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by

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Abstract

To explain emergent cultural phenomena, this paper argues, it is inevitable to understand the evolution of complex human cognitive adaptations and their links to the population-level dynamics of cultural variation. On the one hand, the process of cultural transmission is influenced and constrained by humans' evolved psychology; people tend to acquire some cultural variants rather than others. On the other hand, the cultural environment provides cultural variants that are transmitted to or adopted by individuals via processes of social learning. To gain insights into this recursive relationship between individual cognitive dispositions at the micro level and cultural phenomena at the macro level, the theory of gene-culture coevolution is applied. Moreover, a model of cultural evolution demonstrates the dissemination of novelty within a population via biased social learning processes. As a result, some unique facets of human behavior and cumulative cultural evolution are identified.

Keywords: Cultural Evolution – Social Learning – Diffusion Dynamics – Coevolution – Evolutionary Economics

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1. Introduction

The social sciences have long been occupied with the "micro-macro problem". If a theoretical concept starts from individual behavior, like most economists do, how can we ever get to a proper account of society-scale – emergent – phenomena? On the other hand, if we start with collective institutions, like many sociologists do, how do we account for individual behavior? A theory of cultural evolution addresses a micro and a macro level (see Henrich and Boyd, 1998): (1) At a cultural level it is shown how cultural variants spread and persist within a population via processes of cultural learning. (2) At the genetic evolutionary level the conditions are analyzed under which natural selection favors the psychological mechanisms underlying the cultural evolution of groups. Therefore, to understand the evolution of the psychological mechanisms that shape culture, it is necessary to analyze how individual psychology shapes the cultural environment and how that environment conditions the behavior that people acquire. The theory of gene-culture coevolution clarifies the recursive connection between humans' innate psychological predispositions and the macro-level institutions in which humans are always embedded.

Moreover, to provide some additional insights into the dynamic aspects of cultural evolution, this paper models the transmission of cultural contents via processes of social learning and expounds how these influence the diffusion of novelty in a population. As will be shown, cultural transmission is biased; people tend to acquire some cultural variants rather than others.[1] The process of cultural transmission is influenced and constrained by humans' evolved psychology that shapes what we learn, how we think, and whom we imitate. The proposed model seeks a middle ground between the methodological individualism of many social sciences and methodological collectivism. This is done by relying on a population-based model of cultural evolution and insights on human cognition stemming from evolutionary biology, anthropology, cognitive science, and other disciplines that serve as this approach's micro-foundation.

Given such a "naturalistic" approach, which implies a behavioral model of human agents that is based on our knowledge about human nature, it can be argued that the Darwinian theory of biological evolution is relevant for the social sciences in a very basic

[1] A cultural variant is defined as an idea, skill, belief, attitude, or value that is acquired by social learning and that influences an individual's behavior.

sense: the human species is, after all, a result of natural (Darwinian) evolution. However, this relevance does not directly affect the analytic concepts of theorizing in the social sciences. Natural evolution has shaped the ground and still defines the constraints for man-made, or cultural, evolution. The historical process of cultural evolution can therefore be conceived as emerging from, and being embedded in, the constraints shaped by evolution in nature. Darwinian theory explains the origins of cultural evolution in human phylogeny and fosters the understanding of the lasting influence of innate elements, dispositions, and programs on behavior, which are results of the forces of natural selection and which impose limitations on cultural evolution (Witt, 2003, ch. 1). Evolutionary selection has established a set of cognitive devices that influence human behavior (see, e.g., Singer, 2000). From this perspective, the biologically evolved foundations of social cognition, learning, and reasoning directly enable and affect cultural evolution with its own modes of transmission and its much faster pace. Therefore, Darwinian concepts explain the origins of the human adaptation for culture and the lasting influence of certain evolved cognitive traits (see Cordes, 2004). They cannot, however, do justice to cultural evolution in general and socio-economic evolution in particular which follow their own rules (see Cordes, 2006).

The remainder of this paper is organized as follows: the next section will introduce some of the evolved cognitive dispositions that take effect in cultural transmission. Section 3 demonstrates how gene-culture coevolution gives rise to uniquely human cognitive features. The dissemination of cultural novelty in a population given certain biases in cultural learning that originate from evolved cognitive dispositions are the subject matter of a formal model in Section 4. Section 5 concludes this chapter.

