

The Origin of Culture: Selective conditions for Horizontal Information Transfer

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Abstract

Culture is a central component in the study of numerous disciplines in social science and biology. Nevertheless, a consensus on what it is and how we can represent it in a meaningful and useful way has been hard to reach, especially due to the multifaceted aspects of its nature. In this work we dissect culture into its most basic components and propose horizontal information transfer as the most crucial aspect of it. We discuss the two fundamental processes that are required for culture to emerge in an evolutionary context, namely: high imitation error rates and survival selection. To show how each of these components affect the emergence of culture, a genetic algorithm was explored for a range of conditions. Here, we formalize when and how a population is said to move from biological to cultural evolution and why such a transition radically changes its evolutionary dynamics. Our results suggest that horizontal transfer of information in cultural systems requires the evolution of survival enhancing traits rather reproduction enhancing ones. We consider this requirement to be key for the evolution of rich cultural systems, like the one present in humans.

Introduction

Not only has the human species been able to adapt to a massive range of environments, but we have also transformed them to suit our needs. Culture is said to be one of the primary drivers for the accelerated pace at which we are able to establish and grow in new areas. (Boyd, 1985; Richerson and Boyd, 2006). Its origins are not fully understood but we know that our biological evolution must have set the stage for its emergence. In other words, just before we became a cultural species, we evolved to a point where primitive forms of social learning were possible (Richerson and Boyd, 2006). Literature offers numerous concepts of culture, for some researchers in the social sciences a superorganic view of culture, that is detached from biology, seems to offer a better and more useful explanation for the phenomena that we observe in our societies (Kroeber, 1948; Ingold, 1986). From this point of view culture would start from our biological nature but once it takes off it will be an independent process with no major feedbacks with our biological traits. For others, biology is in constant relation with

culture in deeply intertwined ways (Richerson and Boyd, 2001; Rogers, 1988). We agree, as many studies suggest, that culture has been shaped by our biological history and in return our genetic traits have evolved in response to it (Richerson and Boyd, 2006; Holden and Mace, 1997). Nevertheless, in this work we focus on the disengagement process between genes and phenotype for a particular set of evolving characteristics represented as a vector of binary traits to be optimised. This might associate our model with a more superorganic view of culture, but as it will be discussed, our analysis focuses on the evolution of traits that would spark the emergence of culture rather than on the long term interactions between genes and cultural evolution.

We maintain that culture is an outcome of genes giving rise to and interacting with an evolving environment of ideas and behaviours. Cultural variants, the equivalent of alleles in genetic systems, compete for a space in our minds and are transmitted by means of social learning (imitation and teaching), they can alter our behaviour and in many ways override some of our most basic hardwired instincts. But culture, is also population level phenomena and needs to be defined as one. Considering this, we could say that culture is: the set of behavioural traits that are not the direct result of genetic expression but rather the product of an evolving pool of variants that are stored and transmitted within and between overlapping generations of individuals, by means of social learning. This important concept is discussed in the literature and sets a starting point for our dissection (Avital and Jablonka, 2005; Richerson and Boyd, 2006). A way to understand such a concept is to think of an individual developing in social isolation. This individual would not have the culturally evolved traits that form the phenotype of its socially interacting peers, but not all the traits missing in a socially isolated organism can be considered culture. Some are the result of instinctive interactions between members of a social group and these are also hard wired in genes. It is only when we take these life history and socially instinctive traits out, that we can identify culture as the missing set of traits.

As we said before definitions of culture are numerous and,

depending on which one we select, it can be identified as a unique trait of our species or a repeatedly occurring one in nature (Laland and Janik, 2006; Laland and Hoppitt, 2003; Avital and Jablonka, 2005; Heyes and Galef, 1996). Our definition includes several animal cases like species of birds that learn their song by imitation (Jenkins, 1978; Heyes, 1994), chimpanzees that learn to use tools and simple protocols for nut cracking (McGrew, 1998), cetaceans imitating hunting strategies and mating calls (Rendell and Whitehead, 2001) and others (Laland and Galef, 2009). Even though in animal cases the complexity and repertoire of culturally evolved traits is limited, it is in principle sensible to consider a general mechanism for the emergence of culture. Our intention, as well as previous models on the evolution of culture, is to show the adaptive character of it. But before we consider the adaptive value of culture we need to describe its peculiarity and some valuable existing contributions.

