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Original Article

A Bayesian approach to the evolution of social learning

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Abstract

There has been much interest in understanding the evolution of social learning. Investigators have tried to understand when natural selection will favor individuals who imitate others, how imitators should deal with the fact that available models may exhibit different behaviors, and how social and individual learning should interact. In all of this work, social learning and individual learning have been treated as alternative, conceptually distinct processes. Here we present a Bayesian model in which both individual and social learning arise from a single inferential process. Individuals use Bayesian inference to combine social and nonsocial cues about the current state of the environment. This model indicates that natural selection favors individuals who place heavy weight on social cues when the environment changes slowly or when its state cannot be well predicted using nonsocial cues. It also indicates that a conformist bias should be a universal aspect of social learning.

Keywords: Cultural evolution; Learning psychology; Conformism; Bayesian learning; Bet-hedging; Origin of culture

1. Introduction

Social learning is an essential part of human adaptation and is likely a key factor generating our remarkable ecological success over the last 50,000 years (Richerson & Boyd, 2005). Social learning has been observed in a wide range of other species in diverse taxa including mammals (Galef & Laland, 2005; Perry & Manson, 2003), birds (Benskin et al., 2002; Lefebvre, 2000), fish (Brown & Laland, 2003), and even invertebrates (Leadbeater & Chittka, 2007).

There has been much interest in understanding the evolution of social learning (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Kameda & Nakanishi, 2003; McElreath & Strimling, 2008; Rendell, Fogarty et al., 2010; Rogers, 1988; Whiten et al., 2001). Investigators have tried to understand when natural selection will favor individuals who imitate others, rather than learning on their own. They have also tried to understand how selection shapes the process of imitation. What happens if there are a number of potential models exhibiting different behavior? How should observable characteristics of models, such as indicators of fitness, affect the imitation process?

In all of this work, social learning and individual learning are treated as alternative, conceptually distinct processes. Social learning is conceived as a transmission process in which the determinants of behavior are transmitted socially from one individual to another. This transmission process may be subject to errors, biases, and systematic transformations, but most work assumes that social learning leads to reasonably accurate copying. Then, to build models of cultural evolution, investigators modify mathematical models drawn from population genetics or epidemiology to account for the novel features of social learning. Most important among these are that (1) behaviors that are acquired or modified by individual learning can subsequently be transmitted and (2) social learning can be biased so that some variants are more likely to be transmitted than others. These processes are modeled as deviations from accurate, unbiased transmission. Often, it is assumed that natural selection determines the relative importance of social and individual learning so as to maximize genetic fitness. This work has been widely influential, transforming the idea of cultural evolution from a vague analogy to an active area of both theoretical and empirical research (Mesoudi, 2011).

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A number of authors have criticized this approach to the evolution of social learning on the grounds that social learning and individual learning are not psychologically distinct processes (Heyes, 1994; Plotkin, 1988). Indeed, both individual learning and social learning involve cue-based inferences about what is the best behavior in the organism's environment. Other authors have complained that much of the theoretical literature has assumed that social learning and individual learning are alternatives competing for determination of phenotype when in fact they are usually complementary processes that lead individuals in the same direction (Laland, 2004).

Here we present a simple model in which both individual learning and social learning are modeled as arising from a single learning process. We assume that learning can be modeled as Bayesian inference. This provides a useful framework for studying learning and cognitive development (Perfors & Tenenbaum et al., 2011). In this case, the environment varies, and the adaptive problem is to infer the current state of the environment using two sources of information: the behavior of the individuals from the previous generation (social cues) and information about the current state of the environment that is learned individually, such as through a trial-and-error process (environmental or nonsocial cues). There is no assumption that behavior is transmitted or copied. Rather, the central adaptive problem faced by individuals is how to behave given the observed social and environmental cues. Answering this question is tricky because the usefulness of the social cue depends on how individuals in previous generations combined social and environmental cues. When environmental cue allows accurate inference about the current environment, social learning might not be needed. Returning to home base empty-handed for several days might be a good indication that game is rare in the region and that hunting there is not the best idea. However, many adaptive problems are difficult because the environment does not provide clear cues to the best behavior. What is the best design for a bow? What causes malaria? It is not clear what decision rule will be favored by selection when the environmental cue does not allow accurate inference. The problem is that the quality of the social cue depends on the long-term effects of how individuals in the population integrate social and environmental information in their decisions. Thus, to determine the optimal reliance on social cues, it is necessary to model the coevolution of the culturally transmitted pool of information and the genes that determine how this information is transmitted. This problem is further complicated by the fact that these genes will respond to selection on individuals, not to the effect of the average quality of information on the population as a whole.

Below, we derive the evolutionary stable learning rule that specifies how much weight individuals should put on social information given some environmental cue. We find that (1) a reliance on imitation is favored when individual learning is inaccurate and environments are not too variable; (2) social learning increases average fitness because it allows individual learning to be restricted to situations in which it is accurate; and (3) when learners can observe the behavior of three or more individuals from the previous generation, they should show a conformist bias, that is, they should place a disproportionate weight on the more common behavior.

2. The model

2.1. A learning model with two cues

Consider a large population that lives in an environment that has two states: *state 1* and *state 2*. Each generation, the environment switches from the state that it is in to the alternate state with probability γ and stays in the same state with probability $1-\gamma$. Thus, over the long run, the environment is equally likely to be in each state. Individuals acquire one of two behaviors: *behavior 1* and *behavior 2*. Individuals exhibiting behavior 1 have fitness $1+d$ when the environment is in state 1 and have fitness 1 when the environment is in state 2. Similarly, behavior 2 has fitness $1+d$ when the environment is in state 2 and has fitness equal to 1 when it is in state 1. Thus, individuals need to determine the current state of the environment in order to choose the favored behavior. Individuals with the favored behavior have higher reproductive success, transmitting their genotype at a higher rate to the next generation.

Individuals have access to two cues that provide information about the current state of the environment. We assume that both cues can be represented by numbers and that the values of the cues observed by a given individual are x and y. Let $\Pr(x|1)$ and $\Pr(x|2)$ be the probability that an individual observes cue value x in environments 1 and 2, respectively. Similarly, let $\Pr(y|1)$ and $\Pr(y|2)$ be the probability that an individual observes cue value y in environments 1 and 2. Using Bayes law, the conditional probability that the environment is in state 1 given the cue values x and y is (see Electronic Supplementary Material for derivation, available on the journal's website at www.ehbonline.org):

$$Pr(1|\mathsf{x},\mathsf{y}) = \frac{Pr(\mathsf{x}|1)Pr(\mathsf{y}|1)}{Pr(\mathsf{x}|1)Pr(\mathsf{y}|1) + Pr(\mathsf{x}|2)Pr(\mathsf{y}|2)} \quad (1)$$

The conditional probability that the environment is in state 2 is just $1-\Pr(y|1)$.

Due to the symmetry of the model, an organism maximizes expected fitness by choosing the behavior that is best in the environment that is most likely given the observed cues. If state 1 is more likely to be the current state $\Pr(1|x, y)>1/2$, choose behavior 1; if state 2 is more likely, $\Pr(1|x, y)<1/2$, choose behavior 2. Thus, to maximize expected fitness, individuals should choose behavior 1 when the joint probability of the observed cues given