

# Evolution of social learning does not explain the origin of human cumulative culture

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## Abstract

Because culture requires transmission of information between individuals, thinking about the origin of culture has mainly focused on the genetic evolution of abilities for social learning. Current theory considers how social learning affects the adaptiveness of a single cultural trait, yet human culture consists of the accumulation of very many traits. Here we introduce a new modeling strategy that tracks the adaptive value of many cultural traits, showing that genetic evolution favors only limited social learning owing to the accumulation of maladaptive as well as adaptive culture. We further show that culture can be adaptive, and refined social learning can evolve, if individuals can identify and discard maladaptive culture. This suggests that the evolution of such “adaptive filtering” mechanisms may have been crucial for the birth of human culture.

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## 1. Introduction

How did humans evolve the extraordinary social learning abilities that set us apart from other animals? Because the transmission of non-genetic information is a cornerstone of culture, this question dominates current thinking on the evolutionary origins of human culture (Dawkins, 1976; Cavalli-Sforza and Feldman, 1981; de Waal, 2001; Boyd and Richerson, 1985; Tomasello et al., 1993; Heyes and Galef, 1996; Laland and Brown, 2002). Theory suggests that social learning can be favored by genetic evolution if it enables individuals to obtain information that is otherwise costly or difficult to learn (Boyd and Richerson, 1995; Richerson and Boyd, 2005), but also shows that significant bottlenecks may contrast the evolution of social learning (Boyd and Richerson, 1996). These conclusions derive from models that consider how

imitation affects the transmission and adaptive value of a single cultural trait. Here we ask whether they also hold for culture as a whole. Our approach recognizes that human culture is cumulative, consisting of very many traits elaborated over many generations (Sahlins, 1960; Boyd and Richerson, 1996; Tomasello, 1999), and that it must have a net adaptive value for social learning to be favored by genetic evolution.

## 2. The accumulation of adaptive and maladaptive culture

Assume we can partition all culture in a population into adaptive and maladaptive traits. The former promote fitness (i.e., individual survival and reproduction) while the latter detract from it. By “cultural trait” we mean anything that can be influenced by processes of social learning (Rogers, 1988), such as actions or rules for action, ideas, values and artifacts. We assume that new cultural traits are invented at a rate  $\gamma$  per generation; a fraction  $q$  of these are adaptive. Additionally, we assume that cultural traits are lost, owing to errors in social transmission, at a rate of  $\lambda$  per generation. Equivalently, we can say that the

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average lifetime of a trait is  $1/\lambda$  generations. We assume that improved abilities for social learning result in longer trait lifetimes, or smaller values of  $\lambda$ . The case  $\lambda = 0$  corresponds thus to perfectly efficient social learning, while  $\lambda = 1$  is interpreted as no social learning, since traits disappear at the rate whereby generations replace each other (inventions die with their inventors). Current models seldom consider that culture can be lost, yet losses can be an important force in cultural evolution (Henrich, 2004; Nowak, 2000). How to make a tool, process a food or use plants for healing, for example, can be lost if knowledgeable individuals fail to pass on relevant information. The balance between gains and losses appears thus an important determinant of the adaptive value of culture.

A further key observation to understand adaptive culture is that changes in the social, ecological or physical environment may turn a trait from adaptive to maladaptive (Boyd and Richerson, 1985, 1995; Rogers, 1988; Richerson and Boyd, 2005). For instance, shortage of a given prey type may render a hunting technique maladaptive. Often habits or behaviors lose adaptive value as a consequence of cultural evolution itself. The value of preserving food by fermentation, for example, has been reduced among Alaska natives after the adoption of plastic bags as food containers, in place of traditional earthen pits. Plastic bags favor the growth of botulism bacteria: the rate of death by botulism in some parts of Alaska is now more than 20 times higher than in the rest of the USA (Lancaster, 1990; Chiou et al., 2002). A famous example from technological change is the QWERTY layout that dominates computer keyboards. Designed at the end of the 19th century to avoid jamming of the typebars on mechanical typewriters, it results in suboptimal typing speed and unnecessary hand strain on modern keyboards (Noyes, 1983; Diamond, 1997). To summarize these processes, we assume that adaptive traits turn maladaptive at a rate  $\theta$  per generation ( $\theta > 0$ ), which we call the *corruption rate* of culture. Maladaptive traits may also turn adaptive by chance, but as long as this is unlikely (there are many more ways of doing things wrong than right) our results do not change.