2. The micro foundations of cultural transmission processes

During human evolution, man adapted for culture in ways other primates did not.[1] Biologically evolved novel forms of social cognition and cultural learning formed the micro-foundation for cultural evolution and exclusively human ways of behavior. The key adaptation has been the one that enabled humans to understand other individuals as intentional agents like the self – a capability necessary for reproducing someone else's

[1] The following discussion draws on Cordes (2004).

behavioral strategies (Tomasello, 1999). The sophisticated human skills of social cognition, such as imitative learning, do not just mimic the surface structure of an observed behavior. They also mean a reproduction of an instrumental act understood intentionally. Humans do not just reproduce the behavioral means but also the intended end to which the behavioral means was applied. This unique cognitive skill of human beings underlies behavioral patterns such as joint attentional activities, discourse skills, the learning to use tools, the creation and use of conventional symbols, and the participation in, and creation of, complex social organizations and institutions. These species-unique aspects of human cognition are socially constituted. This means that human social organization is an integral part of the process that resulted in the special characteristics of human cognition (see also Section 3). The partly innate, partly learned behavioral repertoire is the basis on which cultural evolution rests. Social-cognitive learning is a crucial element here (Bandura, 1986, ch. 2). It allows for a fidelity of transmission and diffusion of behaviors and information among the members of a population not feasible in genetic transmission (see Kruger et al, 1993). It also enables humankind to accumulate a multitude of modifications in the course of socio-economic evolution and to pool collective cognitive resources both contemporaneously and over historical time.

Although culture evolves according to its own mechanisms, humans have not transcended biology. Therefore, a deeper understanding of emergent cultural phenomena necessitates an analysis of the underlying human cognitive learning capacities. Cultural transmission is based on complex psychological mechanisms that are likely to have been shaped by natural selection (Henrich and Boyd, 1998).[1] To grasp cultural macro phenomena it is important to understand the nature of these evolved psychological mechanisms – the micro foundation of culture – because they determine which cultural variants spread and persist in human groups.

Most variation between human groups is cultural: genetically similar people live in similar environments showing different patterns of behavior due to different, culturally acquired cultural variants. What is more, individuals living in the same group tend to behave in similar ways and hold similar moral values, which is partly due to conformist

[1] In this context, biases can consist of an innate component and a cultural component acquired in an earlier episode of social learning (Richerson and Boyd, 2005, p. 66).

cultural transmission (see below). These cultural variants are transmitted within social groups by various forms of social learning. On a micro level, Boyd and Richerson (1985) and Richerson and Boyd (2005, p. 99ff) have conceptualized cultural transmission as the product of a series of analytically separable cognitive learning mechanisms or transmission biases that allow humans to effectively and efficiently acquire cultural variants in a complex cultural environment. Evolutionary considerations suggest that humans' cognitive dispositions consist of learning rules that preferentially select and evaluate sensory data from prescribed subsets of externally produced information (see also Henrich and Boyd, 1998). These learning heuristics provide "rules of thumb" that bias humans toward certain cultural variants without exhaustively examining the immense amount of available social and environmental information. The addition of cultural transmission creates many more links between individuals and the populations they live in. Therefore, human culture is an example of an emergent macro phenomenon for it is based on social learning processes taking place on a micro level.

One of the psychological mechanisms in cultural transmission is the well-studied conformist bias (see, for an overview, Aronson et al., 2002, ch. 8; Kameda and Diasuke, 2002; Henrich, 2004; Richerson and Boyd, 2005, p. 120ff). This bias uses the commonness or rarity of a cultural variant as a basis for choice. Due to the conformist bias, agents pick the cultural variant that is used by most of the models in a population (see also Henrich and Boyd, 1998). Boyd and Richerson (1989) show that a tendency to acquire the most common behavior exhibited in a society was adaptive in a simple model of evolution in a spatially varying environment, because such a tendency increases the probability of acquiring adaptive cultural variances. Moreover, a fairly modest conformist bias will maintain intergroup variation in the face of fairly high intergroup migration rates, an important feature in models of cultural group selection (see Section 3). Conformist transmission belongs to the class of frequency-dependent biases and has been a simple heuristic that improves the chance of acquiring the locally favored cultural variant (Boyd and Richerson, 1985, p. 216ff; 1989). In general, frequency-dependent bias will occur if the probability that social learners acquire a variant depends nonlinearly on the frequency of the variant among the set of models. Especially if the environment changes slowly and the information available to an individual is poor, a strong reliance on social learning evolves that favors a strong conformist tendency. There is a synergistic relationship between the evolution of imitation and the evolution of conformism. The fact that humans can imitate implies that conformism is likely to be an important component of human social learning.

