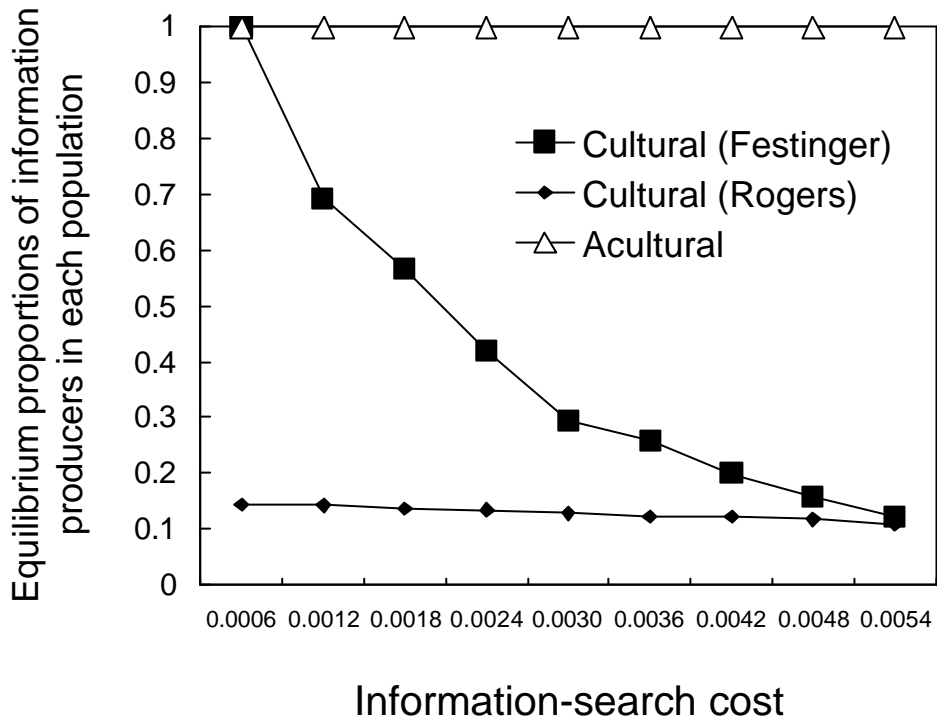
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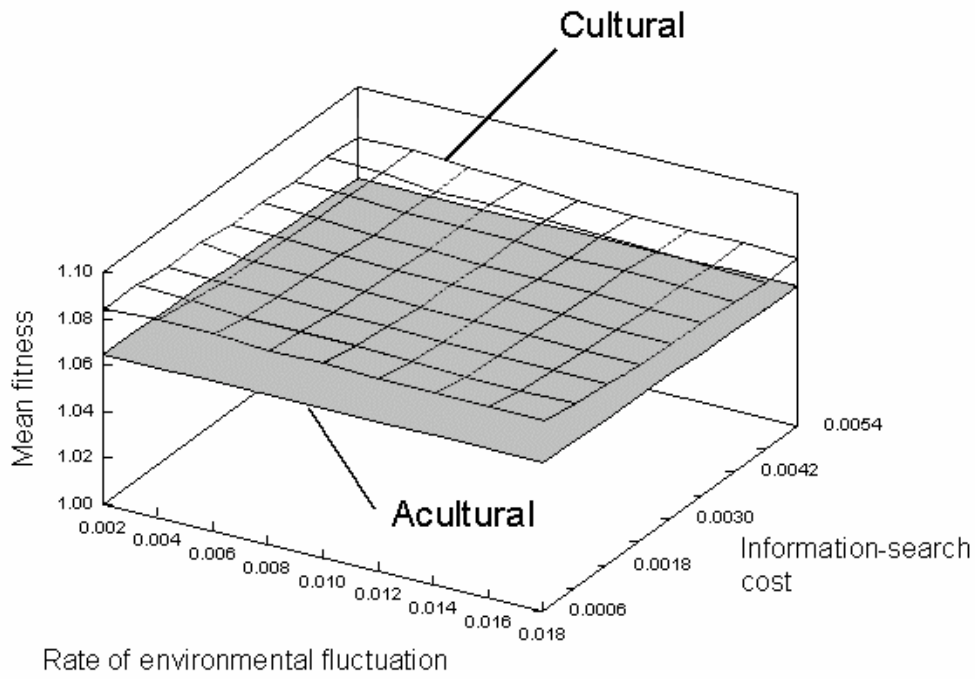
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