

The Transmission of Genes and Culture: A Questionable Analogy

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Abstract Modes of cultural transmission are, by analogy with modes of genetic transmission, ways in which cultural information is transmitted between individuals. Despite its importance across the behavioral sciences and for theories of cultural evolution, no attempts have been made, to our knowledge, to critically analyze this analogy. We here aim at such detailed comparison and show that the fundamental role of modes of transmission in biology results mainly from two properties of genetic transmission: (1) what is transmitted generally does not influence the way in which it is transmitted; (2) there is a limited number of simple and stable modes. In culture however, modes of transmission generally lack these two fundamental properties. In particular, in culture it is often the rate of evolutionary change that determines the mode of transmission. We offer some tentative explanation regarding the origins of such a fundamental difference and we conclude that cultural transmission modes are not causal mechanisms that govern the transmission of culture but mere descriptions of the way culture happens to be transmitted at a given time in a given

community. This shows the limit of the analogy between biological and cultural evolution and suggests that evolutionary models and theories differ substantially between the two domains.

Keywords Cultural evolution · Memetics · Dual inheritance theory · Social learning · Imitation

Introduction

“Au clair de la lune, mon ami Pierrot	“By the clear moonlight, my dear friend Pierrot
Prête-moi ta plume, pour écrire un mot.	Please lend me your quill, to write something down.
Ma chandelle est morte, je n’ai plus de feu.	My candle is dead, my fire is gone.
Ouvre-moi ta porte, pour l’amour de Dieu.”	Please open your door, for the love of God.”

First verse of a French traditional lullaby (Dumersan and Ségur 1866, our own translation).

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Our mothers used to sing this lullaby before we fell asleep. They themselves learned the song in similar conditions from their mothers; our grandmothers, in turn, have probably learned it from their mothers who learned it from their mothers, and so on and so forth since at least 1866, when Durmesan and Ségur recorded it in their survey of traditional French songs. If we assume this song is mostly transmitted from mothers to their children, can we use this information to infer interesting evolutionary properties of the song? Based on an analogy with biological inheritance, it has been argued that the evolution of cultural items is

determined by their mode of inheritance; items inherited from parents for instance, should evolve more slowly than items transmitted outside the family. This article questions the importance of transmission modes (TMs) to understand cultural evolution and sheds new light on the analogy between genes and culture.

Studies of cultural and biological evolution proceed largely independently of each other, but analogies between biological and cultural evolution have always been an important source of inspiration for biologists and social scientists alike. Famously, Darwin and Wallace were deeply influenced by Malthus's laws governing the growth of populations (Malthus 1809; Darwin 1859; Wallace 1905; Bowler 2003). Maynard-Smith was inspired by the work of economists and developed the field of evolutionary game theory and the concept of an evolutionarily stable strategy (Maynard Smith 1982). Of course, the transfer of concepts and methods does not always flow from the social sciences to biology. For instance, biological evolutionary theories played a central role in the debate opposing two conflicting views of cultural evolution, one defended by Tylor, Morgan and Spencer involving a determinist, teleological view of cultural change and another, more Darwinian approach defended by Boas (see Lewis 2001a, b on this topic). Another more recent example is the major breakthrough that happened with the use of phylogenetic methods to study language evolution (see Gray et al. 2009; Currie et al. 2010; Dunn et al. 2011 for instance). This complex history of interdisciplinary dialogue, exchanges and borrowings, sometimes leading to important advances and at other times deceiving researchers; has taken on a new form when scientists in the 70's have suggested that cultural evolution is *in itself* a Darwinian process.

The development of memetics (Dawkins 1976; Dennett 1995; Blackmore 1999; Aunger 2000a, 2002; Hull 2000) and gene-culture coevolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Durham 1991; Feldman and Laland 1996; Richerson and Boyd 2005) has revived the debate regarding the similarities and differences between biological and cultural evolution, with the possibility of new, modern Darwinian theories of cultural evolution (see Aunger 2000a; Wheeler et al. 2002, for overviews of diverse opinions on that topic). Proponents of these theories insist that cultural evolution meets the minimal requirements of Darwinism and therefore that a general Darwinian theory of cultural evolution is possible (Gerard et al. 1956; Mesoudi et al. 2004, 2006). By contrast, opponents argue that large differences between the two processes impede their integration in the same evolutionary framework. However, the criticisms that have been addressed to Darwinian theories of cultural evolution have failed to show that cultural evolution cannot be integrated into the Darwinian framework for two reasons.

First, some of the criticisms, such as the fact that cultural items, unlike genes, are not particulate entities for instance (Daly 1982; Bloch 2000; Kuper 2000; Atran 2001; Aunger 2002; Bloch 2005), have been construed against a stereotypical view of evolution and genetics that is not perfectly accurate. The notion of gene in evolutionary biology is as much confused as the notion of trait in social sciences (see Lyman and O'Brien 2003 for an historical discussion of the notion of cultural trait).