The boundedness of human rationality in the face of a complex world induces individuals often to adopt culturally transmitted behaviors without independent evaluation of their outcomes (Richerson and Boyd, 2001). The constrained psychological resources of human actors are a fundamental part of cultural evolution. This implies that these approaches abandon the assumption that agents rationally choose utility-maximizing items from a given set of alternatives. Instead, it is assumed that an important force in learning is social observation. Agents are aware of only a fraction of the available information. Therefore, imitating or learning from others is one of the most important means by which humans finesse these bounds of rationality (Boyd and Richerson, 1993). This can lead to adaptive but also myopic choice among the cultural variants observed.[1]

Conformist transmission implies that on the (micro) level of an individual there is a propensity to preferentially adopt the cultural traits that are most frequent in the population, i.e., at the population level, conformist transmission causes more common traits to increase in frequency. On the other hand, the frequency of a trait among the individuals within the population – a macro level property – provides information about the trait's adaptiveness. Therefore, in the case of conformist transmission, the frequency of a cultural variant, a population property, affects its probability of being imitated by individuals (see Richerson and Boyd, 2005, p. 247).

Moreover, anthropologists have likewise found that the choice of cultural traits is based on the observable attributes of the individuals who exhibit the trait (Richerson and Boyd, 2005, p. 69; Harrington Jr., 1999). In human phylogeny, selection favored social learners who have been able to evaluate potential models and copy the most successful among them, thereby saving the costs of individual learning (see also Rogers, 1983; Henrich and Gil-White, 2001; Labov, 2001). Hence, model-based learning includes a predisposition to imitate successful or prestigious individuals. In general, a model-based bias results if social learners use the value of a second character that characterizes a model (e.g. prestige) to

[1] Therefore, rational choice is a weak process relative to cultural transmission in the construction of behavioral repertoires. For a similar argument in economics see Eshel et al. (1998).

determine the attractiveness of that individual as a model for the primary character (e.g. a certain behavior). This method of evaluating different cultural variants is likely to be much less costly than directly evaluating these variants (Boyd and Richerson, 1985, p. 135). In Section 4, amongst others, this bias will be used to model the diffusion of novelty in a population.

Finally, individuals are more likely to adopt some cultural variants based on their content (Boyd and Richerson, 1985, p. 135; Richerson and Boyd, 2005, p. 69). Such a content-based or direct bias can result from the calculation of costs and benefits associated with alternative variants or from cognitive structures that cause people to preferentially adopt some cultural variants rather than others, i.e., it results from cues that arise from the interaction of specific qualities of a cultural variant with our social learning psychology. This procedure is likely to entail some kind of experimentation on the part of the agent.[1] In general, a cultural transmission rule is characterized by direct bias if one cultural variant is more attractive than others. A directly biased transmission creates a force that increases the frequency of the culturally transmitted variant that is favored by the bias. A relatively weak direct bias can have important effects on the frequency of different cultural variants in a population. An example for a direct bias – favoring cooperative cultural traits – will be the subject matter of the next section.

To provide another example for a direct bias, Cordes (2005) has, with reference to hypotheses from evolutionary psychology, argued that there are specialized psychological mechanisms that have evolved during human phylogeny to solve cognitive problems linked to the making and using of tools. These mechanisms show considerable content sensitivity with respect to observational learning of how to apply tools and play a role in directing attentional processes. Thus, innate cognitive dispositions contribute to what information will be subject to profound contemplation, what information will easily diffuse within a population of agents, and whether it may be an input to creative activity. Such a bias influences culturally engendered and institutionalized attitudes toward, for example,

[1] As long as this experimentation is not too expensive, it is plausible that directly biased transmission might evolve, as is indicated by abundant empirical evidence (e.g., Lumsden and Wilson, 1981, p. 38ff; Rogers, 1983, p. 217f; Labov, 1994). However, when it is difficult or costly to evaluate the consequences of the cultural variants available in the population directly, then frequency-dependent or model-based bias may be more advantageous.

productive and useful work, the compliance with certain cultural norms, or the aesthetic sense for an appreciation of skill and dexterity.

As a consequence of these thoughts, biological, Darwinian, concepts account for some of the aspects of the relation between individual and collective phenomena (see Richerson and Boyd, 2005, p. 247). This is a feature of many biological concepts for the basic biological theory already includes the genetic level, individuals, and populations, i.e., what happens to individuals affects the population's properties and *vice versa*. The cultural transmission biases mentioned above are a case in point.

3. Interactions between the cultural and genetic levels: the dual inheritance theory

The dual inheritance theory provides another explanation for important facets of the recursive relationships between a (genetic) micro and a (cultural) macro level. It explains the evolution of uniquely human cognitive dispositions that are not amenable to a purely reductionist approach.

The central tenet of evolutionary theory is that behavior of organisms should maximize genetic fitness. Furthermore, as a corollary of this principle, natural selection leads to cooperation among large numbers of individuals only if they are genetically closely related. With the exception of humans, this result seems consistent with the available data (Wilson, 1975). In human organizations, cooperation – including non-relatives – readily emerges spontaneously in small- and medium-sized groups. Cooperation seems to be a kind of first choice for human actors.[1] This disposition is rare in nature if not uniquely human. The question is then, what are the origins of this inclination toward cooperation? If genes spread because hey enhance the survival and reproduction of their carriers, how can altruistic / cooperative behavior evolve at all? Existing genetic evolutionary approaches – that focus on the genetic micro level – cannot explain the degree of prosociality (cooperation, altruism, moralistic punishment) observed in humans.