At the population level culture acts as a whole new evolutionary system. In this system, evolution can only take place as long as all the ingredients of an evolutionary process are present: Reproduction, Inheritance, Mutation and Selection. The equivalent to reproduction and inheritance is implicit in the act of social learning: information gets passed from one individual to another and most of it is received. Mutation is then introduced by errors in imitation; these errors can have positive or negative effects and in this sense are fundamentally different from the effect of individual learning, which tends to improve or adapt variants during lifetime. The balance between inheritance and mutation is crucial for any evolutionary process to occur; too much mutation and the system fails in an error catastrophe. On the other hand, excessive fidelity on information transfer and the system gets stuck on a single solution (Jong, 2002). Some critics of cultural evolution point out that the equivalency of genes with cultural variants (AKA memes) is not a sensible one, due to the low signal to noise ratio of cultural transmission (Burman, 2012). This is a valid observation, but we seem to intuitively understand that ideas learned from others are very similar to the original ideas that those others hold; if this was not the case communication would be impossible. A way to reconcile these positions is to consider the convergent nature of learning towards useful forms of variants (Dawkins, 1976). When we collate new information, noise can be dramatically reduced with further practice or reinforcement because we tend to converge to the useful form of that variant. An example: nut cracking techniques that might be transmitted with a lot of noise from adults to young chimpanzees in natural populations. Maybe the original attempt is different from the proper technique but this will eventually converge to a copy of the original strategy due to the useful result obtained by it (i.e., the nut!).

Selection in cultural systems can come in a variety of forms, different biases in transmission have been identified and some of them are directly related to fitness enhancement

(Enquist et al., 2007) others are frequency dependent (conformism) (Henrich and Boyd, 1998) and some are driven by social status (Richerson and Boyd, 2006). These biases have been discussed in the literature as potential explanations for the adaptive nature of culture. Most authors refer to the seminal paper of Rogers (1988), in this paper a very simple model showed how culture is not inherently adaptive just by means of its defined characteristics or the characteristics of an evolutionary process under natural selection (Rogers, 1988). Its premise is that adapting to a new environment by means of finding an individual solution implies a cost for the learner; this cost can be avoided by imitating others, so that in a non-changing environment an invasion of imitators would be the ESS of the system due to the avoided cost. But if environmental change gets taken into consideration then individual learners increase in frequency due to the advantage that they have over imitators copying environmentally uncorrelated information. In this way, the ESS would be a mixture of individual learning and imitation determined by the rate of change in environmental conditions. Rogers's model found that the point of equilibrium does not confer any adaptive advantage to a cultural population vs. a non-cultural one; the evolution of culture considering the lack of intrinsic adaptive value is known as the Rogers's Paradox.

To solve this paradox several interesting and useful theoretical models have been developed, including extensions with transmission biases (Enquist et al., 2007), spatial dynamics (Boyd and Richerson, 1988) and population structure (Rendell et al., 2010). Here, we would like to take a step in a different direction. Rather than finding equilibria of strategies, biases or spatial structure that increase the adaptive value of culture we focus on the exploratory nature of cultural systems when it comes to finding new solutions in a fitness landscape. Particularly, we focus on the hybrid system present at the moment of transition, showing how culture originates and which are the minimal conditions for it. Our model does not consider environmental change because it focuses on the exploration and exploitation properties of biological vs. cultural systems when challenged to find novel solutions to temporally stable problems. Also, the model does not include individual learning; it merely shows the transition from instinctive behavioural traits to culturally acquired ones.