Our assumptions result in the following differential equations for the expected number  $u$  and  $v$  of adaptive and maladaptive traits, respectively:

$$\dot{u} = -\lambda u - \theta u + q\gamma, \quad (1)$$

$$\dot{v} = -\lambda v + \theta u + (1 - q)\gamma, \quad (2)$$

where the terms  $-\lambda u$  and  $-\lambda v$  represent the loss of culture due to faulty transmission, the terms  $-\theta u$  and  $+\theta u$  represent the transformation of adaptive culture into maladaptive culture, and the terms  $+q\gamma$  and  $+(1 - q)\gamma$  refer to the creation of adaptive and maladaptive culture. These equations are an attempt to model the dynamics of adaptive and maladaptive culture directly at the population level, and they are consistent with the above description of processes that influence adaptive and maladaptive culture. We consider them as a useful first step before the

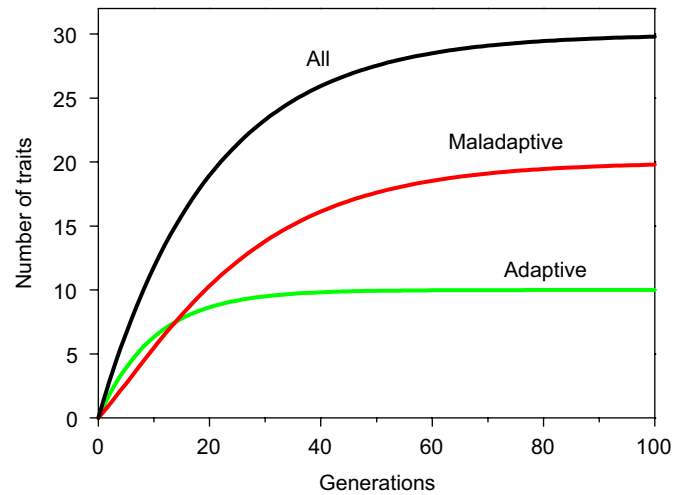


Fig. 1. Accumulation of adaptive and maladaptive culture ( $u$  and  $v$  in Eqs. (1) and (2), respectively), starting from a situation without culture. In this example adaptive traits are invented at a higher rate, yet maladaptive culture eventually dominates. Parameter values:  $\lambda = \theta = \frac{1}{20}$ ,  $\gamma = \frac{3}{2}$ ,  $q = \frac{2}{3}$ . See Appendix for explicit expressions for  $u(t)$  and  $v(t)$ .

development of a more complete, but also much more difficult, theory of the adaptive value of culture based on individual-level processes. According to Eqs. (1) and (2), adaptive and maladaptive traits reach the following cultural equilibrium values (Fig. 1, see also Appendix):

$$u_{\infty} = \frac{q\gamma}{\lambda + \theta}, \quad (3)$$

$$v_{\infty} = \frac{\gamma}{\lambda} - \frac{q\gamma}{\lambda + \theta}. \quad (4)$$

### 3. Genetic evolution of social learning leads to culture without adaptive value

We now consider the difference between adaptive and maladaptive culture, which we call the *adaptive value of culture*,  $a = u - v$ . By definition, culture promotes genetic fitness if  $a > 0$ . Assuming that cultural evolution is much faster than genetic evolution, we consider culture at equilibrium when studying genetic evolution. By Eqs. (3) and (4), the value of  $a$  at cultural equilibrium is

$$a_{\infty} = u_{\infty} - v_{\infty} = \gamma \frac{(2q - 1)\lambda - \theta}{(\lambda + \theta)\lambda}. \quad (5)$$

According to this expression adaptive culture is possible—yet for most parameter values maladaptive traits outnumber adaptive ones. The main reason is that the average time that a trait exists as adaptive is  $1/(\lambda + \theta)$ , which is smaller than the average lifetime of a maladaptive trait,  $1/\lambda$ . The adaptive value of culture decreases as the corruption rate increases ( $da_{\infty}/d\theta < 0$  for meaningful parameter values), and eventually becomes negative (Fig. 2a). Note that  $\theta$  does not influence the total amount of culture: as  $\theta$  increases adaptive culture decreases at the

