Vol. 3 No.2 (2012) 12-16.

LETTERS ON EVOLUTIONARY BEHAVIORAL SCIENCE



Change in One-to-Many Social Transmission When Cultural Variants Are Not Selectively Neutral

Motohide Seki^{1,*}, Yasuo Ihara²

¹ Faculty of Environmental Earth Science, Hokkaido University, N10W5, Kita-ku, Sapporo, Hokkaido 060-0810, Japan

² Department of Biological Sciences, The University of Tokyo, Hongo 7-3-1, Bunkyoku, Tokyo 113-0033, Japan

*Author for correspondence (seki.evol@gmail.com)

Cultural transmission between individuals can take various forms. One-to-many transmission refers to the case when each individual in a population socially acquires cultural traits from one particular individual who occupies a special social status, such as teacher or powerful authority. Researchers have argued that one-to-many transmission accelerates cultural change compared with one-to-one transmission, which occurs between a pair of individuals. In contrast, a recent mathematical analysis has demonstrated that the rate of cultural change is not necessarily higher with one-to-many transmission under the assumption that cultural variants are selectively neutral. Here we analyze models of one-to-one and one-tomany transmission in a situation where cultural variants are not selectively neutral. Our analysis suggests that one-to-many transmission tends to show higher rate of cultural change than one-to-one transmission when cultural variants are selectively disfavored.

Keywords

cultural evolution, learning, teacher

Introduction

A profound similarity between genetic and cultural evolution has been highlighted by many researchers (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). A genetic mutation in a single individual may be lost when the individual dies, or may increase its frequency in a population until it completely replaces the previous wild type. Similarly, a cultural innovation made by a single individual may be lost when the individual dies or abandons it, or may spread throughout the population by social transmission and eventually replace the older form. As an analogy to the rate of molecular evolution in population genetics, Aoki, Lehmann, and Feldman (2011) defined the rate of cultural change, R, as $R = Nu\pi_1$, where N is the population size, u is the innovation rate per individual per generation, and π_1 is the fixation probability of an innovation that is initially made by a single individual (i.e., the probability with which such an innovation will eventually be acquired by all individuals in the population).

An important discrepancy between genetic and cultural evolution is that while genes are inherited exclusively from parent to offspring (one-to-one transmission), cultural inheritance could take various forms. For example, an individual may decide which cultural variant to adopt by observing multiple members of the population (many-to-one transmission). Individuals may also acquire the variant possessed by one particular individual who occupies a special social status (one-to-many transmission). Aoki et al. (2011) developed a mathematical framework to compare the rates of cultural change, R, under various modes of social transmission.

The focus of this paper is on one-to-many transmission (see Pigeot, 1990, for a possible example of one-to-many transmission). With this mode of transmission, cultural change could be very fast: all members of the society will quickly adopt the trait possessed by their teacher or powerful authority. Accordingly, as Aoki et al. (2011) have pointed out, previous studies described the rate of cultural change under one-to-many transmission as "very rapid" (e.g., Lycett & Gowlett, 2008; see Aoki et al., 2011, and references therein). However, this argument was not supported by Aoki et al. (2011), who revealed that the rate of cultural change is not necessarily higher in their one-to-many transmission model than in the oblique (i.e., one-toone) transmission model.

Here we extend Aoki et al.'s (2011) analysis on one-to-many transmission by considering a case when cultural variants are not selectively neutral. On the one hand, cultural variants are not selectively neutral if different variants have different effects on the bearer's survival and/or reproduction. On the other hand, cultural variants are also regarded as non-neutral if certain variants are more likely to be retained and/or imitated than others. Accordingly, we incorporate parameters that represent relative "viability" and "fertility" of a newly innovated variant itself or its carriers. Additionally, although Aoki et al. (2011) assumed a birth-death process (one individual is born and then another dies during a unit time) in their models, we instead adopt a death-birth process (one dies and then another is born during a unit time) because we believe that the latter is more consistent with our second interpretation of non-neutral cultural variants.

In what follows, we first present our one-to-one transmission model as a baseline case and then introduce a one-to-many transmission model. The model outcomes are compared numerically and implications are discussed.