We recognize the inherent complexities of gene-to-instinct mapping and the potentially intricate mechanism for overwriting such behaviours with imitation. However, we consider that for the scope of our question such processes can be drastically simplified. Is for this reason, that in the description of our model a simple 1-to-1 map of genes to behaviour is proposed and the potential to overwrite such information with a copied behaviour is controlled by a binary switch.

Before we move our attention to the model description let us focus on individual learning and vertical imitation, both

of them important for the evolution of culture, but not included in the scope of our analysis.

There is no doubt that individual learning and cultural evolution are constantly interacting and affecting one another (Richerson and Boyd, 2006; Avital and Jablonka, 2005; Rogers, 1988). Nevertheless our question looks at the adaptive value of culture as an evolutionary algorithm and this allows us to treat individual learning as an extension of instinctive behaviours. Here we consider both to be, albeit in different ways, a result of genes and developmental conditions and even though they may differ at a mechanistic level the notion that individual learning has a cognitive tax is not relevant for the scope of our question.

Also, it is sensible to assume that vertical transfer of variants is the ancestral form of imitation. Parents tend to be the most present and readily available source of information to imitate (Avital and Jablonka, 2005). Nevertheless, systems that depend entirely on vertical imitation would not be fundamentally different from genetic systems and would merely represent the same algorithm with an added substrate for information transmission. In order for culture to represent a novel evolutionary system where ideas and not organisms are selected, horizontal transmission should be included. For this reason we concentrate mostly on this sort of transmission in our analysis, only exploring its vertical counterpart in a later section. From here on we will equate the evolution of culture with the evolution of horizontal transmission, unless otherwise specified.

The Simulation Model

The model is a steady-state genetic algorithm in which each individual is represented by two strings of bits. The first string is considered the phenotype and the second the genotype. A 1-to-1 mapping from genotype to phenotype represents genetic expression. Fitness evaluations are made considering only the phenotypic information. Genotypes have an extra bit that acts as an imitation switch: if its value is 1 the individual will substitute the genetic expression string of bits in its phenotype for the phenotype of a randomly selected individual in the population. If the value is 0 the genotype string is copied into the phenotype, excluding the imitation bit. The action of imitation takes place at birth for each individual and once it has happened the phenotype remains unchanged for its lifetime.

Phenotypic imitation has an associated mutation rate, here described as μ_p . In the same way, genetic reproduction incorporates a mutation rate μ_g which also affects the extra imitation bit (switch) in the genotype string. Genetic expression, that is genotype to phenotype copying when the switch value is 0, does not include any errors. For all the results shown in this paper the value of μ_p and μ_g are fixed with a bitflip chance of 0.01 and 0.001 respectively, unless specified.

The population is initially set with an imitation switch

value of 0. and the second half of both strings of bits is set to 0s and, the first half is set to 1s. This is done to avoid mutation biases that would create an upward trend in fitness under lack of selective pressure. The fitness landscape explored in this paper is the one defined by the sum of ones in the string of bits. In this way a string of all-1 represents the optimal solution. For all the results shown here the length of the bit string is two hundred bits ($L = 200$), and the size of the population is one hundred individuals ($N = 100$). The general results can be reproduced with larger populations and larger strings of bits; smaller populations can produce different results between individual simulations but on average they would follow the behaviours here described. The processes we discuss here are relevant when the bit string is long enough for a search and optimization period of several iterations to take place. Single-digit bit strings, for example, might not reproduce the results we describe here.

Selection is established by the joint action of a reproduction function and a death function. Reproduction selects an individual of the population with a probability P_r from a Boltzmann-weighted function distribution of Fitness (Eq. 1). The death function uses the same method but with the complement of the number of ones in the phenotype vector rather than the fitness value $L - L_1$ calculating in this way the chance of dying as P_d (anti-fitness) (Eq. 2). On each iteration a mutated copy of the individual selected by the reproduction function will substitute the individual one selected by the death function.

$$P_r = e^{\frac{L_1}{x_r}} \quad (1)$$

$$P_d = e^{\frac{L-L_1}{x_d}} \quad (2)$$

Different combinations of strength between survival and fertility were considered by changing the value of the exponents x_d and x_r . Random selection for reproduction and random selection for death are also included in our results. Figure 1 illustrates the algorithm we have described here.

