Behavioral constraints and the evolution of faithful social learning

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Abstract   Behavioral "traditions", i.e. behavioral patterns that are acquired with the aid of social learning and that are relatively stable in a group, have been observed in several species. Recently, however, it has been questioned whether non-human social learning is faithful enough to stabilize those patterns. The observed stability could be interpreted as a result of various constraints that limit the number of possible alternative behaviors, rather than of the fidelity of transmission mechanisms. Those constraints can be roughly described as "internal", such as mechanical (bodily) properties or cognitive limitations and predispositions, and "external", such as ecological availability or pressures. Here we present an evolutionary individual-based model that explores the relationships between the evolution of faithful social learning and behavioral constraints, represented both by the size of the behavioral repertoire and by the "shape" of the search space of a given task. We show that the evolution of high-fidelity transmission mechanisms, when associated with costs (e.g. cognitive, biomechanical, energetic, etc.), is only likely if the potential behavioral repertoire of a species is large and if the search space does not provide information that can be exploited by individual learning. Moreover we show how stable behavioral patterns ("traditions") can be achieved at the population level as an outcome of both high-fidelity and low-fidelity transmission mechanisms, given that the latter are coupled with a small behavioral repertoire or with a search space that provide substantial feedback. Finally, by introducing the possibility of environmental change, we show that intermediate rates of change favor the evolution of faithful social learning [*Current Zoology* 58 (2): 307–318, 2012].

Keywords   Animal social learning, Cultural evolution, Cultural transmission, Copying fidelity, Individual based modeling

Examples of behavioral "traditions", i.e. behaviors acquired with the aid of some forms of social learning, and which are relatively stable in groups, have been found in several species (Laland and Galef, 2009). The existence of these traditions has been usually considered as a strong indication of the presence of faithful social transmission mechanisms that guarantee both the successful diffusion and the stability of the behaviors involved (Huffman, 1996; Horner et al., 2006; Marino et al., 2007). In particular, since imitation - i.e. the high-fidelity copy of novel behaviors through the reproduction of action sequences of observed individuals (Call and Carpenter, 2002; Tennie et al., 2006; Whiten et al., 2009) - has often been viewed as the learning mechanism that best explained the emergence of human traditions (Boyd and Richerson, 1996; Tomasello et al., 1993; Tomasello, 1999), it is assumed that also non-human traditions are supported by similar imitative capacities (Claidière and Sperber, 2010).

However, it has been recently questioned whether non-human social learning is actually faithful enough to produce such stable behavioral patterns. For example, it has been shown that in experimental settings great apes tend to scarcely use imitation (Tennie et al., 2006; Tennie et al., 2009; Tennie et al., 2010). On a more theoretical side, Claidière and Sperber (2010) argued that the fidelity of social learning, as deduced by transmission chain studies in different species, may explain the propagation, but not the stability, of non-humans behavioral traditions.

Accordingly, researchers have begun to examine whether, and how, non-human animals, unequipped with faithful social learning capacities, could be able to develop behavioral traditions (Huber et al., 2009; Shea, 2009). It has been suggested that stable behavioral patterns could also result from transmission mechanisms less faithful than imitation, such as emulation, social and local enhancement, or even from trial-and-error learning (Caldwell and Millen, 2009; Franz and Matthews, 2010;


Heyes, 1993; Laland and Hoppitt, 2003; Matthews et al., 2010; Whiten et al., 2003). Finally, it has been proposed that the observed stability could be the result of constraints that limit the number of possible alternative behaviors, more than the result of the fidelity of transmission mechanisms (Tennie et al., 2009; Claidière and Sperber, 2010).

In this paper we investigate the relationship between behavioral constraints and faithful social learning through an evolutionary individual-based model in which a hypothetical "species", first unequipped with high-fidelity copying mechanisms, may evolve them under different conditions. More specifically, we assumed that increasing the fidelity of social learning had some costs (e.g. cognitive, energetic, etc.) and also that the behavior of this species was variously constrained.

We introduced two kinds of constraints into our model. The first series of constraints limited the variety of individuals' behavioral repertoires. In real-life those constraints would translate into a set of "internal" factors, such as cognitive limitations (e.g. poor working memory capacities limit the number of behavioral sequences a species can plan or copy; van Leeuwen et al., 2009), cognitive biases (e.g. preference for certain classes of stimuli or certain types of demonstrators towards which one directs its behaviors; van de Waal et al., 2010), or bodily (biomechanical) architecture of acting individuals (e.g. limited degrees of freedom of effectors restrict the flexibility by which one can interact with external objects; Desmurget et al., 1995). In our model those constraints determined the number of the possible behavioral alternatives a species was provided with. Note that this indicates the distribution of *potential* behaviors, limiting the space in which the search for the optimal behavior is made, while the actual behaviors a population will show is a subset of those.