A second set of criticisms however, have addressed the more fundamental issue of the role of Lamarckian processes (in the sense of directed changes; see Kronfeldner 2007) in cultural evolution (Daly 1982; Sperber 1985, 1996; Fracchia and Lewontin 1999; Sperber and Claidière 2006, 2008; Claidière and Sperber 2007; Kronfeldner 2007; Gabora 2011). Cultural evolution, it is argued, is largely determined by the transformation of culture resulting from the work of cognitive processes rather than by blind replication leading to selective processes (Sperber 1985, 1996). The contribution of transformative processes to evolution and their place in Darwinism is also a biological question (Jablonka et al. 1998; Jablonka and Lamb 2006) but the problem is exacerbated in the cultural case. Defenders of Darwinian approaches to culture however, readily recognize the existence of transformative processes (such as 'guided variation' for instance, Boyd and Richerson 1985) but do not see this as a fundamental problem for Darwinian models of culture. Rather, these differences justify the development of new evolutionary models, specifically tailored to deal with cultural phenomena (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Shennan 2002; Bentley et al. 2004; Richerson and Boyd 2005; Runciman 2005).

In this article, we highlight a more fundamental difference between biological and cultural evolution. A central feature of population genetics is the reliance on the concept of *transmission modes* (TMs). A TM is a way in which genetic material is transmitted between individuals. Bi-parental transmission with fair meiosis for instance is the TM that characterizes most chromosomal DNA. Maternal transmission on the other hand characterizes mitochondrial DNA. TMs are important because they influence the evolution of contents: different modes have different properties and therefore influence the evolution of genes in different ways. This dichotomy between *transmission modes* and transmitted *contents* is at the heart of evolutionary thinking in biology.

By analogy with genetic TMs (GTMs), cultural TMs (CTMs) have been defined as ways in which cultural information is transmitted between individuals. Vertical transmission for instance, is the transmission of cultural information from biological parents to offspring, horizontal transmission is the transmission of information between

individuals of the same age group and oblique transmission is the transmission of information from older individuals to younger ones. The notion of CTM is now broadly used across the behavioral sciences, including evolutionary game theory (Taylor and Jonker 1978; Binmore and Samuelson 1992; Weibull 1997; Hofbauer and Sigmund 1998; Skyrms 2004; Nowak 2006), microeconomics (Gintis 2006), anthropology (Aunger 2000b; Hewlett et al. 2002; McElreath and Strimling 2008; Victoria et al. 2009), animal culture (Deecke et al. 2000; Laland et al. 2000; Krutzen et al. 2005; Garland et al. 2011) and archaeology (Barton and Clark 1997; Shennan and Steele 1999; Borgerhoff Mulder et al. 2006; Tehrani and Collard 2009). It also plays a fundamental role in modern Darwinian theories of cultural evolution, such as memetics (Dawkins 1976; Dennett 1995; Blackmore 1999; Aunger 2000a, 2002; Hull 2000; Distin 2005) and dual inheritance theory (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Durham 1991; Allison 1992; Feldman and Zhivotovsky 1992; Feldman and Laland 1996; Takahasi 1999; Richerson and Boyd 2005).

As in biology, CTMs are important because they affect cultural evolution. Different modes have different properties and therefore influence the evolution of cultural items in different ways (see Table 1 in Guglielmino et al. 1995 for instance). As an illustration, Cavalli-Sforza et al. (1982) summarize the findings of their survey of Stanford student in the following way:

A survey designed to evaluate the importance of some components of cultural transmission on a variety of traits showed that religion and politics are mostly determined in the family, a mode of transmission which guarantees high evolutionary stability and maintenance of high variation between and within groups. (p 19)

Despite their broad acceptance and the fact that TMs constitute a fundamental aspect of population genetic-like models of cultural evolution, to our knowledge, the actual relevance of an analogy between CTMs and GTMs has never been discussed in a systematic manner. We here aim at such detailed comparison and our analysis reveals key differences between the two domains that compromise, we think, the attempt to understand cultural evolution on par with genetic evolution.

In what follows, we start by explaining why the dichotomy between transmission modes and transmitted contents plays such an important role in evolutionary biology. We show that the relevance of this distinction results mainly from two fundamental properties of genetic evolution: (1) in general, what is transmitted does not influence the way in which it is transmitted; what we call the ‘independence assumption’; (2) there are a limited number of simple and stable TMs. We argue that these two

properties are fundamental if the notion of TM is to be useful for understanding evolution (genetic or cultural).

Having identified elements that make the notion of TM useful in biology, we argue that CTMs generally lack these two fundamental properties. We show that in the cultural domain the independence assumption is often violated and that there are an indefinitely large number of CTMs that are not generally stable. This conclusion emphasizes the limit of the analogy between biological and cultural TMs: in biology, a large proportion of genetic evolution can be modeled using the concept of TM, but in culture, evolutionary models based on TMs have limited applicability.

Briefly reviewing previous empirical studies on this topic, we show that the classical assumption that TMs determine the rate of evolution of cultural items can in fact be turned upside down. If cultural items are more stable (evolving slowly), they are more likely to be transmitted vertically. If they are less stable, they are more likely to be transmitted horizontally. In culture it is therefore the rate of evolution that determines the transmission mode. This raises important doubts regarding the causal influence TMs can have on cultural evolution.