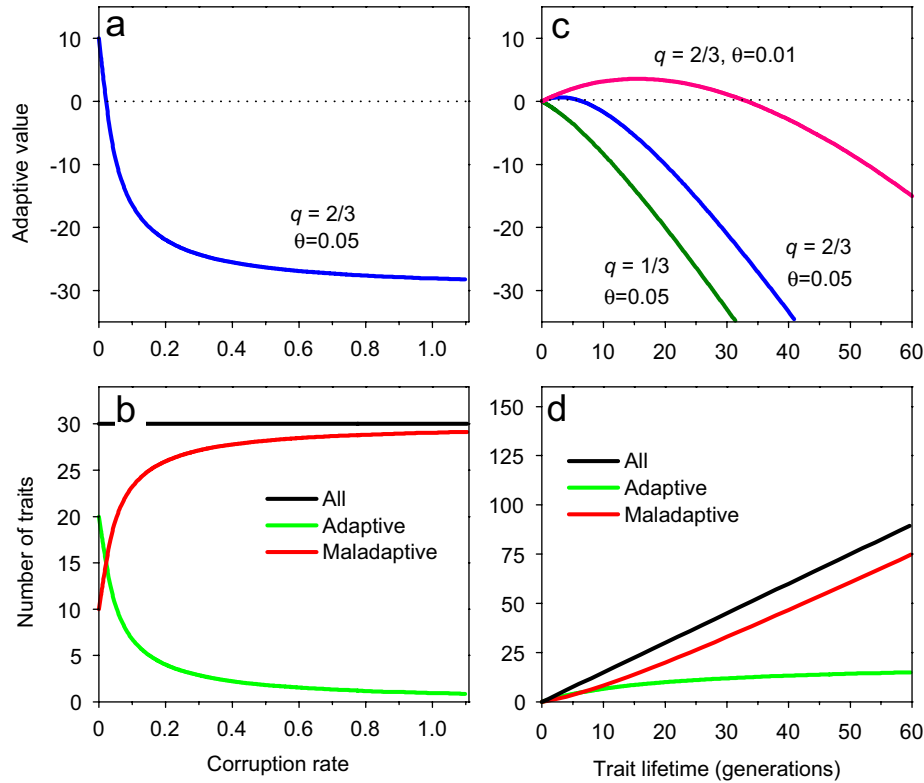


Fig. 2. The amount and adaptive value of culture as functions of corruption rate and average trait lifetime: (a) adaptive value of culture as a function of corruption rate  $\theta$ ; (b) number of adaptive and maladaptive traits as a function of  $\theta$ ; (c) adaptive value of culture as a function of trait lifetime  $1/\lambda$ , for some combinations of  $\theta$  and  $q$ ; and (d) number of adaptive and maladaptive traits as a function of trait lifetime,  $1/\lambda$ . Parameter values as in Fig. 1 unless otherwise noted.

same rate as maladaptive culture increases and their sum is constant:  $u_\infty + v_\infty = \gamma/\lambda$  (Fig. 2b). Eq. (5) also implies that culture can be adaptive ( $a_\infty > 0$ ) only if newly invented traits are on average adaptive ( $q > \frac{1}{2}$ ). In this case, the adaptive value of culture can be positive, and it is maximized by a trait lifetime of

$$\frac{1}{\lambda_{max}} = \frac{\sqrt{2q} - 1}{\theta}. \tag{6}$$

This value is remarkably small, unless the corruption rate  $\theta$  is very small. In the example in Fig. 1, for instance, a trait could stay adaptive for 20 generations ( $\theta = \frac{1}{20}$ ) yet we have  $1/\lambda_{max} \simeq 3.1$  generations (Fig. 2c).

The maximization of the adaptive value of culture, however, has no direct bearing on the genetic evolution of social learning. Since an individual acquires a fraction of the available culture, genetic evolution favors better social learning as long as adaptive culture is more common than maladaptive culture, that is as long as  $a_\infty > 0$  (we assume for now that social learning is cost free). We may thus envision the following gene-culture coevolutionary scenario. Initially there is no social learning ( $\lambda = 1$ ). Short-lived innovations are produced at a rate of  $\gamma$ , and  $q\gamma$  of these are adaptive. If  $q > \frac{1}{2}$ , social learning abilities can develop by genetic evolution, if genetic variation in such abilities exists. Thus the loss rate  $\lambda$  decreases and average trait lifetime increases. At the beginning of this process the