The second series of constraints pertained to the specific task one has to resolve and can be exemplified by a set of "external" factors (e.g. ecological) that shape the structure of the search space in which the candidate solutions takes place (Acerbi et al., 2011; see also Goldstone et al., 2008). For example, finding the ripest fruits on a tree is a very different problem with respect to choosing an edible fruit among different (perhaps including poisonous) fruits. In the former case an individual can try different fruits and, given adequate sensory and cognitive capacities, can choose to eat the sweetest ones; a strategy that is clearly not efficient in the latter situation. Here, we identified three distinct search spaces (see Fig. 1), distinguished by the way payoffs were distributed among possible behaviors and, by consequence, by their tendency to enable individual search strategies. In the Methods section we describe the three spaces used in the model in detail and provide a real-life example for each.

The model we developed is individual-based (Grimm and Railsback, 2005), meaning that we simulated interactions at the level of single individuals, and evolutionary, i.e. an evolutionary algorithm (Holland, 1975) is used to optimize the behavior of individuals. The evolutionary algorithm acted on a variable that encoded the fidelity of social learning of each individual. Individuals that performed better resulted in proportionally more "offspring" than others. Even though they generally represent simplifications of reality, the use of evolutionary individual-based models is increasing in animal behavior studies. The reason is that they enable the identification of different selective pressures under varying ecological conditions, thus helping researchers to select the data needed to understand otherwise opaque phenomena (see also Acerbi and Nunn, 2011).
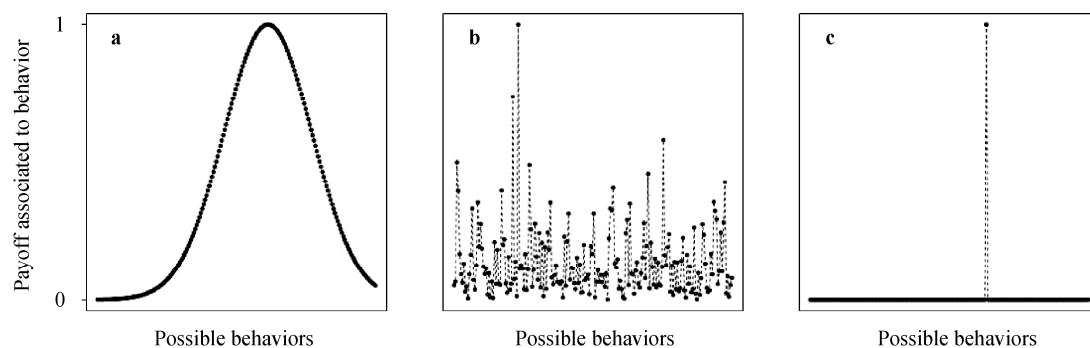
Fig. 1   Search spaces used in the simulations
Schematic representation of the three payoff distributions used in the simulations determining the three different search spaces. **a**. Smooth space. **b**. Rugged space. **c**. Peaked space (See text for details).

In the next section, we describe the implementation and the features of the model in detail, before presenting the results. We first investigated in which conditions a species, starting from completely unreliable social learning capacities, and thus relying upon individual learning only, was likely to evolve costly faithful social learning mechanisms. Secondly, we analyzed how population behavioral homogeneity (i.e. behavioral traditions) could be reached under different behavioral constraints, i.e. varying the size of the behavioral repertoire as well as the tasks' search spaces. Finally, we run other simulations allowing the possibility of environmental change, and we tested its effect on the evolution of faithful social learning. In the last section, we discuss the relevance of our results for the study of animal social learning and culture, limitations and possible extensions of our model, as well as some broad implications for modern human culture.

1 Materials and Methods

1.1 General description of the model

All simulations involved populations of individuals (n=100) that interacted in discrete time steps (until T=10000). At the beginning of the simulations each individual was assigned a behavior, randomly chosen among all possible behaviors characterizing its population. Populations varied with respect to the size of their behavioral repertoire (S): we distinguished three different experimental conditions, with populations disposing of a repertoire of 10, 100, or 200 possible behaviors.

At each time step, individuals interacted in pairs. Each individual (the *learner)* was paired with another individual (the *demonstrator*) randomly chosen among the ten individuals of the population with the highest payoffs (see below for how payoffs were calculated). Thus, each learner attempted to copy the behavior of its paired demonstrators. The accuracy of social learning depended on an individual characteristic, determined by the parameter α (fidelity of social learning). At the beginning of the simulations, α was initialized equal to zero for all individuals (making social learning completely unreliable for all individuals) and its value evolved through time.