Finally, we speculate on the origin of the fundamental differences between biological and cultural transmission. Why is genetic information, and not cultural information, generally transmitted through a few stable TMs? Our own view is that the answer is linked to differences in opacity between the two domains. In biology, genes coding for the rules of genetic transmission (what evolutionary biologists call the “genetic system”) can only evolve toward constant rules that work ‘on average’; they cannot evolve the ability to select only beneficial genes, reject deleterious alleles, and so on. On the other hand, in culture, the relationship between a behavior and its consequences on fitness is more transparent, and cognitive systems have evolved the ability to select behaviors according to elaborate, content and context dependent rules, and not stereotyped, content-independent TMs.

This article therefore specifies the fundamental properties upon which the analogy between cultural and genetic transmission modes rest, suggests different interpretations of previous data, raises challenging modeling opportunities and develops a new hypothesis regarding the origin of the difference between biological and cultural transmission.

Evolutionary Genetics and the Transmission of Genetic Information

Genetic evolution, the temporal change of the genotypic composition of a population, is usually modeled using a recursion relating the genotypic composition of the population at a certain time (or generation) t , to its composition

later in time (or at a later generation), $t + 1$. Consider for instance a population of haploid individuals and a focal locus with two alleles, A and B, coding for a phenotypic trait. Denote p_t the frequency of A alleles in generation t . To model the evolution of the trait under study we usually characterize the genetic composition of the population at $t + 1$ as a function of its composition at t . Since the evolutionary synthesis (Fisher 1930; Haldane 1932; Wright 1968), it has proven relevant and useful to separate the recursion into two independent sub-processes (see also Lewontin 1974).

First, we characterize the effect of genes on the next generation. If B individuals have a fecundity of 1 and A individuals a fecundity of $(1 + s)$, if $s > 0$ A is advantaged by selection. In that case, the population at $t + 1$ contains a proportion $p_t(1 + s)/(1 + sp_t)$ of individuals who are offspring of A, and a proportion $1 - p_t/1 + sp_t$ of offspring of B. However, simply characterizing the effect of genes is not sufficient to determine the genotypic composition of the population at $t + 1$. To do this, we have to define the TM of the genotype, i.e. the genotype of the offspring of A and B individuals. For instance, we may assume that mutations occur at a rate u between A and B alleles, and thus that the offspring of A have a probability $(1 - u)$ of being A and a probability u of being B (and vice versa for B individuals). Under this assumption, the full difference equation is $p_{t+1} = [(1 - u)p_t(1 + s) + u(1 - p_t)]/(1 + sp_t)$. One part of the recursion describes how genes control the phenotype and influence the inclusive fitness of individuals. The other part of the recursion describes the way genotypes are transmitted from parents to offspring.

What this example illustrates is that population genetics models are based upon the assumption that it is *useful and approximately correct* to consider GTMs as constant and independent of the contents they serve to transmit. Metaphorically speaking, TMs are constant physical channels through which genetic information circulates. Each channel has its peculiarity, it can transform and bias information in different ways, but it does so systematically—it always has the same effect on any information that may come to circulate in it. Knowledge or assumptions on the way genes are transmitted (the channel) is therefore necessary to predict or understand the evolution of their contents.

Of course, the validity of the independence assumption is biologically justified in most circumstances. GTMs are indeed, generally, simple and constant rules that transmit equally all genetic content. Arguably, GTMs can be relatively diverse and more complex than what we have suggested so far. For instance, mutation and recombination rates potentially vary across the genome, with hotspots of mutation or recombination around specific genes (see Metzgar and Wills 2000 for a review). Some genes in bacteria can be more subject to horizontal transmission

than others (Jain et al. 1999; Gogarten and Townsend 2005). Transmission modes also vary between nuclear genes and cytoplasmic ones (see Zeh and Zeh 2005 for some of the consequences of maternal inheritance). Furthermore, sometimes the independence assumption is also violated, in particular in models dealing with the evolution of the genetic system—the evolution of genes (so called modifier genes) that control the transmission of all genes (Kimura (1956), Nei (1967) and see Otto (2009) for a recent review). However, despite these complications, population genetics models remain tractable because transmission modes are few, stable and relatively simple rules. In culture, as we shall see, things are strikingly different.

Assumptions of Population Genetics are not Generally Satisfied in Culture

It is generally useful to consider genetic evolution as the result of two independent causes (the effect of transmitted contents and the effect of transmission modes) because in genetics (1) TMs and transmitted contents are to a large extent independent, and (2) TMs are relatively simple and stable rules. This however, is specific to genetic evolution. In this section, we argue that in culture, (1) TMs change with the very content they transmit and (2) TMs are indefinitely numerous and highly unstable. As a result, the scope for models of cultural evolution based upon a parallel with genetics is rather limited.