adaptive value of culture increases, but when the value given in Eq. (6) is passed it starts to decrease (Fig. 2c and d). Nevertheless, genetic evolution continues to favor better social learning, because individuals would still benefit from acquiring culture. Gene-culture coevolution is thus expected to improve social learning until  $u_\infty = v_\infty$ , i.e., until culture has no adaptive value. The outcome of genetic evolution is thus the trait lifetime for which  $a_\infty = 0$  (cf. Eq. 5):

$$\frac{1}{\lambda^*} = \frac{2q - 1}{\theta}, \tag{7}$$

with the same parameters as above (Fig. 1) we have  $1/\lambda^* \simeq 6.7$  generations, while  $a_\infty$  is maximum for  $1/\lambda \simeq 3.1$  generations (Eq. (6)). If a cost of social learning is added to the model, gene-culture coevolution would result in even poorer social learning.

#### 4. Adaptive filtering promotes adaptive culture and the evolution of social learning

The result that genetic evolution of imitation does not by itself create adaptive culture is consistent with some models that consider a single cultural trait (Giraldeau et al., 2003; Rogers, 1988), but is at odds with the impressive ecological success of humans (Fernández-Armesto, 2000; Richerson and Boyd, 2005). To see what is wrong with the model, let

us consider the fate of all innovations produced by a given generation. According to the model, these innovations gradually disappear and, moreover, those that remain become less and less adaptive as time passes. To prevent accumulation of maladaptive traits, it appears that each generation must “filter out”, or discard, at least some maladaptive culture. Such *adaptive filtering* is an important addition that may increase the adaptive value of culture. Assume thus that maladaptive traits are discarded at a rate  $\psi$  per generation. This decreases the average lifetime of maladaptive traits from  $1/\lambda$  to  $1/(\lambda + \psi)$  and results in the following dynamics:

$$\dot{u} = -\lambda u - \theta u + q\gamma, \tag{8}$$

$$\dot{v} = -\lambda v + \theta u - \psi v + (1 - q)\gamma. \tag{9}$$

In this model adaptive and maladaptive traits accumulate to the following equilibrium values (see Appendix):

$$u_\infty = q \frac{\gamma}{\theta + \lambda}, \tag{10}$$

$$v_\infty = \left( q \frac{\theta}{\theta + \lambda} + 1 - q \right) \frac{\gamma}{\lambda + \psi}. \tag{11}$$

The impact of the corruption rate,  $\theta$ , is qualitatively the same as in the previous model (higher  $\theta$  yields less adaptive culture), but the dependence on trait lifetime,  $1/\lambda$ , is different. Now the adaptive value of culture may stay positive, and even increase, when trait lifetime increases. At cultural equilibrium the adaptive value of culture is

$$a_\infty = \gamma \frac{(2q - 1)\lambda - \theta + q\psi}{(\lambda + \theta)(\lambda + \psi)}. \tag{12}$$

We explore this expression by first considering the case  $q > \frac{1}{2}$ . When  $1/\lambda$  increases, starting from zero, the adaptive value of culture at first increases and becomes positive (Fig. 3a). This increase continues forever if

$$\psi \geq \frac{\theta}{2} (1 + \sqrt{1 + 4/q}). \tag{13}$$

If this condition is not fulfilled,  $a_\infty$  reaches a maximum and then starts to decrease. If, however,

$$\psi > \frac{\theta}{q}, \tag{14}$$

such a decrease is limited and culture stays adaptive for any  $1/\lambda$ . In the case  $q < \frac{1}{2}$ , culture is not adaptive for small values of  $1/\lambda$ . As  $1/\lambda$  increases, the adaptive value either continues to decrease or starts to increase as a minimum is passed. In the latter case culture will eventually become adaptive if  $\psi > \theta/q$ .

The possibility of adaptive filtering changes dramatically the coevolutionary scenario for the evolution of social learning. As we saw earlier, in the absence of adaptive filtering genetic evolution is expected to improve social learning until culture is no longer adaptive ( $a_\infty = 0$ ). The latter also occurs in the present model, if  $\psi < \theta/q$ . If