The One-to-One Transmission Model

Consider a population of N individuals, each of which carries either but not both of two cultural variants, A and B ($N \ge 2$). We assume that the following two-step process (i.e., death-birth process) takes place during each time step: first, one individual is chosen from the N individuals; and second, this individual is replaced by a copy of another individual chosen from the remaining N-1individuals. The process can represent two distinct phenomena: the first individual dies and is replaced by a newborn, who acquires the second individual's variant through vertical or oblique transmission (biological death), or the first individual abandons its cultural variant to acquire the second's variant through horizontal transmission (cultural death). In order to consider the possibility that the cultural variants are not selectively neutral, we assume that an individual carrying B (B-individual) is vtimes more (v > 1) or less (0 < v < 1) likely to be chosen at the first step of the death-birth process than an individual carrying A (A-individual). We also assume that an A-individual is s_1 times more $(s_1 > 1)$ or less $(0 < s_1 < 1)$ likely to be chosen than a B-individual at the second step of the process.

The state of the population is specified by the number of A-individuals, $i \ (0 \le i \le N)$. Denote by p_{ij} the transition probability from state i to state j, that is, the probability that the population will be in state j at time t+1 given that it is in state i at time t. The system has two absorbing states, 0 and N, each of which is always followed by the same state (i.e., $p_{0,0} = p_{N,N} = 1$). For $1 \le i \le N-1$, state i is followed by state i-1 (i+1) if and only if an A-individual (a B-individual) is chosen at the first step of the death-birth process and a B-individual (an A-individual) is chosen at the second step. Hence, we have

$$p_{i,i+1} = \frac{\nu(N-i)}{i+\nu(N-i)} \cdot \frac{s_1 i}{s_1 i+N-i-1} , \qquad (1a)$$

$$p_{i,i-1} = \frac{i}{i + \nu(N-i)} \cdot \frac{N-i}{s_1(i-1) + N-i} , \qquad (1b)$$

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1} . (1c)$$

The population will eventually reach one of the two absorbing states. The fixation probability of variant A, π_i , is the probability that the population in state *i* will eventually reach state *N*. The following should hold:

$$\pi_{i} = \begin{cases} 0 & \text{for } i = 0 \\ p_{i,i+1}\pi_{i+1} + p_{i,i}\pi_{i} + p_{i,i-1}\pi_{i-1} \\ \text{for } 1 \le i \le N - 1 \\ 1 & \text{for } i = N \end{cases}$$
(2)

Solving (2), we have

$$\pi_{i} = \begin{cases} \frac{i[(2N-1)\nu - 1 - i(\nu - 1)]}{N(N-1)(1+\nu)} & \text{if } s_{1} = \frac{1}{\nu} \\ \frac{1 - \frac{1}{(s_{1}\nu)^{i}} \left[1 + \frac{i(s_{1}-1)}{N-1 + (s_{1}-1)/(s_{1}\nu - 1)} \right]}{1 - \frac{1}{(s_{1}\nu)^{N}} \left[1 + \frac{N(s_{1}-1)}{N-1 + (s_{1}-1)/(s_{1}\nu - 1)} \right]} & \text{otherwise} \end{cases}.$$
 (3)

Note that when the cultural variants are selectively neutral ($s_1 = v = 1$), (3) reduces to $\pi_i = i/N$. The fixation probability of A when it is introduced by a single individual, π_1 , is obtained by substituting i =1 into (3):

$$\pi_{1} = \begin{cases} \frac{2\nu}{N(1+\nu)} & \text{if } s_{1} = \frac{1}{\nu} \\ \frac{1 - \frac{1}{s_{1}\nu} \left[1 + \frac{s_{1} - 1}{N - 1 + (s_{1} - 1)/(s_{1}\nu - 1)} \right]}{1 - \frac{1}{(s_{1}\nu)^{N}} \left[1 + \frac{N(s_{1} - 1)}{N - 1 + (s_{1} - 1)/(s_{1}\nu - 1)} \right]} & \text{otherwise} \end{cases}$$
(4)

The One-to-Many Transmission Model

The one-to-many transmission model differs from the one-to-one transmission model in that the population regularly has one special individual, which we call the "teacher." During each time step, one individual is chosen to die and is replaced by a newborn who acquires the teacher's variant. In case the teacher is chosen to die, a new teacher is chosen from non-teachers before the newborn's learning event (biological death). An alternative interpretation of the process is that one individual is chosen to abandon its own cultural variant to acquire the teacher's (if the learner is a non-teacher) or a non-teacher's (if the learner is the teacher; cultural death). As in the one-to-one transmission model, the probability that a B-individual is chosen to die is *v* times that of an A-individual. In addition, we assume that an A-individual is s_2 times more (s_2 > 1) or less $(0 < s_2 < 1)$ likely to be chosen as the new teacher than a B-individual is.