In order to understand this phenomenon, we require a theory that explains why humans, but not other organisms, are capable of large scale cooperation among non-relatives. Boyd

[1] See the abundant evidence from game theory and experimental economics (e.g., Bolton and Ockenfels, 2000; Güth and van Damme, 1998; Fehr and Gächter, 2000; Fehr and Schmidt, 1999; Rubin, 1982).

and Richerson (1982; 2002) and Richerson and Boyd (2005) propose that the disposition for cooperation has evolved: by a process of cultural group selection. Humans are also unique in the degree to which they depend upon socially transmitted information, i.e., culture – a macro level phenomenon, to create complex adaptations (see also Tomasello, 1996). While genetic variation between human groups is very hard to maintain due to intergroup migration, cultural variation between groups can resist the destruction of intergroup variation.[1] The reason for the fact that cultural variation can more easily respond to group selection are mechanisms peculiar to culture that maintain variation even when migration rates are appreciable. One of these mechanisms in cultural transmission that culturally homogenize groups is the conformist bias mentioned above; another one is the role model bias. Other cultural processes, like symbolic markers of group identity, also tend to limit the flow of ideas from group to group (McElreath et al., 2003). Moreover, the patterns of group formation and group competition in small-scale societies satisfy the requirements of cultural group selection models (Soltis et al., 1995). As a result, the capacity for culture enables behavioral equilibria consisting of combinations of cooperation and punishment that are not available to genetic evolutionary processes.

The ancestors of modern humans became highly cultural in the Middle Pleistocene, perhaps 250,000 years ago (McBrearty and Brooks, 2000). If cultural group selection became an appreciable evolutionary force about that time, it would have set in motion a process of gene-culture coevolution.[2] The prevalent level of cooperation based upon the prevailing social transmitted institutions in a group would exert selection on innate human social dispositions, i.e., here we have a direct interaction between a micro (genes) and a macro (culture) level resulting in a certain cognitive set-up of human agents. Over many generations this coevolutionary dynamic generated a social psychology that facilitated cooperation. This coevolutionary dynamic makes genes as susceptible to cultural influences as *vice versa* (Richerson and Boyd, 2005, p. 191ff).

We imagine a long period of repeated gene-culture coevolutionary cycles in which primitive social institutions, such as the rule to treat cousins like brothers, became established in populations, and in turn exerted a coevolutionary response, for example,

[1] The first aspect is the central problem of any genetic explanation of group selection.
[2] To enable this process to start, a group-beneficial variant must become common in an initial subpopulation only once. Then, the conformist effect will favor its further increase by group selection.

down-regulating testosterone production when confronted with relatively distantly related males who might be mating competitors. Once males became a little more docile, then a more tolerant culturally transmitted norm that encouraged cooperation between still more distantly related males might invade. Over many generations this coevolutionary dynamic generated a cognitive set-up that facilitated cooperation, even sometimes with strangers. By systematically altering the social (macro) environment in favor of prosocial phenotypes, cultural processes create the conditions for natural selection to favor prosocial genes on a micro level, for example, genetically coded dispositions for in-group altruism, cooperation, and punishment (see Boyd and Richerson, 1982). By focusing on competition among cultural groups, these models demonstrate how the cultural transmission of behaviors related to cooperation may explain otherwise puzzling patterns of human prosociality.

The selective mechanisms involved in this process can favor quite different behaviors from those favored by selection on genes alone. As a result, any gene that contributed to pro-social behavior or anti-social conduct would have been undergone selection by coevolution. Culturally evolved social environments favored an innate psychology that is suited to such environments, for example, a psychology aiming at gaining social rewards and avoiding social sanctions.[1] In this way, cultural institutions set up a moral community.[2] The complex societies of the sort we live in only began to evolve about 5,000 years ago, too little time for much, if any, evolution of the innate aspects of our social psychology. Hence, complex societies are based upon the cultural evolution of institutions that use our tribal social predispositions as their raw material (Richerson and Boyd, 1999).

In this context, cultural group selection meets a fundamental evolutionary principle: costly group-beneficial behavior cannot evolve unless the benefits of this behavior flow non-randomly to individuals who carry the genes that give rise to the behavior. Moreover, the evolution of moralistic strategies has been guided by cultural group selection – a macro-level property – for cooperative traits and represents another crucial mechanism in creating cultural differences between groups: the coevolutionary process between genes and culture is maintained by a system of moral rules that sanction bad behavior and reward good

[1] Evidence from neuroscience, for example, shows that cooperation leads to the activation of brain regions involved in the release of dopamine and in pleasure behavior thus reinforcing cooperation (Rilling et al., 2002). Cultural rules that are affectively evaluated in a positive way may be transmitted preferentially.