This model does not include crossover functions; we recognize that recombination advantages can be added to the cultural process by increasing the source of possible models to follow. Future work would be oriented towards exploring the advantage of cultural multi-parent crossover vs. bi-parental crossover in genetic reproduction. Here, we decided to focus on the effects of horizontal transfer of information.

Results

Simulations were run for a range of values (mutation rates, population size, vector length and selection strength). Results suggest that the relation between mutation rates and the type and strength of selection are critical for the evolution of horizontal information transfer to take place. Before

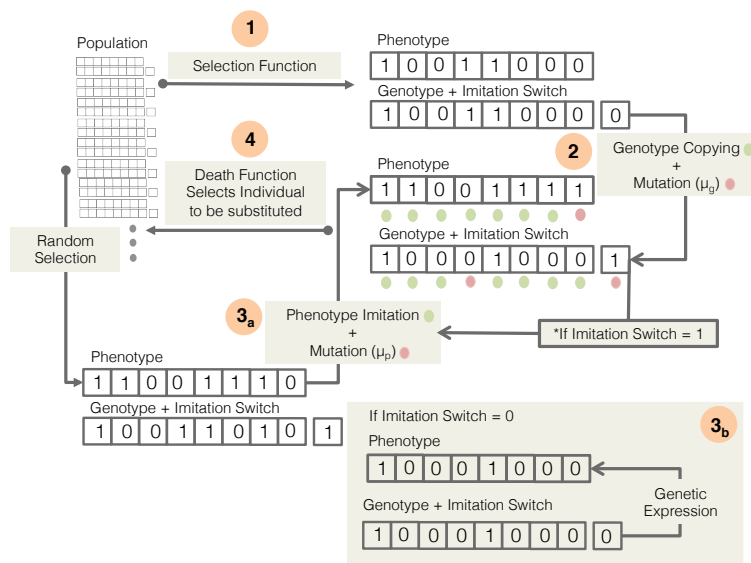


Figure 1: The diagram shows an iteration of the algorithm: (1) the selection function picks an individual from the population, (2) its genotype string is copied including the imitation switch (mutations may occur), (3a) if the imitation switch is equal to one, a random individual from the population will be selected and its phenotype will be copied with an associated imitation error. (3b) if the switch is equal to zero the bit string in the genotype will be copied into the phenotype with total fidelity. (4) The resulting combination of phenotype and genotype will replace an individual selected by the death function.

discussing these critical points it is important to describe the three possible behaviours emerging from these simulations. Figure 2 describes these scenarios.

In case A disengagement between phenotype and genotype fitness takes place early in the simulation along with a rapid growth in the proportion of imitators. Here, survival selection establishes a fitness-proportional life length for cultural variants. This case distinctively shows how the evolutionary process is taken over by horizontal imitation. Selection only evaluates phenotypes while genes get masked as soon as imitation frequency rises. Further evolution increases the gap between phenotype and genotype, making it even more costly to stop imitating and start expressing information from the genome. Eventually an evolutionary process entirely dependent on social learning finds the optimal solution and information is then maintained in individuals' actions rather than genes.

Case B is similar to A but here the selection strength for the phenotype is not enough to reach the optimal solution, this case occurs when survival selection is low ($x_d \gg 1$). Imitation, with its high mutation rate, will initially outper-