Evolutionary dynamics resulted from a death-birth process in which newborns inherited the value of α from fittest individuals. Below we describe the details of the model's implementation.

1.2 Behavioral repertoire and search spaces

Experimental conditions varied with respect to the size of the population's behavioral repertoire (S=10, 100,

and 200 possible alternative behaviors) as well as to how payoffs were distributed among possible behaviors, determining three different "search spaces". Behavioral payoffs varied between 0 and 1, and only a single behavior, randomly selected, brought the maximum payoff to individuals in all spaces.

1.2.1 The smooth space In *smooth spaces* (see Fig. 1a), different behaviors laid on a payoff gradient, and the "closest" a behavior was to the optimal one, the higher its payoff. Payoffs were modeled as a Gaussian distribution (as in Boyd and Richerson, 1985 and Mesoudi and O'Brien, 2008). Smooth spaces represent tasks for which, even if an optimal solution exists, sub-optimal alternatives are similar in terms of payoff returns. Moreover, the existence of a payoff gradient provides a way to orient individual searches so that individual learning (e.g trial and error learning) can potentially be as effective as social learning (Acerbi et al., 2011). Even complex behaviors like chimpanzees' ant dipping have aspects that may be considered searches in smooth spaces (Humle and Matzusawa, 2002). An individual, for example, can repeatedly experiment with sticks of different length, self-evaluate the outcomes of different attempts, and then arrive at the measure that is most appropriate in a given situation.

1.2.2 The rugged space Rugged spaces (see Fig. 1b) represent "difficult" tasks for which only few good solutions exist. Contrary to smooth spaces, the structure of such tasks does not provide ways to orient individual searches. In our simulations rugged spaces were generated by assigning to every possible behavior a random payoff drawn from an exponential distribution with mean=1 (rescaled between 0 and 1), so that a single behavior led to the maximum payoff, while a restricted number of alternatives approximate it and a vast majority led to low payoffs. One real-life example of a task represented by a rugged search space could be foraging in a patchy, heterogeneous, environment (see e.g. Gil and Wolf, 1977). In such a situation, an individual can potentially try different sources of food, with only few of them being fruitful, without knowing in advance which one will be the richest. The knowledge of one source, furthermore, does not give information about the quality of the other sources present in the environment.

1.2.3 The peaked space Finally, peaked spaces (see Fig. 1c) represent even more difficult tasks, for which only a single behavior provides a payoff to individuals, distinguishing it from the two other search spaces described above. In Acerbi et al. (2011) we argued that many real-life tasks, especially in human culture, fit this

description. One simple example is tying a knot: performing a behavior similar – but not equal – to the one requested to tying the knot does not produce a "less effective" knot, but in general does not produce any usable result. For this kind of task it is likely that any form of individual learning would be very ineffective, since there is nothing in the search space that could orient the search and there is only a single rewarding solution.

1.3 The copying process

The outcome of the copying process depended on the observer's value of α. Fig. 2 illustrates how the new behavior was picked up by the observer. Once the demonstrator was chosen, a new behavior was randomly selected in the search area included between $\pm\frac{S}{2}(1-\alpha)$ with respect to the demonstrator's behavior, and retained by the individual if its payoff was equal or higher with respect to the current payoff.
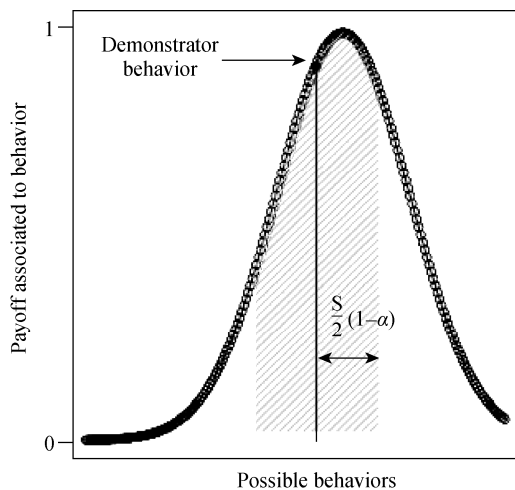
Fig. 2 Schematic representation of the copying process (in a smooth search space)

Given the demonstrator behavior, the learner will randomly pick up one behavior in the gray area. The size of the area is given by $\pm S/2(1-\alpha)$, where S is the size of the population's behavioral repertoire and α represents the learner's fidelity of social learning. (See text for details).