In Culture, Transmitted Contents and Transmission Modes Cannot Generally be Separated

To illustrate our general argument, we shall follow in some details one classical study of CTMs, but similar conclusions would be reached in other studies (such as Cavalli-Sforza et al. 1982; Guglielmino et al. 1995; Aunger 2000b; Lozada et al. 2006). In a pioneering study of Aka pygmies' foraging techniques, Hewlett and Cavalli-Sforza (1986) asked 40 adults, 16 children (7–12 years old), and 16 un-married adolescents whether they possessed particular skills and if so, whether it was one person, or a group of people, who had shown them how to perform the skills. Fifty skills such as hunting techniques, food gathering techniques, child care, singing and dancing... were studied. Hewlett and Cavalli-Sforza found that adults reported that their biological parents had taught them the skills on more than 80% of cases on average. Despite the vagueness and observer-influenced nature of the data (see McElreath and Strimling 2008 for a discussion of methodological problems associated with this and similar studies), similar

results have been reported in other studies (Cavalli-Sforza et al. 1982; Shennan and Steele 1999; Lozada et al. 2006). The authors state:

One conclusion, however, seems inescapable on the basis of the data: vertical (parent–child) transmission is by far the most important mechanism, accounting for about 80% of the cases studied. This is, according to the model, a conservative mode of transmission; it assures slow evolution while allowing individual variation. (p 932)

A similar finding is described by Guglielmino et al. (1995) in a comparable study of cultural transmission in sub-Saharan Africa:

In conclusion, cultural transmission mechanisms with their different degrees of conservativeness, determine the stability of cultural traits. [...] This investigation indicates that the conservation of many cultural practices and beliefs in traditional societies is the result of vertical transmission and family group pressure. (p 7589)

Of course, to a certain extent, models of cultural evolution are abstract conceptualizations and the details of a particular application do not bear on the general validity of the results (horizontal transmission will always be faster than vertical transmission; how much faster however is an empirical issue). The conclusions just cited have had an important theoretical and *practical* impact on discussions of cultural transmission (see for instance the discussion of the transmission of ethnobotanical knowledge in Ohmagari and Berkes 1997; Lozada et al. 2006; Victoria et al. 2009) and at this stage, it can be enlightening to lay out the practical implications of these claims fully.

Consider two alternative hunting techniques used by Aka pygmies: the crossbow and the bow and arrow it replaced. According to Hewlett and Cavalli-Sforza (1986), hunting techniques are transmitted vertically from father to sons in most cases. Let us assume that the rate of vertical transmission is 80%, a conservative rate given that hunting techniques are generally more vertically transmitted than other skills. 80% of sons therefore learn the technique from their fathers and the remaining 20% learn the technique from someone else. Further assume that the advantages of the crossbow are so flagrant that all individuals who do not learn to hunt from their father, learn to use the more efficient crossbow. Given these conservative assumptions we may ask: how long would it take for the new crossbow technique introduced by a few innovators to rise to fixation among Aka hunters?

If the proportion of crossbow users in a group at generation t is x_t , in the next generation it is $x_{t+1} = x_t + 0.2(1-x_t)$. Starting with a fraction of 5% of Aka hunters who

use the new technique, it is straightforward to show that it takes seven generations for the crossbow to become used by more than 80% of hunters, and fourteen generations for less than 5% of hunters to use the old, bow and arrow technique. Pygmies are known for their very high generation turnover (see Migliano et al. 2007 for a study of pigmy groups demography), but even with an average age at which mothers give birth of 20, 14 generations still represent 280 years. Therefore, if hunting techniques, or any other skills, are transmitted vertically at 80%, it takes at least 280 years for the technique to rise to fixation (by which we mean being used by more than 95% of the population). Today, in occidental societies, cultural rate of turnover can obviously be much higher (particularly technological turnover), but could it be, or rather have been, so slow in hunter-gatherer societies? We doubt that it is the case and in fact there is evidence to the contrary:

Some of these [hunting techniques], like crossbow construction, are of recent introduction. Ethnohistoric records (Bruehl 1910; Regnault 1911) show the crossbow being used in the region by Bantu farmers in the late 19th and early 20th century but not by Aka, who continued to use the bow and arrow. Demesse (1958) noted that by 1958 some Aka used the crossbow in the Sangha region, but many still used the bow and arrow. In 1965 most Aka were reported using the crossbow and today [1986] all Aka use the crossbow and no Aka use the bow and arrow. (Hewlett and Cavalli-Sforza 1986, p 932)

The discrepancy between the predictions of the model and the observed cultural change is considerable. It took 28 years for the crossbow technique to spread from introduction to complete fixation, 75 years if we consider the time lapse between the last documented observation of a total absence of crossbow to their total fixation in 1986, and only 7 years between the observation that some Aka use crossbow and the observation that most of them do. The time span predicted by the model (280 years) is thus between *four* and *forty* times the time span observed. Interestingly, the authors themselves point toward a likely explanation of this difference, but apparently without realizing the consequences for their model of cultural evolution:

For instance, the crossbow is a relatively new hunting technique (acquired less than 40 years ago), and less than one-third of the adult males know how to make one (see Table 2). Therefore, a boy whose father does not know the skill must watch other skilled males to learn. Many Aka today acquire a cross-bow through trade. (Hewlett and Cavalli-Sforza 1986, p 929)

The authors note that contact with different behaviors may often incite individuals to change, at least temporarily,

the source of their knowledge and thus *to change the transmission*. Hunting techniques are therefore transmitted vertically, except in the very situation where it would have a significant effect on their evolution: when there are several alternative techniques to compare.