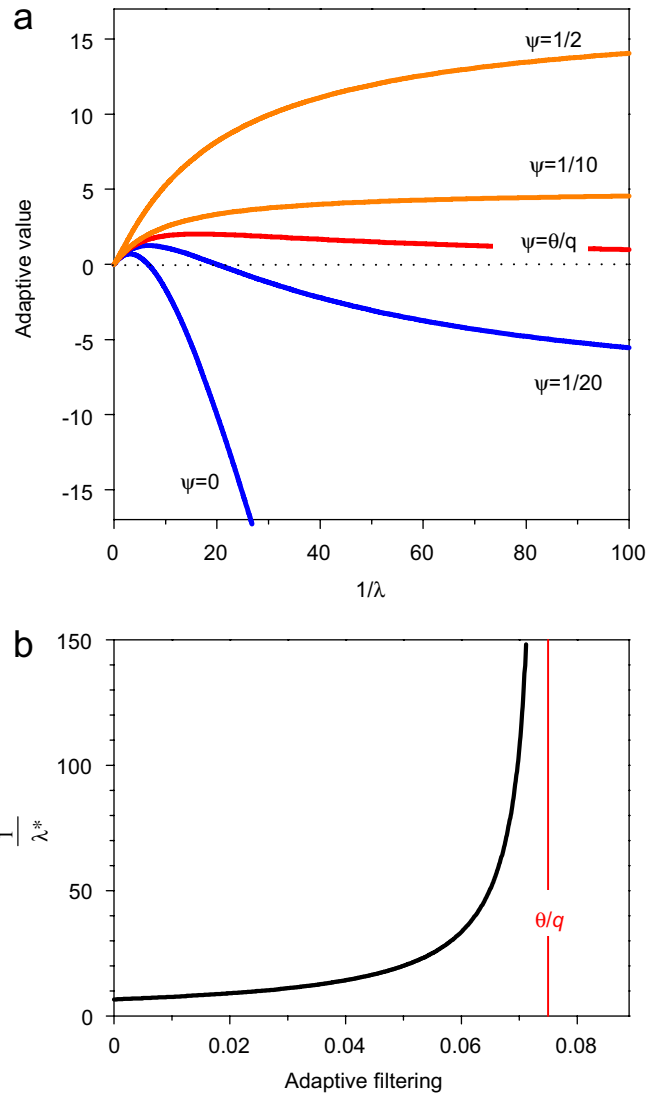


Fig. 3. The impact of adaptive filtering on the adaptive value of culture and the evolution of social learning: (a) the adaptive value of culture as a function of average trait lifetime  $1/\lambda$  for some values of the adaptive filtering rate,  $\psi$ ; and (b) the value of evolved trait lifetime,  $1/\lambda^*$ , for which the adaptive value of culture is zero as a function of the adaptive filtering rate,  $\psi$ . When  $\psi > \theta/q$  no such value exists, meaning that genetic evolution always favors improved social learning. From Eq. (12) we have  $1/\lambda^* = (2q - 1)/(\theta - q\psi)$ . Parameter values as in Fig. 1.

adaptive filtering is sufficiently strong, however, culture is adaptive for all values of  $1/\lambda$ . Thus if genetic factors for adaptive filtering evolve so that  $\psi$  passes  $\theta/q$ , genetic evolution of social learning no longer brings culture to a point where it is not adaptive. Fig. 3 illustrates the dramatic effect of adaptive filtering. If  $\psi = 0$  (blue line) we obtain the previous scenario, in which evolution of imitation occurs until  $1/\lambda^* \approx 6.7$  generations. If  $\psi = 0.05$  we have  $1/\lambda^* \approx 20$  generations (purple line) and when the threshold  $\psi = \theta/q \approx 0.075$  is reached social learning can improve without bound because culture is always adaptive (red, orange and yellow lines). With sufficient adaptive

filtering, adaptive culture is possible even if  $q < \frac{1}{2}$ , i.e., even if new traits are on average maladaptive (Eq. (12)). Genetic evolution favors individual capacities for adaptive filtering under broader conditions than capacities for social learning, because selection for adaptive filtering depends on the number of maladaptive traits,  $v_\infty$ , rather than on the difference  $u_\infty - v_\infty$  ( $\psi$  appears only in the expression for  $v_\infty$  in Eq. (10)). Thus there can be selection for adaptive filtering even when the adaptive value of culture is small, suggesting that selection for adaptive filtering may have been stronger than selection for social learning at the dawn of human culture.

## 5. Discussion

In this paper we developed a macroscopic (population-level) model of the adaptive value of cumulative culture. This strategy is similar to that employed, for instance, in much of macroeconomics (Barro and Sala-i-Martin, 2004), and it has similar advantages and disadvantages. It allowed us to avoid most of the complexities of individual-level approaches and to analyze the model formally, but it also raises some issues. In particular: What does it mean that a population “contains” a given number of traits? And are our dynamical equations good approximations to what one could derive from individual-level approaches? We have no definitive answers but there are several reasons why we think our approach can be useful.