When α is close to 1 – such that the fidelity of the learner's copy is almost perfect – this expression is close to 0, meaning that individuals will assume a behavior closely approximating the demonstrator's behavior (with α=1 the copied behavior will be exactly the demonstrator's behavior, so, in this case, social transmission equates to replication). On the contrary, when α is close to 0, the expression is close to $S/2$, covering a large range of the behavioral repertoire. Since behaviors that decrease individual's payoff are discarded, α=0 can be

considered cases of pure individual learning.

1.4 Average payoff and evolutionary algorithm

A basic assumption of our model was that faithful social learning has some cost, and this cost modulated the payoff an individual received from performing a behavior. Individual payoff was hence determined both by the behavior performed and by the fidelity of social learning represented by their value of α.

In more detail, the payoff of individuals (P_i), at each time step, was equal to:

$$P_i = P_b - \alpha C$$

that is, the payoff obtained by the behavior performed (P_b), minus the value of α multiplied for a factor *C:*

We varied the value of *C* from 0 (no cost) to 0.5 (highest cost), with steps of 0.1, representing alternative situations in which using (and evolving) faithful social learning could be more or less costly.

The *average* individual payoff, used to select individuals for reproduction in the evolutionary algorithm, was simply the sum of all payoffs an individual had had in the course of its life, averaged for the number of time steps it was alive.

Individuals were selected for reproduction according to their average payoff. At each time step one individual, randomly chosen among the entire population, was replaced by a "newborn". The newborn individual inherited the value of α from another individual that was randomly chosen among the ten individuals with the highest average payoffs. The behavior of the newborn was initialized randomly. In other words, the fidelity of social learning, and not the behavior *per se*, was genetically inherited and, hence, subject to evolutionary pressures.

Finally, with a small probability of mutation (μ=0.05), the inherited value of   α was randomly reinitialized with a value comprised between 0 and 1.

1.5 Simulation procedures

In a first set of simulations we studied three different sizes of behavioral repertoires (S=10, 100, and 200) for each payoff distribution (smooth space, rugged space, and peaked space). For each condition, we varied the cost factor of fidelity (C=0, 0.1, 0.2, 0.3, 0.4, and 0.5) and we ran 100 simulations for every value of C, recording the average value of fidelity evolved.

We then analyzed how, in peaked search spaces, the interaction between the fidelity of social learning and the size of the behavioral repertoire impacted the populations' behavioral diversity, namely, the number of behavioral patterns present in a population. To calculate behavioral diversity we used Simpson's diversity index. Simpson's diversity index was developed mainly to as-

sess ecological diversity, taking into account both the number and relative abundance of species present in a given environment (Simpson, 1949). Recently it has been used to assess behavioral diversity in cultural evolutionary models (Kandler and Laland, 2009; Enquist et al., 2010). According to this index the diversity of a population can be represented as:

$$D = 1 - \sum_i \chi_{(i)}^2$$

where $\chi_{(i)}$ is the frequency of the i variant in the population. The value of D tends towards 1 as the behavioral diversity of a population increases, and is equal to 0 when all individuals share the same behavioral variant.

We also measured directly the number of existing behaviors at the end of simulations, comparing the effect of the three different search spaces, keeping the other parameters constant (S=200, C=0.2).

In a second set of simulations, we added the possibility of environmental changes. An additional parameter (p_c=0.001, 0.01, and 0.1) determined at each time step the probability of the payoff distribution to be fully reinitialized. Note that reinitialization of payoffs did not change the structure of the search space but it changed the distribution of payoffs among the behaviors. In smooth spaces as well as in peaked spaces, this involved the "shifting" of the optimal behavior in a different position, and in rugged spaces the re-assignment of a random payoff to every possible behavior drawn from the exponential distribution described in subsection 2.2.2. Notice that when p_c=0 this condition reduces to the basic simulation (Table 1).

Table 1 Main parameters and their value used in the model

| Symbol	Short description	Values
N	Population size	100
T	Number of time steps	10000
S	Size of the behavioral repertoire	**10, 100, 200**
C	Cost factor of fidelity	**0, 0.1. 0.2, 0.3, 0.4, 0.5**
μ	Mutation rate	0.05
p_c	Probability of environmental change	**0, 0.001, 0.01, 0.1**

Bold typeface values are values varied in different experimental conditions.

2 Results

2.1 Faithful social learning evolves with large behavioral repertoire and in peaked spaces

The results of our simulations showed that, in stable environments, costly faithful social learning evolved only if two conditions were simultaneously met: the populations had a large behavioral repertoire, and the task structure was a peaked space (see Fig. 3).