If the transmission is not vertical but changes according to costs and benefits of acquiring new skills, maybe more complex transmission rules, belonging to the family of “payoff-biased” imitation would be appropriate (also sometimes called ‘imitate your Best Neighbour’; e.g. Henrich 2004; Skyrms 2004; Ohtsuki et al. 2006). Payoff-biased imitation however, as any other model that could possibly explain the pattern of transmission just described, is strongly dependent of the content of what is being transmitted and the context in which it is transmitted and therefore differs substantially from the notion of TMs as it is used in biology.

To make a biological analogy, imagine that genes are transmitted according to the benefit they provide to individuals and the costs of acquiring them, or for instance vertically if they do not mutate, horizontally when a new advantageous mutation arises, and not at all when a deleterious mutation appears; this would certainly require a major revision of population genetics models. The fact that, in culture, the independence assumption is not generally valid creates a fundamental difference between biological and cultural evolution.

If there were only two alternative behaviors (crossbow vs. bow and arrow) and three TMs (horizontal, vertical and no transmission), we could imagine building more complex population genetics-like models that would take these new properties into account. As we will see in the next section however, the non-independence of contents and modes in culture corresponds with extremely diverse and unstable CTMs.

Cultural Transmission Modes are Indefinitely Many and Highly Unstable

The list of CTMs can be viewed as largely incomplete and representing only a first step toward the full description of cultural transmission. Implicit in this undertaking is the idea that it is in fact possible to list all, or most, CTMs. However, when examined carefully, the list of CTMs should be much longer than what has been described so far and the proper characterization of each mode should involve a great many details. For instance, consider the transmission of an idea about the proper medical response to breast cancer. The description of the TM of this idea should specify that, in occidental societies, this idea can be efficiently transmitted by medical doctors with sufficient self-confidence or by persons who have recovered from the

treatment. It would not be accurate to give a more general description. The transmission could not be described simply as ‘horizontal transmission’ for instance, because only specific individuals can influence all age classes. It could not be described as ‘prestige biased’ either, because more prestigious but less competent individuals would not be able to transmit this idea. The population in which the idea is transmitted is important too. Among Christian Americans this idea might spread according to the pattern we just described, but this might not be the case in Amish populations for instance.

Ideas about health are simply transmitted according to a very specific TM and the same is true for most cultural domains and items (food habits, language skills, scientific knowledge, social norms, etc.). For instance, Lutz and Keil (2002) show that children as young as 3 years old already have an understanding of the division of cognitive labour, in the sense that they understand that different pockets of expertise are associated with different individuals, car mechanics and doctors should not be asked the same questions (see also Danovitch and Keil 2004; Keil et al. 2008).

In addition to being highly diverse and specific, CTMs are also extremely unstable. The example of hunting techniques in Aka described previously shows that the transmission mode of a cultural item can be affected by its own evolution. Extrinsic factors can also have the same effect. In general, any change in the environment is susceptible to lead to a change in the way information circulates. Changes in familial organization, geographic distances among individuals, trading routes, political conflicts, the economy... are all susceptible to affect CTMs. Ohmagari and Berkes (1997) for instance, in their study of the transmission of Cree’s bush techniques conclude:

Given the changes that have occurred in the last half century, it is perhaps surprising that about half of all traditional Cree bush skills are still being transmitted. The losses can be explained by the realities of village life and changing economic conditions. First, those skills that are no longer needed or no longer essential for livelihoods in the village have not been transmitted. People can buy commercially manufactured clothing, goods, and foods. Some kinds of fur preparation skills are no longer essential either, because the fur economy has declined. Second, those skills that are still needed but take a considerable time to master, such as reading animal movements, orientation in bush, and tanning hides, are transmitted incompletely because urban life makes it difficult for young people to invest enough time to learn them. Finally, the most important concern in the transmission system, as voiced by Cree elders themselves,

may be the *incomplete* transmission of bush skills and knowledge. Many women of the younger generation are familiar with a skill, but the level of mastery of the skill tends to be low compared to that of the older generation. (p 218)

In summary, cultural items are transmitted according to an indefinitely large number of unstable TMs.

Is Cultural Stability a Consequence of Transmission or is it the Opposite?

In this section, we highlight one particularly interesting consequence of the instability of CTMs: the reversal of the causality between the rate of evolution of a trait and its transmission mode. In genetics, TMs affect the evolution of contents in specific and predictable ways because there are a few, stable, content-independent rules. As we have seen, this line of reasoning has been transposed in culture: the fact that cultural items are vertically transmitted should cause them to evolve more slowly and thus to be more stable than if they were horizontally transmitted. In many cases however, the causal relationship is probably the other way around.