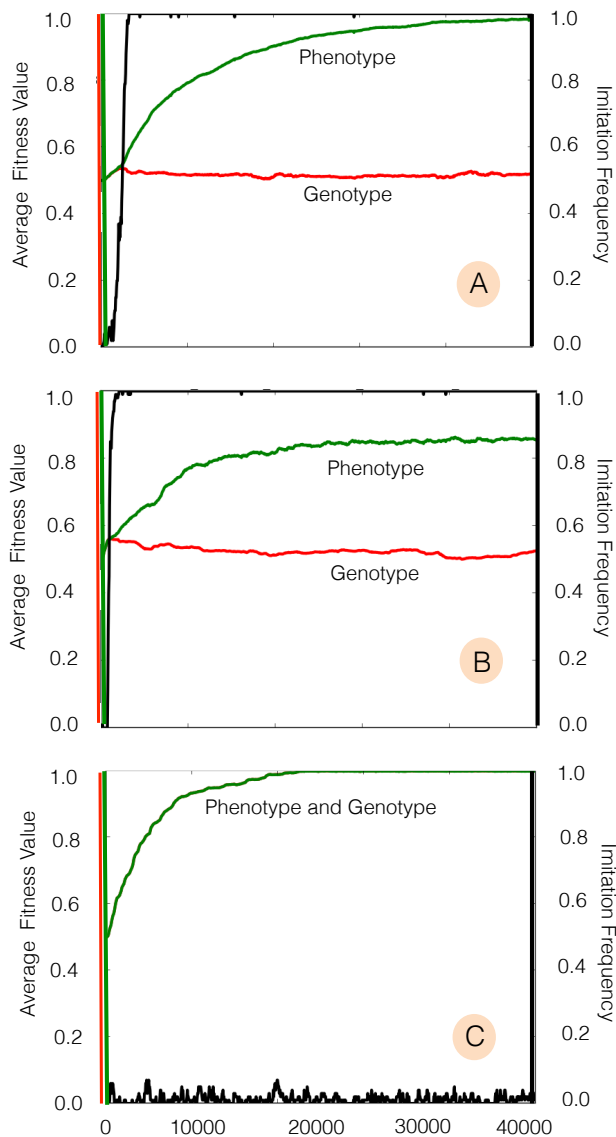


Figure 2: Single runs showing the three different scenarios: (A) Culture emerges early in the simulation under strong survival selection and the fitness disengagement between phenotype (green line) and genotype (red line) is accompanied by the sudden increase of imitation frequency (black line) ($x_d = 1, x_r = \infty$). (B) The fixation of imitators is also accompanied by fitness disengagement, but in this case the balance between selection and mutation prevents the phenotype from reaching the optima while the high frequency of imitation masks the genotype from selection. This case takes place under weak survival selection ($x_d = 5, x_r = 1$). (C) Disengagement is not present when survival selection is absent, both imitation rates stay low. Genetic evolution dominates ($x_d = \infty, x_r = 1$).

form the search ability of genes but eventually fail to reach the optima after disengagement. Selection on the genotype is masked making it impossible for genes to catch up. Variations of case B are rarely found under lack of survival selection; in these cases there is a chance that genetic fitness will eventually match phenotype fitness, if this trend goes beyond mid way the solution gradient (average of a drifting pattern), imitation frequency will drop to zero and the population will evolve genetically from then on.

Case C shows a standard genetic evolution scenario where both phenotype and genotype correlate all the way to the optimal solution; in this case imitation rate remains low. These genetic systems rely on vertical inheritance, which, under reproductive selection alone, is the only way to consistently optimize solutions. Simulations tend to converge to case C under lack of survival selection.

Types of Selection in Cultural Systems

In order to find the minimal conditions for horizontal transfer to evolve, we explored a range of combinations of the Boltzmann exponents in equations 1 and 2. These exponents control the strength of fitness based selection for survival P_d and reproduction P_r . The larger the value of x_d and x_r the weaker the strength of selection. Figure 3 shows a distribution of the three different cases discussed in the previous section for different combinations of Boltzmann exponents.