When faithful social learning was cost-free (C=0), all populations converged towards high average values of α, showing that high-fidelity transmission mechanisms proved advantageous to individuals in all conditions. However, when copying mechanisms involved costs that impacted on the individual's payoff (C>0), these costs were only worthwhile in situations where an individual search was ineffective. This occurred in peaked search spaces, and with populations characterized by a sufficiently large behavioral repertoire (see Fig. 3c).
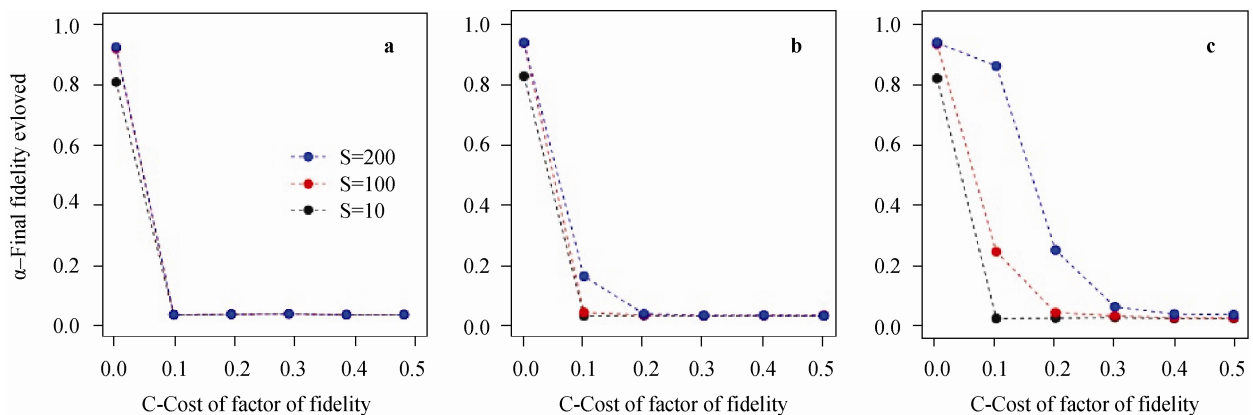
Fig. 3 Average fidelity evolved at the end of simulations versus cost factor of fidelity
a. Smooth space. **b**. Rugged space. **c**. Peaked space. Different lines colors in the three conditions represent different sizes of the behavioral repertoire: blue line: S=200; red line: S=100, black line: S=10. (Each data point is an average on 100 runs).

2.2   Behavioral homogeneity results from both high-fidelity social learning mechanisms and low-fidelity mechanisms

Fig. 4 depicts the evolutionary trajectories of typical runs in the peaked space condition, for populations having different sizes of behavioral repertoire and for three different values of C. We have chosen to analyze in detail the peaked space condition because in this condition faithful social learning evolves also when is costly (see results in Fig. 3). Each point in the plots represents the "position" of a population with respect to its behavioral diversity (x-axes) and its average fidelity of social learning (y-axes), sampled at an interval of 100 time steps, during each run. Populations that are in the left part of the graphs are behaviorally homogeneous populations and populations that are on the right side are behaviorally diverse. With respect to y-axes, populations that are in the lower part of the graphs lack hi-fidelity social learning abilities while population in the upper part posses them.

Populations always "started" in the bottom right corner of the graphs, i.e. they were diverse (at the beginning of the simulations behaviors were randomly initialized) and individuals also did not possess hi-fidelity social learning abilities (α was initialized at 0 for all individuals). When faithful social learning was cost-free (C=0, Fig. 4 left), populations, irrespective of their behavioral repertoire's size, "moved" towards the high left corner of the plot during the simulation run, i.e. towards behavioral homogeneity and faithful social learning. It is worth noting that populations with a small behavioral repertoire (black line) could move to the left area of the plot (i.e. towards behavioral homogeneity) without individuals being required to increase their social learning ability

(this happened only in later stages of the simulation). On the contrary, populations with larger behavioral repertoire (blue and red lines) were required to increase the faithfulness of social learning ("moving up in the plot") in order to move towards behavioral homogeneity.

For intermediate costs of faithful social learning (C=0.1, Fig. 4 center), the evolutionary trajectories of populations with large behavioral repertoire were similar, while the population with small behavioral repertoires reached homogeneity without developing faithful but costly social learning. Finally, when faithful social learning was even more costly (C=0.2, Fig. 4 right), even populations with large behavioral repertoires did not evolve it, and their behavioral diversity remained high.

In sum, while behaviorally diverse populations (right part of the plots) were the outcome of a large behavioral repertoire coupled with low-fidelity social learning mechanisms (Fig. 4 right), behavioral homogeneity (i.e. low diversity, left part of the plots) could be the product either of faithful social learning (Fig. 4 left) or of low-fidelity social learning, provided that the behavioral repertoire was small (Fig. 4 center, black line).