When culture is stable through time (i.e. it is evolving slowly), it is also often homogenous in space. Therefore, because every individual in the community has similar knowledge, there is no incentive to look beyond one's closest social relationships (generally one's family) for knowledge. In this case, transmission is mostly vertical. On the contrary, when culture is unstable through time (i.e. it is evolving rapidly), it is also often less homogeneous in space, especially when generations are overlapping. In that case, the contact with alternative behaviors may incite individuals to investigate beyond their closest relatives, and transmission thus becomes oblique or horizontal.

The change in transmission with the diffusion of a new hunting technique just described is one such example. Another is the acquisition of language. At first glance, first language transmission seems to be very similar to genetic transmission and it can be used as an indicator of relatedness among individuals (Guglielmino et al. 1995; Hewlett et al. 2002; Mace and Holden 2005). From a developmental perspective, language transmission happens during a child's first few years of life through experience with individuals who, during this period, are most frequently relatives. If someone is asked from whom they learned to speak their first language, the most likely answer is from their parents, which is why the first language is also called 'native language' or 'mother tongue'. On all these accounts, language transmission is vertical and its evolution should therefore be slow.

However, the above description of language acquisition reflects only stable conditions, when a child's family accurately speaks the dominant language in the environment. The TM changes when the conditions become less stable: when a child's parents do not speak or speak poorly the dominant language, the child nevertheless acquires the correct form of the language from non-family members. The TM of language therefore changes from vertical to horizontal precisely when the vertical mode would have had an effect—by slowing down evolution when there is a contact between populations speaking different languages.

This conclusion is not specific to language or even to humans; the same point can be raised with respect to animal culture. For instance, the famous example of macaque potato washing illustrates the passive role of CTMs. The study of the spread of the 'potato-washing' behavior among macaques (*Macaca fuscata*) is a paradigmatic example of the diffusion of a new behavior in an animal community (Kawai 1965). Briefly stated, in 1953, Japanese primatologists observed a female macaque washing sweet potatoes in water to remove sand from it. This new habit slowly spread among other monkeys and led to several changes in the lifestyle of the community. The potato-washing behavior is an example of a persistent cultural difference between communities of macaques since it has now been observed for more than 50 years.

At present, young macaques acquire the potato washing behavior at a very young age from their mother. Potato washing is therefore transmitted vertically, from mothers to offspring. Accordingly, one might think that the spread of the behavior must have occurred through the progressive birth and death of individuals. As documented by Kawai (1965) however, when the young female Imo first started washing potatoes, it slowly spread to her peers and her mother and from her peers to their mothers. Note that this would correspond to a yet unstudied TM we could name bottom-up vertical transmission combined with horizontal peer to peer transmission. The results of the study showed that the behavior spread slowly in the population, but much faster than would have been predicted by vertical transmission only.

Furthermore, the study of potato washing and other studies on social learning in primates, suggest that social and physical proximity are key factors explaining cultural transmission (Kawai 1965; Perry et al. 2003). When a new beneficial behavior appears, it usually spreads to all individuals who are in close contact with the inventor—whether they are family or not. Once the behavior is common however, young individuals learn it at an early age from their closest relatives—who in many cases are their mothers.

In conclusion, in general it is not the TM that constraints the evolution of a cultural item but the evolution of an item

(e.g. its stability or instability) that determines its TM. In contrast with genetics, TMs are not generally among the causal explanations of cultural evolution but rather among its consequences. Other factors must therefore be found to explain the stability or instability of cultural items; they have been studied by anthropologists for a long time (e.g. Bruner 1956), and involve a variety of psychological (Sperber and Hirschfeld 2004), ecological (Diamond 1997) and institutional factors.

Why are Transmission Modes Simple in Genetics, But not in Culture?

So far we have described what we think is a fact about culture: culture and genes are transmitted in fundamentally different ways. Let us now speculate briefly on why this is so: Why has evolution given rise to simple and stable TMs in biology and not in culture?

Genetic TMs are controlled by the genetic system. The genetic system is itself controlled by genes and is a product of adaptive evolution (e.g. Otto 2009). However, in genetics, the causal relationship between genes and their effects on phenotype is often opaque.¹ A consequence of that opacity is that there is not much the genetic system can do to select other genes. Genes cannot foresee the consequences of transmitting or expressing this or that DNA sequence, predict the likely consequences of this or that mutation, or compare a given genetic combination to an alternative. In other words, genes cannot select other genes based on their specific content; they have to rely on content-independent, “work on average” rules. Because of the opacity of the genetic system, GTMs evolve for their overall effect on the transmission of many different genes and as a result, even the most adaptive GTM inevitably lead to many “mistakes”, like the transmission of deleterious alleles, or the integration of viruses into chromosomes. As often, exceptions exist and subtler strategies can sometimes evolve. Mutation rates can be adjusted around

¹ We use the terms opaque and transparent here after Gergely and Csibra (2006). Sylvia’s recipe: The role of imitation and pedagogy in the transmission of cultural knowledge. Pp. 229–255 in S. Levinson, and N. J. Enfield, eds. *Roots of human sociality: Culture, cognition and interaction*. Berg Publishers, Oxford. We simply extend the use of these terms to the relationship between genes and phenotype. A causal relationship A-B is more opaque than another C-D when the causal path linking A to B is longer and more complex than the one linking C to D. The causal path linking a particular gene (A) to its consequences (B) on the phenotype can be extremely long and complex. This makes it difficult for another gene to evolve to control or modify A in order to have a different effect B’ on the phenotype. By contrast, the causal path linking a certain behavior (C) to a certain effect on the phenotype (D) can be short and simple, making it easier for a third observer for instance to modify and adapt C in order to have a certain desired effect D’.

specific genes for instance, but these adjustments remain crude and prone to mistake. Content-independent TMs have evolved in genetics because the relationship between different genes is opaque: when it comes to genetics, TMs are the best of a bad job.