Defining the amount of culture in a population amounts essentially to deciding how many individuals should have a given trait before it “counts” at the population level. This problem is not unique to our model but affects most definitions of culture as, e.g., a set of traits that is “shared” (Brumann, 2002) or “customary of groups of people rather than individuals” (Harris, 1971). A pragmatic solution may be to use an empirical measure, like the number of food dishes or surnames in a standardized sample of individual, and apply models to this measure. An analogy with genetic evolution also suggests that most traits should be either very common or very rare (e.g., Kimura and Crow, 1964), which minimizes the problem.

We are also convinced that our conclusions are qualitatively genuine. For instance, even in a model that explicitly tracks the transmission of culture between individuals, environmental changes would lead to a decrease of the adaptive value of culture with time, whereby (in the absence of adaptive filtering) better transmission would lead to less adaptive culture. We have also run individual-based computer simulations that support the general conclusions from our models (Enquist and Ghirlanda, unpublished data).

### 5.1. Environmental variability and the origin of cumulative culture

Our models predict that cumulative culture should evolve more easily in stable environments (small  $\theta$ ), where

the adaptive value of culture is higher (Fig. 2, Eqs. (5) and (12)) and where a smaller rate of adaptive filtering can make culture adaptive (Eq. (14)). It has been previously suggested that culture is more likely to evolve in a moderately variable environment, based on two considerations: (1) in a highly variable environment it is not useful to learn from the previous generation; and (2) in a slowly varying environment individuals can rely on genetic information (Boyd and Richerson, 1985; Richerson and Boyd, 2005). We agree with point 1 but not with 2, because the possibility that traits be genetically coded is much less relevant to the evolution of cumulative culture than it is for simple culture (e.g., of the kind displayed by living non-human primates). First, cumulative cultural evolution can be advantageous even in a constant environment, because it is much faster than genetic evolution. Second, it seems unlikely that the genes can code for artifacts beyond a certain level of complexity. The most complex tool which has been suggested to rely mostly on genetic information is the Oldowan stone tool (Richerson and Boyd, 2005), while cumulative cultural evolution has brought us much farther than that.

### 5.2. Short- and long-term adaptation

In our second model, traits that have existed for longer time are on average more adaptive (if  $\psi > \theta/q$ ), because maladaptive ones are continuously filtered out. This is what we expect in adaptive culture, and suggests a refinement of the model. In reality, environmental changes do not affect all traits equally: some traits are adaptive in few environments, others in many. For instance, information about food locations may be valid for just a generation, while a knife is almost always useful, as well as general knowledge about how the world works. So far we assumed the same corruption rate for all traits, but in Fig. 4 we explore a case in which 80% of traits stay adaptive on average one generation ( $\theta = 1$ ), while the remaining 20% stay adaptive forever ( $\theta = 0$ ). Thus, given  $q = \frac{2}{3}$  as in most of our examples, about 33% of innovations are maladaptive, 53% short-term adaptive and 13% long-term adaptive. At cultural equilibrium, however, the situation is radically different. With  $\psi = 1$ , for example, there are about 10% maladaptive, 7% short-term adaptive and 83% long-term adaptive traits. Thus adaptive filtering allows cultural evolution to preferentially accumulate traits that stay adaptive despite environmental changes.

### 5.3. Conclusion

We have shown that, if cultural traits can turn maladaptive owing to environmental change, genetic evolution of social learning leads to the accumulation of both adaptive and maladaptive culture—which soon halts the genetic evolution of imitation. But culture can remain adaptive, and imitation abilities continue to improve, if