However, the size of the potential behavioral repertoire was not the only factor that influenced the final behavioral diversity of a population. We analyzed simulation runs with the same behavioral repertoire size (S=200) and the same cost factor for social learning (C=0.2) and we measured the number of behaviors present at the end of the simulations for the three different search spaces (Fig. 5). In smooth and rugged spaces, where faithful social learning did not evolve (see results in Figure 3 a and b), the populations showed approximately 20 different behaviors. In peaked search paces, however, the final number of behavior in absence of faithful social
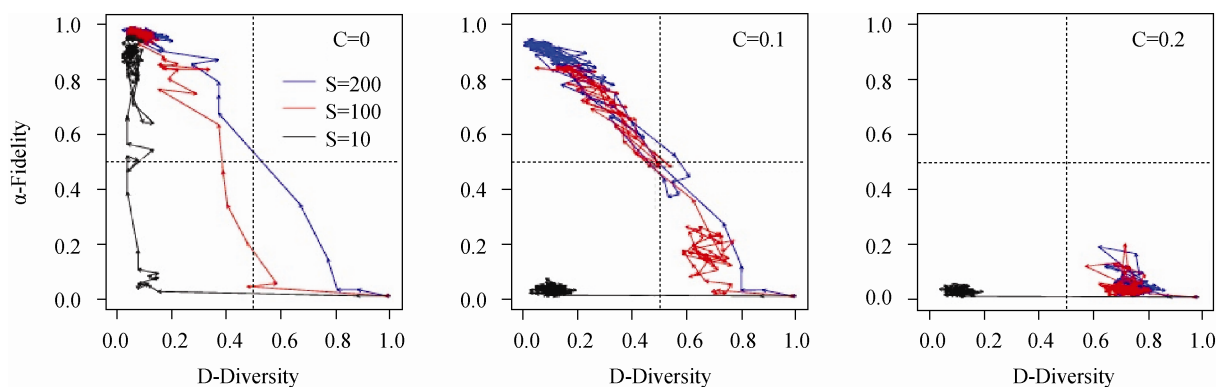
Fig. 4   Evolutionary trajectories of populations
Evolutionary trajectories of populations in respect to behavioral diversity (x-axes) and average fidelity of social learning (y-axes). Each point in the plot represent the "position" of a population at a given stage of the evolution (sampled every 100 time steps in a simulation run).   Different lines colors represent different sizes of the behavioral repertoire: blue line: S=200; red line: S=100, black line: S=10. The cost factor of social learning varies in the three panels: from left to right C=0, C=0.1, C=0.2.
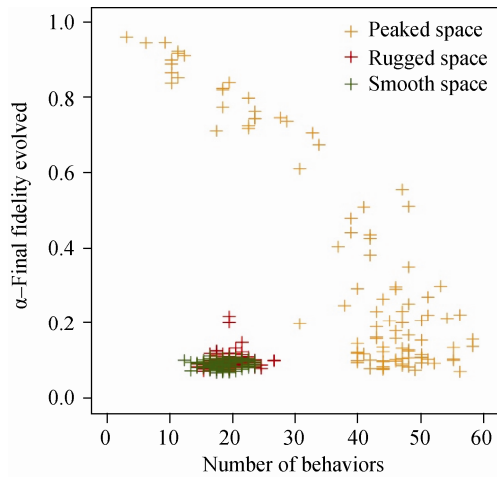
Fig. 5   Final number of behaviors present in populations in the three different search spaces

Each point of the plot represents the results of a simulation in respect to the final number of behaviors present in the population (x-axes) and the average fidelity of social learning evolved (y-axes), keeping fixed the factor cost of social learning (C=0.2) and the size of the behavioral repertoire (S=200). Orange: peaked space, red: rugged space, green: smooth space. (For each space 100 simulations were run).

learning was higher, and the same number of behaviors was reached only when faithful social learning evolved.

2.3   Intermediate rates of environmental change favor the evolution of faithful social learning

Finally, we analyzed the effect of environmental variation on the evolution of faithful social learning, running additional simulations for populations with a large behavioral repertoire (S=200). Populations with a large behavioral repertoire were specifically targeted as the above described results showed that in these conditions faithful social learning was more likely to evolve when the environment was fixed.

In smooth search spaces, environmental variation had no effect on the evolution of faithful social learning (Fig.

6a), and populations remained composed of individuals with poor copying abilities, even when the environment was variable. For rugged and peaked search spaces (Fig. 6b and 6c), we found instead that the evolution of faithful social learning was favored for intermediate rates of environmental variation. In fact, when the rate of environmental variation was too high (p_c=0.1) the average values of fidelity evolved were similar to the condition in which the environment was stable (p_c=0).