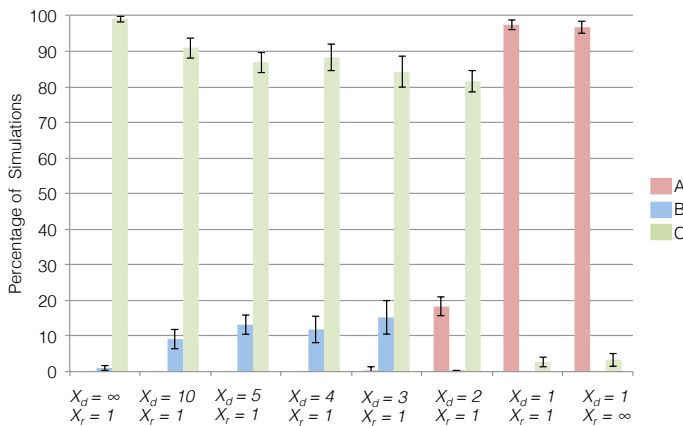


Figure 3: The percentage distribution of cases A, B and C is shown for different combinations of selection strength. Ten replicates of 100 individual simulations were run for each combination; positive and negative error bars represent a single standard deviation.

Cultural cases A and B are more frequent when the strength of survival selection increases but when selection only affects reproductive success case C is dominant. The reason for this has to do with the way horizontal imitation breaks the very notion of inheritance. Without inheritance,

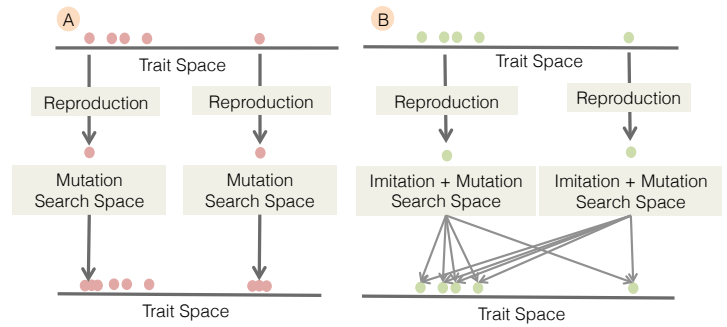


Figure 4: Comparative analysis of cultural vs. genetic search. (A) The genetic case explores an area restricted to the vicinity of the parental position in trait space. (B) Cultural evolution with horizontal information transfer establishes a common search area defined by the current distribution of phenotypes in the population, effectively getting rid of vertical inheritance and eliminating the impact of reproductive selection.

the number of offspring that an individual has is irrelevant.

In genetic reproduction each individual explores the trait space in independent lines from one another. In other words, the space of possibilities for a newborn is limited to the area where its parents currently are plus a surrounding space established by the genetic mutation rate. With horizontal imitation every single newborn in the population has the same search area, that is the current distribution of phenotypes in search space plus the imitation error area around them. A graphical representation of this is shown in Figure 4.

For cultural systems with horizontal transfer it does not matter who produces the new individuals because the algorithm stops looking at them as units of selection and instead it focuses on cultural variants. The bottom line is how long can you survive and serve as a model for others, rather than how many others can you produce. Our model links the selection of variants to the survival of individuals just like in a natural selection scenario, but it is important to reiterate, that this is not the same as selecting for the current state of independent search paths as it happens in biological evolution (figure 4A). This subtlety is a fundamental difference that changes the focus of selection from organism to variants.

These findings lead us to think that in order for horizontal transfer to evolve, with no transmission biases, a strong component of survival fitness should be present for a set of traits in the population. By extension, these types of traits would be fundamental for the emergence of culture.

In natural populations this claim is hard to test because behavioural traits have different mixtures of reproductive and survival fitness components; most species respond to some form of transmission bias (Avital and Jablonka, 2005) and evolutionary races to find new solutions for problems are hard to spot and trace. Nevertheless, we consider the find-

ings of our model interesting from an A-Life perspective, especially due to its characteristic phenotype genotype disengagement behaviour and potential for extensions.

The Culture Advantage of Mutation Rates

Horizontal transfer without any transmission biases can generate faster adaptation compared to genetic evolution. This is mainly because the error rate of imitation is higher than mutation rates in genes. In figure 5 the average path for one hundred replicates compares the performance of a horizontal transfer cultural system (Cultural HT) with a vertical one (Cultural VT). In Cultural VT parents are the only models to imitate; this system is slightly different from a purely genetic case because the evolution of imitation frequency is still considered and both genes and variants are evolving. For comparison, a genetic case with mutation rate equal to the imitation error in cultural systems (Genetic HM) and a genetic system with a low mutation rate (Genetic LM), are included.