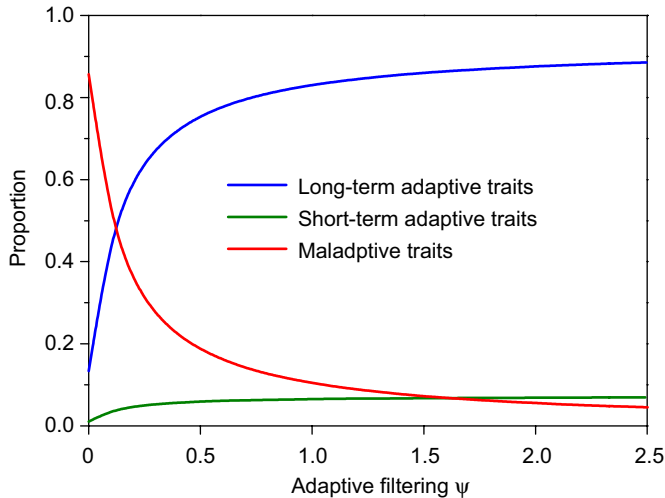


Fig. 4. The result of cultural evolution on a mixture of cultural traits where some are short- ( $\theta = 1$ , 80% of innovations) and other long-term adaptive ( $\theta = 0$ , 20% of innovations), as a function the rate of adaptive filtering,  $\psi$ . Other parameters as in Fig. 1.

maladaptive traits are continuously filtered out. Thus the evolution of adaptive filtering may have been at least as important as the evolution of imitation for the origin of human culture. We may speculate that non-human animals have only rudimentary social learning abilities (compared to humans) not because social learning is especially difficult to evolve, but because it is not useful unless one cannot discriminate between adaptive and maladaptive cultural traits.

An adaptive filter, in our model, is any process or mechanism able to reduce the number of maladaptive traits among cultural traits in a population. Existing literature, while focusing on single cultural traits, contains several suggestions about processes and behavior mechanisms that can maintain or increase the adaptive value of culture. Such suggestions include cultural analogs to selection in genetic evolution, acting on both individual and group levels (Boyd and Richerson, 1985, 2005; Gintis, 2000; Richerson and Boyd, 2005), critical social learning (Galef, 1995; Enquist et al., 2006) or other content biases or direct biases that would allow us to preferentially acquire adaptive cultural traits, e.g., so-called “success bias” (copying successful individuals) and “conformist bias” (copying preferentially what is more common, Boyd and Richerson, 1985; Henrich and Boyd, 1998; Richerson and Boyd, 2005). These mechanisms can improve the adaptive value of a single cultural trait, but their potential impact on culture as a whole remains to be assessed.

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## Appendix

The first model present in the main text consists of two coupled linear differential equations:

$$\dot{u} = -\lambda u - \theta u + q\gamma, \quad (15)$$

$$\dot{v} = -\lambda v + \theta u + (1 - q)\gamma. \quad (16)$$

These can be solved by standard techniques. A possible solution is as follows. Eq. (15) is independent of Eq. (16) and can be solved by the method of separation of variables. The solution is

$$u(t) = u_{\infty} + (u_0 - u_{\infty})e^{-(\lambda+\theta)t}, \quad (17)$$

where  $u_{\infty}$  is

$$u_{\infty} = \frac{q\gamma}{\lambda + \theta}. \quad (18)$$

The simplest way to solve Eq. (16) is to note that the sum  $x = u + v$  obeys the equation

$$\dot{x} = -\lambda x + \gamma \quad (19)$$

(obtained by summing Eqs. (15) and (16)), with solution

$$x(t) = \frac{\gamma}{\lambda} + \left(u_0 + v_0 - \frac{\gamma}{\lambda}\right)e^{-\lambda t}. \quad (20)$$

We then have  $v(t) = x(t) - u(t)$ . The second model in the main text consists of equations

$$\dot{u} = -\lambda u - \theta u + q\gamma, \quad (21)$$

$$\dot{v} = -\lambda v + \theta u - \psi v + (1 - q)\gamma. \quad (22)$$

Eq. (21) is identical to Eq. (15) and thus has Eq. (17) as solution. Eq. (22) can be solved, for instance, introducing the variable

$$z = (1 + \psi/\theta)u + v, \quad (23)$$

which according to Eq. (21), obeys

$$\dot{z} = -(\lambda + \psi)z + (\theta - (1 - q)\psi)\frac{\gamma}{\theta}. \quad (24)$$

This equation has the same form as the ones solved so far. The solution is

$$z(t) = z_{\infty} + (z_0 - z_{\infty})e^{-(\lambda+\psi)t}, \quad (25)$$

with  $z_0 = (1 + \psi/\theta)u_0 + v_0$  and

$$z_{\infty} = \gamma \frac{\theta - (1 - q)\psi}{(\lambda + \psi)\theta}. \quad (26)$$

The expression for  $v(t)$  is then recovered as  $v(t) = z(t) - (1 + \psi/\theta)u(t)$ .

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