[2] For an account of the evolution of relative large, cooperative, egalitarian hunter-gatherer societies from smaller, less cooperative dominance structured ape societies see Boehm (1999).

behavior. “Good” genes get rewarded and “bad” genes penalized by culturally transmitted norms; in this case not by group selection acting directly on the genes. Nevertheless, in the end, the innate elements of human social psychology act much as if they had been subject to group selection. The theory of punishment (e.g., Fehr and Gächter, 2002) describes how the evolved willingness to punish non-conformists – even at a cost to oneself – renders a potentially powerful tool in homogenizing social groups and group competition.[1]

Groups with prosocial moralistic norms for cooperation had a considerable advantage over other, competing groups (Richerson and Boyd, 2005, p. 214ff; Henrich, 2004). By producing multiple behavioral equilibria, including group-beneficial equilibria, cultural evolution generates a macro level mechanism of equilibrium selection that can favor prosociality on the micro level of an individual. Cultural group selection not only favors the evolution of prosocial predispositions, but also the harder element of altruistic punishment of individuals who violate cultural norms. Successful social institutions are based on humans’ propensity toward cooperation reinforced by altruistic punishment, rewards, moral suasion, and social role models, often codified in culturally transmitted norms and rules. Furthermore, institutions have to cope with the problem that there is always a not-insignificant selfish minority that has to be coerced to cooperate. Some sort of policing system must exist to counteract this threat (Richerson and Boyd, 2001; Fehr and Gächter, 2000; Ostrom, 1990). Monitoring, rewarding, and punishment systems are necessary to prevent an increase of selfish behavioral strategies and a collapse of cooperation. These systems function best when they crowd in good behavior in those tempted to defect without crowding out cooperation on the part of those inclined to cooperate. To understand these facets of human behavior, an analysis of the recursive relationship between cultural and genetic transmission is inevitable.

As a result, the coevolutionary selection on genes has given rise to a direct bias taking effect in cultural transmission: the evolved inclination toward group-beneficial or cooperative cultural contents. The gene-culture, or micro-macro, coevolutionary approach provides an explanation for the human capacity of large-scale cooperation in various domains. Human social learning abilities produce cultural evolution and behavioral

[1] Moralistic punishment is a more plausible mechanism for the maintenance of large scale cooperation than reciprocity. For an interesting transfer of this topic to the explanation of international political conflicts see Witt (2001).

equilibria not available to genetic transmission alone. Then, cultural group selection acted on these alternative behavioral equilibria. In the next section, we develop a model of cultural transmission that relies on biases in social learning that explain the diffusion of novelty in a population.

4. The diffusion of novelty as a cultural macro phenomenon

Evolutionary models of cultural change allow one to deduce the population-level evolutionary consequences of individual-level psychologies, decision rules, and behaviors (McElreath and Henrich, 2007). At the same time, the population affects individuals. The micro-level learning biases of individuals taking effect in cultural transmission, which have been discussed in Section 2, have consequences for the population-level dynamics of cultural change. A simple formal model of cultural evolution can depict this interrelationship and explain an important stylized empirical fact – the diffusion of novelty in a population via processes of social learning.[1] The human ability to acquire novel behaviors by observation is the reason that cultural change, i.e., the diffusion of new cultural variants, is cumulative. This contrasts with rational choice models in the social sciences: a core element of these is that individuals rationally choose among given alternative behaviors by performing cost-benefit analyses using payoff-relevant data.

To understand how a population's culture evolves, we need to account for the processes that increase the frequency of some cultural variants, for example, a novel practice, idea, or technology, and reduce that of others, for example, established ways of behavior. A complex interplay of such processes will constantly affect any population's culture. In this context, the agents' behavioral repertoire is crucially influenced by processes of social learning. In the following, we illustrate how these considerations can be translated into a stylized mathematical model (see, as points of origin for this method, Cavalli-Sforza and Feldman, 1981; Boyd Richerson 1985). The analysis' starting point is the empirical observation that robust "S-shaped" cumulative adoption curves are typically observed in the spread of novel practices, ideas, and technologies. Diffusion rates first rise, then fall over time; a period of rapid adoption is sandwiched between a slow take up and satiation.

[1] This section draws on a model developed by Henrich (2001).

These diffusion curves emerge as an empirical phenomenon from the diffusion of innovations literature and their general shape captures the temporal dynamics encountered in a wide range of diffusion studies (see, e.g., Rogers, 1983; Henrich, 2001). Why do things diffuse slowly if an innovation is advantageous from the beginning? Rational choice models cannot account for these temporal dynamics of the diffusion of an advantageous novelty, especially for the long time lag until the adoption dynamic "takes off", i.e., the "long tails" of the S-shaped diffusion curves. However, as will be shown in the following, models based on biased cultural transmission can reproduce these empirical patterns.