The trajectory described by Genetic LM is similar to that of a horizontal transfer system where the imitation error is set to the same low value as the mutation rate of genes. In similar fashion, if both mutation and imitation errors are set to a high value, the trajectory described by Genetic HM will take place. This shows how the advantage of cultural systems in Cultural VT and Cultural HT relies heavily on high error rates in imitation when compared to its low mutating genetic counterpart.

In nature, genetic mutation rates have a baseline and its random occurrence is considered a physicochemical constraint of DNA replication. Nevertheless, there are corrective mechanisms that can attenuate the effect of mutation during genetic replication (Lodish et al., 2004). The evolution of these mechanisms is considered an adaptation to the high level of contingency existing in development. Higher mutation rates could easily evolve in an organism but such a trait is undesirable due to the associated frequency of deleterious mutations arising from it. In this way, it is sensible to say that genes cannot afford to mutate as much as cultural variants due to the collateral effects on existing adapted traits.

If culture, with its higher mutation rate, is to take over genetic evolution it has to find a way to shield finely tuned behaviours that are critical for life. For this reason we would like to make the point that the term cultural evolution as described in this work should be reserved for newly established problems which could be the result of a sudden environmental change or the introduction of a new social group in the community. Our model does not describe this mechanism in detail and it merely assumes that this is the sort of problem that the hybrid system needs to tackle.

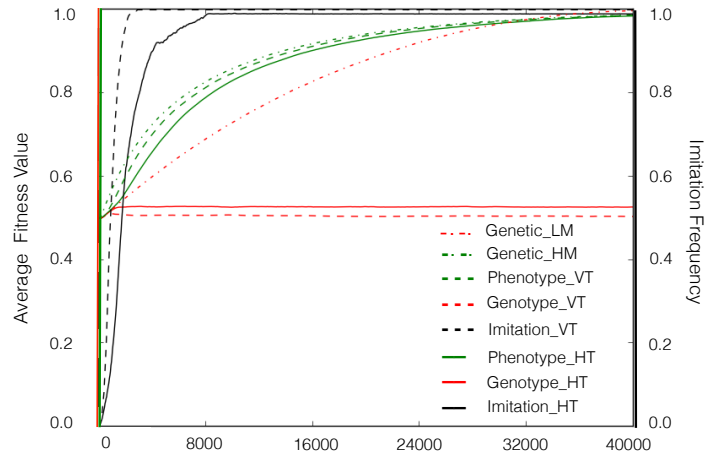


Figure 5: The average trajectory for a hundred individual simulations is shown for an horizontal transfer algorithm HT (continuous lines) and a vertical transfer algorithm VT (segmented line). Dot and segment lines represent paths for genetic evolution algorithms with mutation rates of 0.001 (Genetic LM) and 0.01 (Genetic HM). Here is shown that the fundamental advantage of cultural algorithms relies on the high error rate ($x_d = 1, x_r = \infty$).

Extensions

The model here presented is intended as a building block for future research endeavours. We think it is minimal in its assumptions and yet it produces the fundamental behaviours associated with culture. Current analysis on the embedded evolution of horizontal (vs. vertical) imitation is being developed. In addition, we are looking at the previously mentioned crossover advantage when having numerous models to copy from.

Transmission biases could easily be added by making the selection of a model to copy a function of its fitness, frequency or individual social status. Population structure is just a networked implementation away. On a networked model models to imitate would come from neighbour nodes rather than from the whole population; such a constraint could stimulate the evolution of culture by creating clusters of solutions that rarely exchange information, exploiting in this way the advantage of weak links in social networks (Csermely, 2000; Granovetter, 1983).

A more sophisticated approach would include the idea of frequency dependence and social games. Correlation between strategies in social games has been shown to increase the total benefit for individuals. An extension to the model here explained could show how culture can promote such correlations taking advantage of social learning and imita-

tion in a game theoretic context.

