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Evolution of improvement and cumulative culture

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ABSTRACT

Humans have created highly developed cultures, brought about by iterative improvements in technology. Using a mathematical model, I investigated the conditions under which cultural traits tend to be improved for a higher level of culture to evolve. In the model, I consider three ways of learning: individual learning, simple social learning, and improvements of socially learned cultural traits (social improvement). I obtain the evolutionarily stable number of cultural traits acquired through each way of learning. I show that organisms improve many socially learned cultural traits under the following conditions: (1) environmental stability is intermediate; (2) the environment is severe; (3) the success rate of individual learning is high; (4) the utility of cultural traits acquired by individual learning is large; (5) the accuracy of social learning is high; and (6) the increase in the utility of beneficial cultural traits attained by social improvement is large. I also show that when organisms have greater ability for social improvement, the average utility of the beneficial cultural trait increases, the proportion of beneficial cultural traits among all cultural traits decreases, and the total number of cultural traits acquired by the three ways of learning is constant. These results shed light on the origins of human cumulative culture.

1. Introduction

To investigate the evolution of human learning ability, we must consider the cumulative character of human culture. Human culture evolves over time through iterative improvements in technology and reaches a high level that cannot be invented by a single individual (Boyd and Richerson, 1985; Tomasello, 1999). This property of human culture is often compared to a "ratchet". Although many animals learn the behaviors of others, cumulative culture exists only in humans.

Previous theoretical studies considered only simple social learning and individual (asocial) learning (Boyd and Richerson, 1988; Rogers, 1988; Feldman et al., 1996; Wakano et al., 2004; Aoki et al., 2005; Aoki and Nakahashi, 2008; Nakahashi, 2010). Here, simple social learning is defined as organisms that copy others' cultural traits without modification, and individual learning is defined as learning through organisms leading to the invention of (new) cultural traits independent of others' cultural traits. Although some studies consider social learning biases such as conformist transmission (Henrich and Boyd, 1998; Nakahashi, 2007; Wakano and Aoki, 2007; Nakahashi et al., in press), vertical transmission (McElreath and Strimling, 2008), payoff-biased transmission (Nakahashi et al., in press), and condition-dependent social learning such as conditional social learning and critical social learning (Enquist et al., 2007), these ways of social learning never modify cultural traits. Since neither simple social learning nor individual learning result in cumulative culture, considering only these two strategies when investigating the evolution of human learning abilities is an oversimplification, although this simplification is beneficial for considering the learning abilities of nonhuman animals.

To consider cumulative culture, we must include a learning strategy by which organisms improve or modify socially learned cultural traits. Some theoretical studies have introduced learning strategies and discussed conditions for their evolution. Borenstein et al. (2008) and Aoki (2010) proposed the social learner explorer strategy, in which organisms initially learn a cultural trait socially, then explore the trait individually to acquire a mature trait. Aoki et al. (2012) studied evolutionarily stable learning schedules that include a learning schedule in which social learning precedes individual learning. Ehn and Laland (2012) proposed the individual refiner strategy, in which organisms initially learn a cultural trait socially and then increase its level individually. McElreath (2010) modeled a learning strategy in which organisms acquire behavioral phenotypes through a combination of social learning and innovation, although the order of these processes was not considered.

These studies obtained interesting results, but they also had a number of problems. The most critical problem was the assumption that the process by which a socially learned cultural trait was modified was the same as the individual learning process. For example, Borenstein et al. (2008) suggested that organisms acquire an initial trait innately or by social learning, and that in both cases individuals explore the trait in the same way to acquire a mature

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trait. Ehn and Laland (2012) also considered that an individual refiner increases the level of socially learned cultural traits in the same way as individual learning. However, improving a socially learned cultural trait is a different process from that of inventing a new cultural trait. The former, for which others make a baseline, is sometimes easier than the latter, but it may yield a useless cultural trait when the concept of the socially learned cultural trait is wrong. While many animals can learn individually, few animals can improve socially learned cultural traits, suggesting that improving requires higher intelligence than inventing. Moreover, some studies considered only two environmental states (two temporally changing environments or two environmentally heterogeneous islands) so that every cultural trait was already acquired and new cultural traits never appeared at equilibrium (Borenstein et al., 2008; Aoki, 2010; Aoki et al., 2012). Since continual appearance of new cultural traits is the most important characteristic of human culture, these studies are insufficient to consider cumulative culture. The two environmental states model sometimes yields model-specific results (Aoki et al., 2012). Furthermore, these previous studies have assumed that each organism always obtains only one kind of cultural trait. Since humans learn many kinds of cultural traits, which have different roles and utilities, the assumption of learning only one kind of cultural trait is an oversimplification.

In this paper, I have developed a new model that considers improvement of socially learned cultural traits, in multiple cultural trait situations, by extending the learning capacity model proposed by Nakahashi (2010). I assume that organisms obtain multiple cultural traits through individual learning, simple social learning, and improvement of socially learned cultural traits (called social improvement). The number of cultural traits that organisms acquire under each way of learning (which we call learning capacity) is the strategy of organisms. I obtain the evolutionarily stable strategy (ESS; Maynard Smith, 1982) of learning capacities to investigate under what conditions cultural traits are frequently improved for a higher level of culture to appear.