Within the scope of this model, we will focus on three cultural evolutionary forces that bias transmission, can be traced back to evolved cognitive dispositions, operate at the individual level, and have been described above (see Section 2): the model-based or prestige bias, the conformity bias, and a direct bias. In general, cultural transmission biases are forces that arise because people's psychology makes them more likely to adopt some cultural contents rather than others, thereby changing the frequency of the different types of cultural variants in the population.[1] In this context, biases can consist of an innate component and/or a cultural component acquired in an earlier episode of social learning (Richerson and Boyd, 2005, p. 66).[2] To model the transmission of a dichotomous cultural trait we begin by labeling the variants, say *Trait 1* and *Trait 2*, where *Trait 1* represents the new technology, behavior, or idea and *Trait 2* the existing cultural variant. Tracking only two traits is sufficient to capture the essentials of a typical diffusion process. The state of the population is determined by the frequency of agents with the new variant *Trait 1*, labeled p, which denotes the frequency of the novel *Trait 1* in this population (0 in the beginning); $1\text{-}p$ is the frequency of *Trait 2* (1 in the beginning). Now, the task is to find a recursion equation in discrete time that allows us to predict the frequency of p in the next stage of the transmission process given its frequency in the present stage. Cultural transmission takes place between the members of a population. The model is of the form

[1] The forces of biased transmission acting on cultural variation are much stronger than those that shape genetic variation; they work on shorter timescales and are driven by psychological processes, not demographic events.

[2] Each of these biases of cultural transmission arises from the attempts of social learners to evaluate the adaptiveness of the different cultural variants they are exposed to in a setting in which information is incomplete or costly to acquire (Boyd and Richerson, 1985). This does not imply that all biases are necessarily adaptive, especially in contemporary societies.

$$p_{t+1} = p_t + \textit{cultural evolutionary forces (biases)}.$$

We take a population perspective, i.e., we look at a population of potential adopters. In a large population each individual encounters one potential "cultural model" during each time cycle. During each time step, individuals acquire information on the relative payoffs of the two alternatives, whereby it is assumed that *Trait 1* – the innovation – is superior to *Trait 2* with respect to payoffs. To characterize the evolution of the population, the model must allow us to predict the changes in the frequency of cultural variants in the course of time. We derive a recursion that determines p in the next time step, given the value of p in this period. This is done by specifying the probability that a particular set of role models makes an individual to acquire the cultural variant *Trait 1*.

A direct bias or a model-based bias is represented by the variables r_1 and r_2 in Table 1, i.e., agents compare the r-value of their cultural variant with the model's or the trait's r-value. In the case of the prestige or model-based bias, an individual compares her prestige to the prestige of the potential cultural model and switches and adopts the trait of the more prestigious model. A direct bias causes an individual to compare her own trait to the qualities of the trait possessed by the cultural model. This gives the switching probabilities for each combination of cultural models (the term $r_1 - r_2$ ranges from -1 to 1). With these assumptions, the cultural transmission table showing the probability of agents acquiring *Trait 1* or *Trait 2*, given a particular set of cultural role models (Self, Model), yields:

Table 1 The probability of an agent acquiring *Trait 1* or *Trait 2* given a particular model and the cultural variant hold by the agent herself.

Cultural Variant Of		Frequency of Pairings	Probability That an Agent Acquires *Trait 1* or *Trait 2*	
Self	Model		Pr(*Trait 1*)	Pr(*Trait 2*)
1	1	p^2	1	0
1	2	$p(1-p)$	$\frac{1}{2}(1+(r_1-r_2))$	$\frac{1}{2}(1-(r_1-r_2))$
2	1	$(1-p)p$	$\frac{1}{2}(1+(r_1-r_2))$	$\frac{1}{2}(1-(r_1-r_2))$
2	2	$(1-p)^2$	0	1

For example, let $P(T1|T1T2)$ denote the conditional probability that an agent acquires *Trait1* given that she is exposed to a model with *Trait 2* while holding *Trait 1* herself. After inserting all possible conditional probabilities, the following equation shows the frequency of *Trait 1* after transmission, *p prime*, given that it was *p* before transmission:

(1) $$p' = p^2 P(T1|T1T1) + p(1-p)P(T1|T1T2) + (1-p)pP(T1|T2T1) + (1-p)^2 P(T1|T2T2).$$

This term computes the frequency of each different set of social models, multiplies this times the probability that a particular set of social models results in an individual acquiring a particular cultural variant, and then sums over all possible sets of social models. The frequency of *Trait 1* after cultural transmission is calculated by multiplying the probability of each pairing by the probability of ending up with *Trait 1*. This expression tells how the frequency of the trait will change from one time step to another because of the social learning processes.