Conclusions

Our model shows basic attributes of the evolution of culture. That we see the characteristic fitness disengagement between the phenotype and the genotype co-occurring with the fixation of imitation provides a clear fingerprint for culture. Within the constraints of our model, two conditions are necessary for horizontal transmission to evolve i) a high imitation error rate that provides an exploratory advantage and ii) a strong survival selection function that maintains selective pressure when imitation takes over. The mechanism here presented showed how genotypes can be masked from selection when imitators increase in frequency, and as a result a clear disengagement between phenotype and genotype occurs. We consider this key for the emergence of culture as defined in this work. Potential future extensions that could offer a clearer picture of the interaction between vertical and horizontal transmission, along with the possible effects of transmission biases, population structures, and social games are being developed.

We hope our findings lead the way to a general simulation framework to explore culture emergence and cultural evolution; the model is simple and stripped of most complexities obscuring the basic attributes of hybrid gene-culture systems, which makes it an excellent candidate for future development.

Acknowledgments

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References

- Avital, E. and Jablonka, E. (2005). *Animal Traditions*. Cambridge University Press.
- Boyd, R. (1985). *Culture and the Evolutionary Process*. University of Chicago Press.
- Boyd, R. and Richerson, P. J. (1988). An evolutionary model of social learning: The effects of spatial and temporal variation. In Zentall, T. and Galef, B. G., editors, *Social Learning: Psychological and Biological Perspectives*. Lawrence Erlbaum Associates.
- Burman, J. T. (2012). The misunderstanding of memes: Biography of an unscientific object 1976-1999. *Perspectives on Science*, 12(1).
- Csermely, P. (2000). *Weak Links: The Universal Key to the Stability of Networks and Complex Systems*. Springer.
- Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press.
- Enquist, M., Eriksson, K., and Ghirlanda, S. (2007). Critical social learning: A solution to rogers' paradox of nonadaptive culture. *American Anthropologist*, 109(4).
- Granovetter, M. (1983). The strength of weak ties: A network theory revisited. *Sociological Theory*.
- Henrich, J. and Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and human Behaviour*.
- Heyes, C. (1994). Social learning in animals: Categories and mechanism. *Biological Reviews*.
- Heyes, C. M. and Galef, B. G., editors (1996). *Social Learning in Animals: The Roots of Culture*, chapter 1. Elsevier.
- Holden, C. and Mace, R. (1997). Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology*.
- Ingold, T. (1986). *Evolution and Social Life*. Cambridge University Press.
- Jenkins, P. (1978). Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behaviour*.
- Jong, K. D. (2002). *Evolutionary Computation*. Bradford.
- Kroeber, A. L. (1948). *Anthropology: Race, Language, culture, psychology, pre-history*. Harcourt, Brace and World.
- Laland, K. and Galef, B. G. (2009). *The Question of Animal Culture*. Harvard University Press.
- Laland, K. N. and Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology*.
- Laland, K. N. and Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology and Evolution*.
- Lodish, H., Berk, A., Matsudaira, P., Kaiser, C., Krieger, M., Scott, M., Zipursky, S., and Darnell, J. (2004). *Molecular Biology of the Cell*. WH Freeman, 5 edition.
- McGrew, W. (1998). Culture in nonhuman primates. *Annual Review of Anthropology*.
- Rendell, L., Forgarty, L., and Lanland, K. (2010). Rogers' paradox recast and resolved: population structure and the evolution of social learning. *Evolution*.
- Rendell, L. and Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, 24(02).
- Richerson, P. and Boyd, R. (2001). Culture is part of human biology: Why the superorganic concept serves the human sciences badly. In Maasen, S. and Winterhager, M., editors, *Science Studies: Probing the Dynamics of Scientific Knowledge*. Bielefeld: Verlag.
- Richerson, P. J. and Boyd, R. (2006). *Not By Genes Alone: How Culture Transformed Human Evolution*. University of Chicago Press.
- Rogers, A. (1988). Does biology constrain culture? *American Anthropologist*.