Cultural TMs are controlled by the cognitive system. The cognitive system is itself partially determined by genes and is a product of adaptive evolution. When it comes to acquiring information and making decisions however, there is more to do than using simple and ‘work on average’ TMs, because behaviors are more transparent than genes.

Cognitive systems have evolved to select different alternatives based on context, content, source and likely consequences. When an individual learns complex skills such as fishing for instance, the result is often a complex mix of personal experience and social influence from various sources such as family, successful fishermen, friends, etc.

Even when the consequences of a behavior are opaque for a novice who has never tried that behavior, they are often much more transparent for experts who have mastered it. For instance, at first it might not make sense to open a wine bottle some time before drinking it but experts know that in some circumstances this helps release the aromas. Most naïve wine tasters learn this technique by trusting more knowledgeable individuals who have experienced the effects of letting wine breathe.

The ability to interpret the behavior of others in terms of beliefs and intentions (Sperber and Wilson 1986/1995; Grice 1989), is also an essential clue in deciding which novel behavior to try or avoid. Friends or family for instance might convince you that an otherwise suspiciously dangerous activity such as rock climbing is in fact perfectly safe and worth trying. Finally, even when behaviors are opaque for novices and experts, individuals often have access to rich indirect information. For instance, despite the fact that they cannot experience all the negative effects of smoking, people avoid smoking because they have been told that those who smoke tend to have cancers.

Arguably, sometimes behaviors are probably so opaque that they can only be transmitted according to simple and content-independent rules, just like genes. One example could be the transmission of food habits in traditional societies because their long term health consequences are difficult to evaluate (Henrich and Henrich 2010); however this is an exception rather than the rule.

To conclude, the opacity of culture is orders of magnitude smaller than that of genes. To cope with the opacity of genes, genetic transmission has evolved simple, stable and content independent rules that apply blindly to most genes across the genome. Advantageous and deleterious genes are equally likely to be transmitted to offspring and expressed by them. Mutations are equally likely to occur

across large part of the genome and are blind to their consequences on fitness. In sharp contrast with genetic transmission, behaviors are carefully evaluated, compared to alternatives and screened by evolved content and context sensitive cognitive capacities. Our own experience, our ability to interpret others' behavior in terms of intentions and goals, our capacity to communicate and trust others conditionally, depending on their likely expertise and benevolence (Danovitch and Keil 2004; Mascaro and Sperber 2009), all provides rich information against which behaviors can be carefully assessed and transmitted.

Conclusion: Populational Models of Culture

To what extent and in which ways is cultural evolution different from biological evolution? Previous studies have discussed differences pertaining to the nature of cultural information (Bloch 2000, 2005; Kuper 2000; Atran 2001; Auger 2002), the role of Lamarckian processes (Sperber 1985, 1996; Fracchia and Lewontin 1999; Sperber and Claidière 2006, 2008; Claidière and Sperber 2007; Kronfeldner 2007; Gabora 2011) and the mechanisms of transmission (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Shennan 2002; Bentley et al. 2004; Richerson and Boyd 2005; Runciman 2005). These discussions, however, have led to further *adjustments* of evolutionary models, in which the difference between biological and cultural evolution was generally presented as one of *detail* rather than of *nature*. However, as we have endeavoured to show in this article the extent to which Darwinian models can be adjusted to fit the cultural case heavily rely on the existence of few stable transmission modes in culture and we have argued that this is generally not the case. Let us describe genetic and cultural evolution in parallel in order to highlight, once more, this key difference.

DNA sequences are processed by “computational systems”, the replication and transcription machinery, which use that information to build organisms and generate offspring. Computational systems processing DNA, however, operate in a stereotyped manner: they work essentially in the same way for any sequence they process. In practical terms, therefore, it makes sense to consider constant transmission modes as actual *causal* mechanisms governing the evolution of genetic contents. Population genetics, as a whole, relies on this useful simplification.

Things are different in culture. Any feature of the world can potentially be considered as information, including others' behavior. This information is processed by computational systems: the cognitive system of individuals. Cognitive systems use information in order to generate behavior, and thus produce novel features of the world that

can be used as information by other cognitive devices, giving rise to culture (Sperber 2002). Just like genetic systems, cognitive systems are products of evolution and their function is also to process information. However, in contrast with genetic systems, they process information in flexible ways. They transform information by combining and by enriching them through inferential processes (Sperber and Wilson 1986/1995). As a consequence, they do not give rise to constant, stereotyped, transmission modes. In contrast with genetic ones, therefore, cultural transmission modes are not *causal* mechanisms that govern the evolution of culture, but *descriptions* of the way culture happens to be transmitted at a given time in a given community. In their attempt to establish cultural models based on an analogy with genetic ones, evolutionary biologists have overlooked this fundamental difference.