3   Discussion

3.1   General discussion of the results

The present individual-based model examined the relationship between behavioral constraints and the evolution of faithful social learning. Constraints varied according to the size of the behavioral repertoire of populations (10 vs. 100 vs. 200 possible alternative behaviors) and according to the intrinsic structure of the search space characterizing the task problem (*smooth space* vs. *rugged space* vs. *peaked space*). We firstly analyzed, by varying the cost for individuals to use faithful transmission mechanisms (from *null* to *high* cost), how and in which type of search spaces populations with different sizes of behavioral repertoire would take advantage of such faithful social learning. We also took into account the effects of fidelity of social learning and behavioral constraints on the behavioral diversity at population level. We investigated whether populations unequipped with high-fidelity transmission mechanisms were prone to develop and stabilize novel behavioral patterns in a manner outwardly similar to populations equipped with high-fidelity transmission mechanisms. Finally, the effect of the rate of environmental change in which populations evolved (from *no* to *fast* environmental change) was studied.
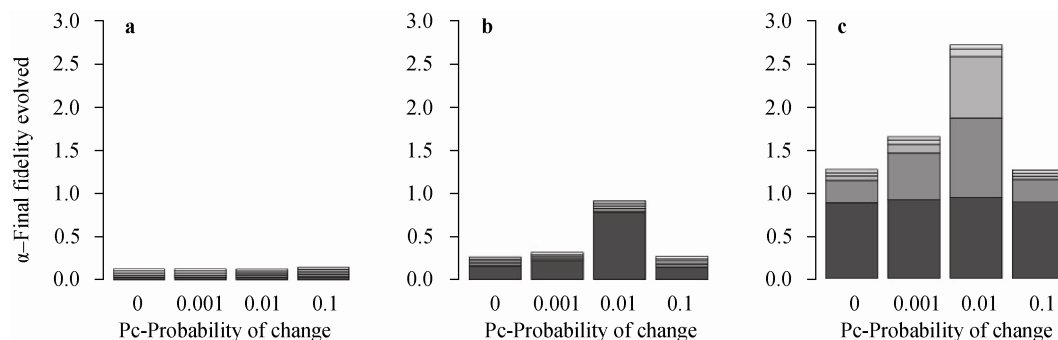
Fig. 6   Stacked bar plot of the average fidelity evolved with different probabilities of environmental change for population with S=200 (size of the behavioral repertoire)

The different colors in the bars represent different values of C (factor cost of faithful social learning) from C=0.1 (darker) to C=0.5 (lighter). We did not take into account C=0 because in this condition faithful social learning always evolved for p_c=0 (see Fig. 3).   **a**. Smooth space. **b**. Rugged space. **c**. Peaked space. (Each data is an average on 100 runs).

Three main results emerged. First, in stable environments, costly faithful social learning evolved only in populations with large behavioral repertoires, and particularly in peaked search spaces. Second, the convergence towards behavioral homogeneity resulted from high-fidelity social learning mechanisms but also from low-fidelity mechanisms, when they were associated with a small behavioral repertoire or with smooth and rugged search spaces. Third, intermediate rates of environmental change favored the evolution of faithful social learning.

The evolution of faithful social learning, when costly, strongly depended on behavioral constraints. According to our results, we should expect to find, in real-life, faithful social learning in conditions in which a species, or a group, has many behavioral alternatives (a large S in our model) and, at the same time, in which the task at hand does not provide any structure useful to orient the individual's search. In particular these conditions were met in peaked spaces. Tasks characterized by this search space had two interesting features. First, only a very narrow number of behaviors-in our model, only one-led to success (i.e. the payoff achievable with sub-optimal behaviors is zero, differently from other spaces). Secondly, performing behaviors other than the single successful solution did not provide any feedback that individuals could use to estimate the optimality of a given behavior. This result confirms and enriches our previous findings (Acerbi et al., 2011) where we showed that, for tasks whose search structure could be modeled as a peaked space, imitation-i.e. a specific instance of high-fidelity social learning mechanism-was more effective than emulation and individual learning.

We also showed that the convergence of a population towards behavioral homogeneity could result, as expected, from high-fidelity social learning mechanisms, but also from low-fidelity social learning mechanisms. An analysis of simulations for peaked search spaces demonstrated that a population with a small behavioral repertoire could become behaviorally homogeneous without developing high-fidelity social learning mechanisms. Additionally, our results also showed that when the number of potential behaviors was large, the search structure had an impact on the number of behaviors actually present in the population. In particular, relative homogeneity in absence of high-fidelity social learning mechanisms was obtained for smooth and rugged search spaces, but not for peaked spaces.