Inserting the conditional probabilities from Table 1, we can rewrite equation (1):

(2) $$p' = p^2(1) + p(1-p)\frac{1}{2}(1+(r_1-r_2)) + (1-p)p\frac{1}{2}(1+(r_1-r_2)) + (1-p)^2(0).$$

Simplifying this, we get:

(3) $$p' = p + (1-p)p(r_1-r_2) = p + p(1-p)B \qquad \text{(with } B = r_1 - r_2\text{)}.$$

The model's r-values may also contain a conformist component that depends on the frequency of the trait in the current population, i.e., agents use the frequency of a trait as an indirect indicator of its worth – a direct interaction between the micro- and the macro-level. On each encounter, individuals assess the relative frequency of the two traits. B now has two components, a constant part and a frequency-dependent part:

(4) $$B = b(1-\alpha) + \alpha(2p-1).$$

The conformist component of equation (4), $\alpha(2p-1)$, varies between -1 and 1. When the frequency of the novel trait is low, this component is negative, which reduces the value of the total bias B. Whereas, when $p > 0.5$, this term increases the conformity bias, thereby favoring the dissemination of the more common trait. Here, α scales the weight given to the frequency of a behavior relative to other biases in social learning, i.e., b

captures other biases, such as the direct or model-based biases introduced above and as shown in the appendix (α varies between 0 and 1; b varies between -1 and 1).[1] We obtain

$$p' = p + p(1-p)(b(1-\alpha) + \alpha(2p-1)). \tag{5}$$

The recursion given by equation (5) models the change of p in the population in the course of time given three potential learning biases. By setting the parameters of the system, we can analyze its long run behavior by conceptually iterating equation (5) recursively through successive time cycles. Its temporal dynamics are plotted in Figure 1:

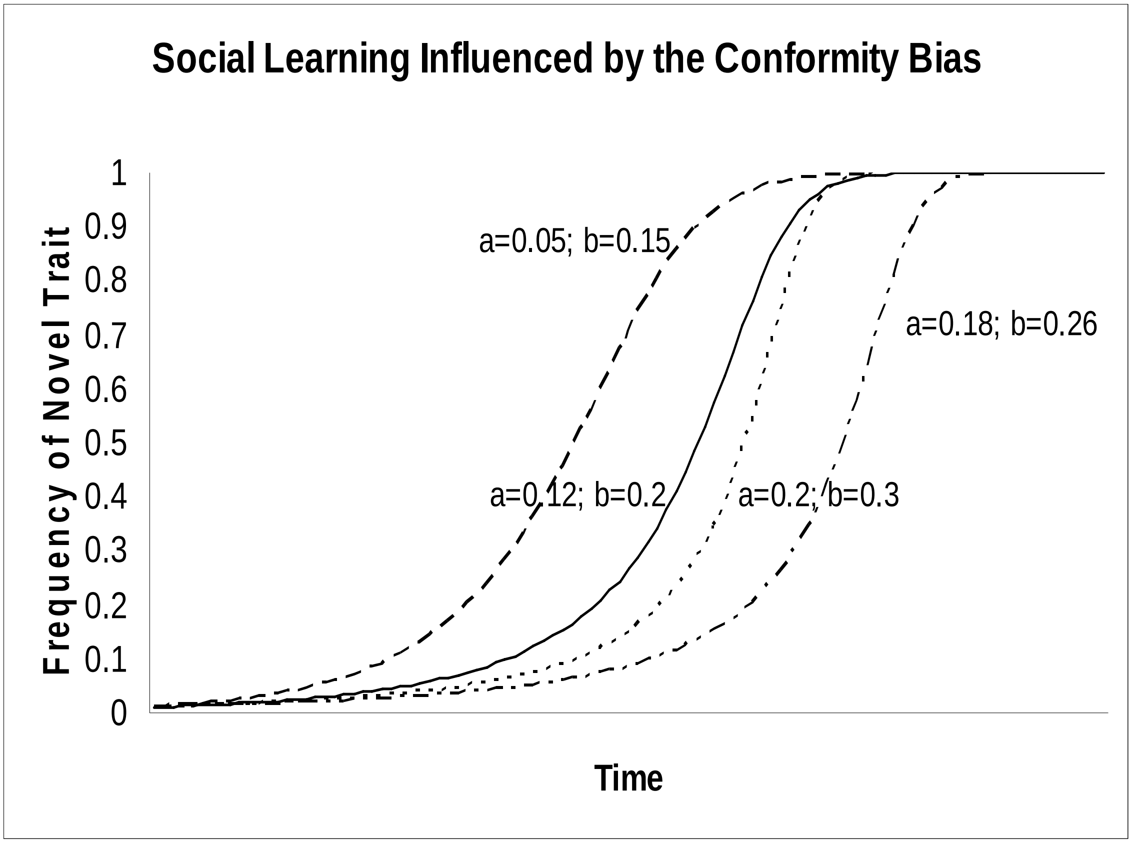

Figure 1: The spreading of a novel trait in a population via processes of biased cultural transmission for different values of α (denoted by "a" in the figure) and b .