Transmission Modes can Sometimes be Used in Culture Too

It is important to stress that the difference between biological and cultural transmission is more quantitative than qualitative. In biology we find genes that affect their own transmission in the way cultural items change their TM. In culture we find cultural items whose TM happens to be simple and very stable and whose evolution can thus be studied with population genetic-like models. This occurs when TMs are strongly constrained by stable ecological or institutional factors.

Examples of ecological factors include population density, gender, geography, etc. In children playground culture for instance, there is a very rapid population turnover because every year older children change school and younger children arrive. Playground games and songs must therefore be transmitted and learned quickly in order to survive the constant renewal of the population (Morin 2010). This rapid turnover constantly affects the transmission of cultural items, and has long-term effects on children culture. A higher rate of turnover favors highly transmissible cultural items over memorable ones for instance, in the same way that extrinsic host mortality favors virulent pathogens (Morin 2010). Because fast turnover is a stable property of children's ecology, it can influence cultural evolution in constant and predictable ways.

Institutions too can have a long and stable influence on the evolution of culture. To give one obvious example, the evolution of surnames is influenced by stable and simple rules of transmission (note that in that case the problem is to explain how the rules can stay put for so long; see Yasuda et al. 1974; Lasker 1985; Zanette and Manrubia 2001; Manrubia and Zanette 2002). Institutions and their

norms regulate the transmission of cultural items in various ways, sometimes by defining which behaviors are to be performed under which conditions (e.g. sing a specific song during birthdays), other times by defining who must learn from whom (priests teach priests to be).

Population Thinking Without Transmission Modes

However, the few instances in which population genetics like models happen to be adequate must not hide the general discrepancy between genetic and cultural evolution. Biological and cultural evolution lie at the two ends of a continuum of cases, between fixed and stable transmission rules and highly flexible ones.

Fortunately, the dichotomy between transmitted contents and transmission modes is not a general property of all populational models, but an idiosyncrasy of population *genetics*. Therefore, populational approaches to culture do not have to rely on such a premise: culture can be studied formally with population thinking, without any reliance on the concept of TM. As we have explained, the drawback of the notion of TMs in culture is that, in contrast with genetics, TMs are not generally *mechanisms* with causal roles. However, this does not mean that there is no other causal mechanism at work in the evolution of culture. If these mechanisms are characterized properly, they can help predict its evolution.

Economists and analytical sociologists consider one such mechanism: rationality. They assume that individuals are rational agents trying to maximize utility, and predict the outcome of the interaction of a population of such agents (Schelling 1978). Although populational in character, these models (1) are not centered on the transmission of some cultural content and (2) do not rely on the existence of stable TMs: they rely on a different mechanism.

For biologists, however, the assumption of rationality has little naturalistic foundations. Rather than the a priori hypothesis that human beings are rational, an alternative approach is to consider models of cultural evolution based on the knowledge of the actual properties of our cognitive system. Human cognitive capacities, such as biases and predispositions, are causal mechanisms that, once implemented into population models, can allow predicting and understanding cultural evolution (Atran 1990; Sperber 1996; Boyer 2001).

For instance, one domain in which populational models of cultural evolution have had an important impact is language evolution and the evolution of the language faculty. Kirby and colleagues have developed an alternative explanation to traditional approaches to the origin of language that usually relies solely on natural selection. They have shown that even weak cognitive biases can have large

consequences on cultural evolution through repeated episodes of transmission (what Kirby et coll. call iterated learning). Languages adapt to cognitive constraints (Kirby et al. 2007; Griffiths et al. 2008; Smith and Kirby 2008). Cultural evolution of language can therefore prevent natural selection to act on language related genes (see also Kirby et al. (2008) and Scott-Phillips and Kirby (2010) for recent experiments strengthening these conclusions).

This suggests that in each domain, specific cognitive mechanisms lead to the emergence of domain-specific cultural dynamics. There is therefore no particular reason to build models of cultural evolution based on an analogy with population genetics (Daly 1982). As Godfrey-Smith (2009) argues:

There are many other ways, beside Darwinian ways, in which a population's past can feed forward to affect its state in the future, in a way that involves aggregations of local individual responses (p158).

There are however, reasons to believe that population thinking (Mayr 1959, 1982; Chung 2003) is a fundamental concept from evolutionary biology that can inspire our understanding of culture (Boyd and Richerson 1985; Sperber 1996; Sperber and Claidière 2006; Godfrey-Smith 2009). Nevertheless, population thinking is only one ingredient of evolutionary biology and the fact that culture shares this ingredient with biology does not entail that it should share all the others. As we have argued in this article, the notion of modes of transmission is not particularly relevant to cultural evolution. Novel concepts and mechanisms, more inspired by cognitive sciences and less by population genetics, are required.

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