The state of the population is specified by the number of A-individuals, *i*, and the cultural variant possessed by the current teacher, α $(1 \le i \le N$ when $\alpha = A$ and $0 \le i \le N-1$ when $\alpha = B$). Denote the transition probability from state *i* α to state *j* β by $p_{i\alpha,j\beta}$. There are two absorbing states 0B and NA, that is, we have $p_{0B,0B} = p_{NA,NA} = 1$. For $1 \le i \le N-1$, state *i*A is followed by state (*i*+1)A if and only if a non-teacher carrying B is chosen at the first step of the death-birth process, and by state (*i*-1)B if and only if the teacher, which carries A, is chosen at the first step and a B-individual is chosen as the new teacher. Similarly, state *i*B is followed by state (*i*-1) B if and only if a non-teacher carrying A is chosen

at the first step, and by state (i+1)A if and only if the teacher, which carries B, is chosen and replaced by an A-individual. Formally, we have

$$p_{iA,(i+1)A} = \frac{v(N-i)}{i+v(N-i)} , \qquad (6a)$$

$$p_{iB,(i-1)B} = \frac{i}{i + v(N-i)}$$
, (6b)

$$p_{iA,(i-1)B} = \frac{1}{i + v(N-i)} \frac{N-i}{s_2(i-1) + N-i} , \qquad (6c)$$

$$p_{iB,(i+1)A} = \frac{v}{i + v(N-i)} \frac{s_2 i}{s_2 i + N - i - 1} , \qquad (6d)$$

$$p_{iA,iA} = 1 - p_{iA,(i+1)A} - p_{iA,(i-1)B}$$
, (6e)

$$p_{iB,iB} = 1 - p_{iB,(i+1)A} - p_{iB,(i-1)B} .$$
(6f)

Let $\pi_{i\alpha}$ denote the fixation probability of A when the population is in state $i\alpha$. The following should be satisfied:

$$\pi_{iA} = \begin{cases} p_{iA,(i+1)A} \pi_{(i+1)A} + p_{iI,(i-1)B} \pi_{(i-1)B} + p_{iA,iA} \pi_{iA} \\ \text{for } 1 \le i \le N - 1 \\ 1 \quad \text{for } i = N \end{cases}$$
, (7a)

$$\pi_{i\mathrm{B}} = \begin{cases} 0 & \text{for } i = 0\\ p_{i\mathrm{B},(i-1)\mathrm{B}}\pi_{(i-1)\mathrm{B}} + p_{i\mathrm{B},(i+1)\mathrm{A}}\pi_{(i+1)\mathrm{A}} + p_{i\mathrm{B},i\mathrm{B}}\pi_{i\mathrm{B}} \\ & \text{for } 1 \le i \le N-1 \end{cases}$$
(7b)

Solving (7), we obtain

$$\pi_{iA} = \begin{cases} \frac{N - 1 + (N - 1 + 1/\nu) \left(-d_0 + \sum_{j=0}^{i-1} d_j \right)}{N - 1 + (N - 1 + 1/\nu) \sum_{j=1}^{N-1} d_j} & \text{if } s_2 = \frac{1}{\nu^2} \\ \frac{s\nu^2 - \left(\prod_{j=1}^{i-1} r_j\right) / r_1}{s\nu^2 - \left(\prod_{j=1}^{N-1} r_j\right) / r_1} & \text{otherwise} \\ \frac{s\nu^2 - \left(\prod_{j=1}^{N-1} r_j\right) / r_1}{N - 1 + (N - 1 + 1/\nu) \sum_{j=1}^{N-1} d_j} & \text{if } s_2 = \frac{1}{\nu^2} \\ \frac{s\nu^2 \left[1 - \left(\prod_{j=1}^{i+1} r_j\right) / r_1 \right]}{s\nu^2 - \left(\prod_{j=1}^{N-1} r_j\right) / r_1} & \text{otherwise} \end{cases}$$
(8b)

where $d_j = v/[Nv^2+v-1-j(v^2-1)]$ and $r_j = 1-(s_2v-1/v)/[j(s_2-1)+N-s_2+s_2v]$. Note that when the cultural variants are selectively neutral $(s_2 = v = 1)$, (8) reduces to $\pi_{iA} = (N+i-2)/[2(N-1)]$ and $\pi_{iB} = i/[2(N-1)]$. Substituting i = 1 into (8), we have the fixation probabilities of A when it is introduced by a single individual:

$$\pi_{1A} = \begin{cases} \frac{N-1}{N-1 + (N-1+1/\nu) \sum_{j=1}^{N-1} d_j} & \text{if } s_2 = \frac{1}{\nu^2} \\ \frac{s_2 \nu^2 - 1/r_1}{s_2 \nu^2 - \left(\prod_{j=1}^{N-1} r_j\right) / r_1} & \text{otherwise} \end{cases} , \quad (9a)$$

$$\pi_{1B} = \begin{cases} \frac{(N-1+1/\nu) d_2}{N-1 + (N-1+1/\nu) \sum_{j=1}^{N-1} d_j} & \text{if } s_2 = \frac{1}{\nu^2} \\ \frac{s_2 \nu^2 (1-r_2)}{s_2 \nu^2 - \left(\prod_{j=1}^{N-1} r_j\right) / r_1} & \text{otherwise} \end{cases} . \quad (9b)$$

Note that $\pi_{1A} \ge \pi_{1B}$ always holds because of $p_{1A,2A} \ge p_{1B,2A}$, $p_{1A,0B} \le p_{1B,0B}$, and the fact that both populations starting from 1A and 1B must pass through 2A to reach *N*A.

Comparison of the Model Outcomes

The rate of cultural change for the one-to-one transmission model, $R_{\rm OtO}$, is given by $R_{\rm OtO} = Nu\pi_1$, where u is the innovation rate (i.e., the expected number of innovations made by an individual per time) of any one individual and π_1 is given by (4). Meanwhile, the rate of cultural change for the one-to-many transmission model, $R_{\rm OtM}$, is given by $R_{\rm OtM} = u_t \pi_{1\rm A} + (N-1)u_{\rm nt}\pi_{1\rm B}$, where u_t and $u_{\rm nt}$ represent the innovation rates of the teacher and of any one non-teacher, respectively, and $\pi_{1\rm A}$ and $\pi_{1\rm B}$ are given by (9).

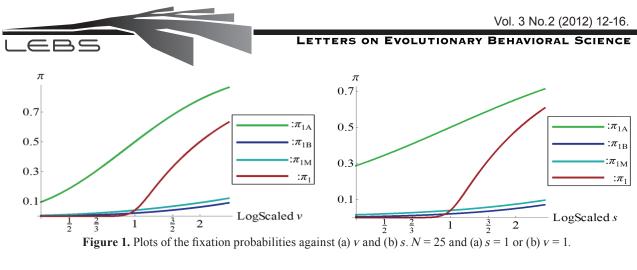
In the simplest case, where $v = s_1 = s_2 = 1$ and $u_t = u_{nt} = u$, we obtain $R_{OtO} = R_{OtM} = u$, which is identical to Aoki et al.'s (2011) result. This means that one-to-many transmission, as compared with one-to-one transmission, neither accelerates nor decelerates cultural change if cultural variants are selectively neutral and the teacher is no more or less innovative than a non-teacher.

Let us now consider the case when the cultural variants are non-neutral. For simplicity, however, we concentrate on the case when $s_1 = s_2 = s$ and $u_t = u_{nt} = u$, in which case we have $R_{\text{otM}}/R_{\text{otO}} = \pi_{1M}/\pi_1$, where $\pi_{1M} = (1/N)\pi_{1A} + (1-1/N)\pi_{1B}$. Note that $\pi_{1B} \leq \pi_{1M} \leq \pi_{1A}$ always holds (because π_{1M} is a weighted mean of π_{1B} and π_{1A}) and that $\pi_1 = \pi_{1M} = 1/N$ if v = s = 1. It is suggested numerically that $R_{\text{otM}}/R_{\text{otO}}$ becomes larger and can exceed unity when v and/or s become smaller (compare π_{1M} and π_1 shown in Figure 1).