When did human (hominid) culture become cumulative? Since the Acheulean tradition can be considered to be an extension of the Oldowan tradition, and the Mousterian tradition an extension of the Acheulean tradition, primitive cumulativeness may have appeared soon after the emergence of the genus *Homo*. However, before the emergence of modern humans (*Homo sapiens*), cultural evolutionary rates had been extremely low. The Acheulean tradition of *Homo erectus* remained much the same in the record for over a million years, which is described as a period of "unimaginable monotony" (Jelinek, 1977). Also, the Mousterian tradition of Neanderthals had been almost static for hundreds of thousands of years (Akazawa et al., 1998). That is, technological improvements had seldom occurred in these Paleolithic traditions. On the other hand, modern human culture changed frequently during and after the Upper Paleolithic in Europe (Bar-Yosef, 2002) and the Middle Stone Age in Africa (McBrearty and Brooks, 2000). Since cumulative culture is brought about by iterative improvements in technology, we can consider that highly cumulative culture appeared after the emergence of modern humans (*Homo sapiens*), though it is unclear whether behavioral modernity emerged gradually (McBrearty and Brooks, 2000) or suddenly (Klein and Edgar, 2002).

Modern humans have larger brains than extant apes and most of the extinct hominids (Robson and Wood, 2008), suggesting that large brains support the ability for highly cumulative culture. However, interestingly, Neanderthals had almost the same (or slightly larger) brain size as modern humans, but their level of cultural cumulativeness was low. The replacement of Neanderthals by modern humans is one of the most interesting problems in anthropology, and a number of hypothetical models of the causes have been proposed and tested. If Neanderthals had had smaller brains than modern humans, many researchers might think that Neanderthals became extinct because their intelligence (learning ability) was lower. Two possibilities may be considered: Neanderthals had the same learning ability as modern humans but lacked high cultural cumulativeness for some reason or Neanderthals had lower learning ability but needed the same brain size for some reason. I will discuss this problem later.

From the beginning of the Upper Paleolithic in Europe (or the Middle Stone Age in Africa), human culture became diverse and complex, and has been called the explosion of culture or the Upper Paleolithic revolution. Many kinds of cultural traits appeared in this age, and some of them (e.g., microliths, fine blades, bone tools, and ivory tools) were obviously highly developed and very useful. However, the significance of some cultural traits (e.g., beads, cave paintings, figurines, and engravings) is uncertain, although researchers tend to assign meanings to them. How can we understand these "strange" cultural traits? I will provide a new viewpoint from model results.

2. Model

Consider an infinite population with infinite kinds of cultural traits (know-how, information, technology, etc.) generated by individual learning, the mistakes of social learning, and the improvement (modification) of socially learned cultural traits. Cultural traits can be classified into two categories, beneficial and useless, and each beneficial cultural trait has different utility. In this paper, the term "utility" means the efficiency of performance of a cultural trait in promoting the acquisition of energy/resources that affect the fitness (fertility) of organisms, and does not mean a subjective measure of satisfaction. Useless cultural traits have no utility and therefore do not affect the fitness of organisms. Organisms cannot distinguish between beneficial and useless cultural traits, and acquire them by individual learning, simple social learning, and social improvement (acquiring a cultural trait by simple social learning and modifying it). The number of cultural traits organisms learn (learning capacity) is determined by their strategy gene, i.e., an organism with strategy (n, m, l) acquires n cultural traits by individual learning, m by simple social learning, and l by social improvement (individual learning capacity is n, simple social learning capacity is m, and social improvement capacity is l). Although many organisms may share the same cultural traits, the possibility that an organism learns the same cultural trait more than once can be disregarded because, by assumption, there are infinite kinds of cultural traits, and organisms acquire finite cultural traits.

In the individual learning process, organisms acquire a new cultural trait by themselves, for example, by trial and error or by insight. Let the probability of acquiring a beneficial cultural trait (success rate of individual learning) be r $(0 < r < 1)$ and the average utility of the beneficial cultural trait (individual learning level) be b.

In the simple social learning process, organisms copy a cultural trait from a random member of their parental generation (oblique transmission) and the cultural trait is randomly picked from the repertoire of the target's cultural traits pool. Let the probability of copying another's cultural trait accurately (accuracy of social learning) be $a (0 < a < 1)$. We reject the possibility that a useless cultural trait becomes beneficial by mistakes of social learning.

In the social improvement process, organisms initially acquire a cultural trait by oblique transmission as simple social learning, and then modify it. If they learn a beneficial cultural trait accurately, they increase its utility. Let the average increase of utility be bu $(u > 0)$. That is, we assume that the increase in utility achieved by social improvement is proportional to the individual learning level, and the ratio is u (improvement level). We reject the possibility that a useless cultural trait becomes beneficial through social improvement.