These diffusion curves generated by the model for different values of the parameters nicely fit the empirically observed diffusion curves. Moreover, the conformity bias explains

[1] If α is large, few if any traits can spread in the population.

the slow growth of p during the initial stages of the diffusion process: it captures the empirical phenomenon of "long tails" – the slow growth period in the beginning of diffusion – and the takeoff points, i.e., when a "critical mass" is achieved, the diffusion process "takes off" and the trait quickly reaches fixation (the takeoff frequencies lie between 0 and 0.5).[1] The existence of takeoff points supports the claim that social learning is a crucial force in the dissemination of novelty. Hence, the different S-shapes generated by this social learning model resemble a wide range of the empirical adoption curves (see Henrich, 2001). This similarity suggests that biased cultural transmission models capture an important component of human behavioral change. The models of cultural evolution consistently produce the particular S-dynamics found throughout the literature.

Therefore, adoption dynamics, i.e., the diffusion of innovations of all kind, indicate that biased cultural transmission (social learning) is the predominant force in behavioral change and sociocultural evolution in general, and not individual-level rational choice, trial-and-error learning, or cost-benefit analysis like it is assumed in many theoretical approaches in the social sciences. Unless payoff information related to the different cultural traits is very clear, people rely on biased cultural transmission. What is more, cultural transmission can also explain the spread of maladaptive or costly behavior against the force of individual learning – such traits are prevalent in cultures throughout the world (Richerson and Boyd, 2005, p. 243ff).

5. Conclusions

Many economists and other social scientists work on how individuals make decisions and how behavior is acquired, while many of them ignore how those decisions and mechanisms of learning aggregate at the population level. On the other hand, many analyses of collective institutions do not account for the micro determinants of individual behavior and the recursive relationship between these levels. As shown, evidence from evolutionary and cognitive science suggests that humans have an evolved psychology that shapes what we learn, perceive, and what we think (Richerson and Boyd, 2005, p. 4). These cognitive

[1] Conformist transmission also predicts socio-spatial clusters of similar traits any time the differences between the costs and benefits of alternatives are relatively small.

dispositions influence the kinds of cultural variants that spread and persist. Moreover, these approaches link the population dynamics of cumulative cultural evolution to the psychological mechanisms that shape social learning. Furthermore, this paper has shown that humans have predispositions toward cooperation and group-beneficial behaviors that have resulted from a process of gene-culture coevolution, i.e., the recursive interaction of a micro and a macro level (Boyd and Richerson, 1982).

In evolutionary models, the classical conflict between explanations at the level of individuals and explanations at the level of the society disappear (see, e.g., McElreath and Boyd, 2007). Population models allow explanation and causation at both levels to exist in one theory. They are about how individuals can create population-level effects which then influence individual behavior and *vice versa*. A model of cultural transmission has been proposed that can be considered as a step toward an applied science of cultural evolution – in this case in the context of diffusion dynamics of technologies, ideas, or behaviors. This learning model is rooted in human psychology, is evolutionarily plausible, and still produces the typical S-curves of most diffusion dynamics found in the literature under a wide range of general conditions.

Models of cultural evolution start with a theory based on individual behavior and also provide an account of society-scale phenomena. In the short run, individual decisions do not have much effect on institutions, but, in the long run, accumulated over many decisions, individual decisions have a profound effect on institutions – they are the driving force of cultural evolution. Delineating both the micro-level psychological mechanisms of cultural transmission, as well as the population-level processes to which they give rise and that again influence individual behavior, may further the understanding of a variety of important social phenomena (see, e.g., Cordes et al, 2006). Evolutionary approaches to cultural evolution account for the basic structure of the relationship between individuals and the collective properties of their societies.

Appendix

The r-values in the case of conformist transmission are:

(A1) $r_1 = b_1(1-\alpha) + \alpha\left(p - \frac{1}{2}\right)$ and

(A2) $r_2 = b_2(1-\alpha) + \alpha\left(1 - p - \frac{1}{2}\right)$.

This gives us the total bias B:

(A3) $B = r_1 - r_2 = (b_1 - b_2)(1-\alpha) + \alpha(2p-1) = b(1-\alpha) + \alpha(2p-1)$.

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