Finally, suppose that v for each innovation follows the log-normal probabilistic distribution;

$$f(v) = \frac{1}{\sqrt{2\pi\sigma}v} e^{\frac{(\ln v - \mu)^2}{2\sigma^2}}.$$
 (10)

As shown in Figure 2, f(v) is distributed symmetrically when plotted against log-scaled v



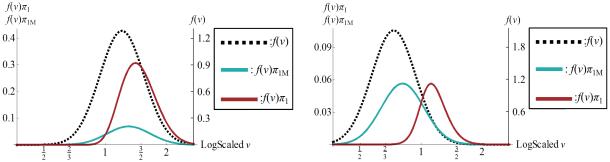


Figure 2. Plots of f(v), $f(v)\pi_1$, and $f(v)\pi_{1M}$ against *v*. The broken curve shows the probability distribution of *v* for an innovation. The area below each of the solid curves corresponds to the expected fixation probability of an innovation. N = 25, s = 1, $\sigma = 1/4$, and (a) $\mu = 1/4$ or (b) $\mu = -1/4$. The expected fixation probabilities are numerically calculated as: (a) 0.225 for the one-to-one transmission model and 0.057 for the one-to-many transmission model; (b) 0.0238 for the one-to-one transmission model and 0.0287 for the one-to-many transmission model.

(note that v is a parameter representing relative magnitude). The expected fixation probabilities of an innovation, which may be more viable (v > 1), neutral (v = 1), or less viable (v < 1) than the existing variant, under the one-to-one and one-to-many transmission models are then given by:

$$\int_{0}^{\infty} f(v)\pi_{1}(v)\mathrm{d}v , \qquad (11a)$$

$$\int_{0}^{\infty} f(v)\pi_{\mathrm{IM}}(v)\mathrm{d}v \quad (11b)$$

Examples of $f(v)\pi_1$ and $f(v)\pi_{1M}$ are also shown in Figure 2.

When we consider multiple cultural traits for each of which an innovation following (10) may be made independently, higher expected fixation probability for each innovation means more accumulation of innovations over the whole set of the traits during a given time period. Hence, our numerical analysis on (11) given in the legend of Figure 2 can be interpreted as follows: when innovations are on average more viable than the existing variants ($\mu > 0$; see Figure 2a), more innovations are expected to accumulate under the one-to-one than one-to-many transmission model, whereas when innovations are on average less viable than the existing variants ($\mu < 0$; see Figure 2b), the one-to-many transmission model predicts greater amount of accumulated innovations than the one-to-one transmission model.

Discussion

Aoki et al. (2011) showed that one-to-many transmission, as compared with one-to-one transmission, does not accelerate or decelerate cultural change so long as cultural variants are selectively neutral and the teacher and a nonteacher have the same chance of making an innovation. In the present study, we have shown that, when cultural variants are not neutral, oneto-many and one-to-one transmission may differ in the rates of cultural change, even if the teacher and non-teachers exhibit the same innovation rate. Our analysis also suggests that one-tomany transmission accelerates cultural change when innovations are on average less viable than the existing variants, but decelerates it when innovations tend to be more viable.

As mentioned earlier, the "viability" of a cultural

EBS

LETTERS ON EVOLUTIONARY BEHAVIORAL SCIENCE

variant has two distinct interpretations. Firstly, a variant that improves the bearer's survival to a greater extent can be regarded as more viable. In this case, a less viable variant may, for instance, harm the carrier's health and the accumulation of such variants could result in the rise of the average mortality of the population. Secondly, a variant that is more likely to be retained by those who have already acquired it can be regarded as more viable. With this interpretation, a less viable variant may be such that is more complicated or harder to practice. Consider, for example, there are two variations in the way a certain tool is made: one that has refined decoration requiring intense efforts and the other that is functionally equivalent but without such decoration. The former may be regarded as less viable in the sense that people are more likely to give up making it than the latter. If innovations tend to require greater efforts (and thus less viable) than the existing variants, accumulation of such innovations are expected to be faster under one-to-many transmission than under one-to-one transmission. In this sense, therefore, one-to-many transmission might serve as a driving force for assembling such delicate traits and accelerate sophistication of culture.

References

- Aoki, K., Lehmann, L., & Feldman, M. W. (2011). Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. Theoretical Population Biology, 79, 192-202. (doi:10.1016/ j.tpb.2011.02.001)
- Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.
- Cavalli-Sforza, L. L., & Feldman, M. W. (1981). Cultural transmission and evolution. Princeton: Princeton University Press.
- Lycett, S. J., & Gowlett, J. A. J. (2008). On questions surrounding the Acheulean 'tradition.' World Archaeology, 40, 295-315. (doi:10.1080/00438240802260970)
- Pigeot, N. (1990). Technical and social actors: flintknapping specialists and apprentices at Magdalenian Etiolles. Archaeological Review from Cambridge, 9, 126-141.