This observation is of importance since the emergence

of behavioral homogeneity in wild populations is often presumed to be a sign of faithful social learning (Huber et al., 2009). While this could certainly be the case – in the simulations presented here faithful social learning does indeed produce behavioral homogeneity – our model provides an alternative explanation. This explanation is based on the existence of behavioral constraints, may they be due to physical and/or cognitive limitations, or ecological factors (shaping the search space of a given task). It has been shown that behavioral constraints can lead to the re-appearance of presumed cultural behaviors in naïve captive individuals (Huffman and Hirata, 2004; Tennie et al., 2008; see also Masi, 2011). With regard to ecological influences, it has long been suggested that these may help explain the distribution of several behaviors across populations (Humle and Matsuzawa, 2002; though see Schöning et al., 2008; Möbius et al., 2008). For a behavior presumed to be a product of faithful social transmission, one has to check whether its diffusion among the population is accounted for by such alternative possibilities (see also Laland and Janik, 2006; Tennie et al., 2009). Of course, as nearly always in modeling, our model represents an ideally simplified situation. However, one could imagine having an estimation of the possible alternative behaviors a species is likely to use (see e.g. Changizi, 2003), as well as an estimation of the search structure of a specific task (for example the distribution of resources in a specific environment and their energetic/caloric contribution). These data can then be used to parameterize the model. In this way one could obtain more realistic results that could be used as a guide to analyze whether, in a specific situation, a given population is likely to make use of social learning.

Finally, by manipulating the probability of environmental change, we showed that intermediate rates of environmental change favored the evolution of faithful social learning. Importantly, with moderate rates of environmental change, costly faithful social learning evolved not only in peaked spaces, but also in rugged search spaces. This is consistent with the idea that the three search spaces we modeled represent three different levels of "difficulty" (see below however for how we intend the meaning of "difficulty" here), with smooth spaces representing "easy" tasks, followed by rugged spaces, and then by peaked spaces as the most difficult ones. More generally, this result is coherent with the broad consensus that the evolution of social learning is more likely to occur for an intermediate rate of environmental change than for no change-where genetic

evolution is favored - or fast change-where individual learning is favored (see e.g. Henrich and McElreath, 2003; Wakano et al., 2004; Aoki et al., 2005).

3.2 Related literature and possible extensions of the model

The results of our model are, in general, consistent with the "costly information hypothesis" (Boyd and Richerson, 1985), according to which social learning is favored when acquiring information individually is costly or inaccurate (see e.g. Rogers, 1988; Boyd and Richerson, 1995; Wakano et al., 2004; Aoki et al., 2005). We aimed to illustrate how this trade-off between social and individual learning could be realized in a scenario analogous to many real-life situations, focusing on the notion of behavioral constraints, and we believe that this illustration may be of some use for field biologists and comparative psychologists who study social learning and cultural evolution.

The role of the variation of search spaces, or adaptive landscapes, have been considered in previous models of cultural evolution (Boyd and Richerson, 1992; Mesoudi, 2008). These models show how multimodal adaptive landscapes-i.e. search spaces with more than one peak - favor social learning, contrary to unimodal adaptive landscapes, where individual learning is favored. Our results add to these previous finding by showing that also in unimodal adaptive landscapes social learning may be favored, as long as the search space does not provide information that can be used to orient individual learning (our peaked space condition).

Previously, other computational models (Hinton and Nowlan 1987) had shown that problems analogous to tasks represented by the peaked space could be solved through a combination of individual learning and genetic evolution. Since we did not consider genetic evolution (i.e. our evolutionary algorithm acted on the accuracy of social learning, and not on the actual behavior), our model is unable to address this question, though we obtained the same qualitative result with respect to the poor performance of individual learning alone. In a later development of Hinton and Nowlan's model (Best, 1999), the possibility of social learning was added, and it was shown that, indeed, the combination of social learning and genetic evolution improved the performance compared to the combination of individual learning and genetic evolution. In Best's model, however, social learning was cost-free and no changes in the search space or in the size of the behavioral repertoire were taken into account.

As with many models, we concentrated here on few parameters that we thought of fundamental importance for our study, namely the cost of acquiring faithfully social information, the size of the behavioral repertoire, the different search spaces, and, as a final check of the validity of our model, the extent of environmental variation. Interesting developments could consist in examining the effects of other factors on the results here reported. For example, we used a basic evolutionary algorithm, mainly intended as a proof-of-concept tool, keeping a fixed-and high-selection pressure, a simple implementation of the mutation-α was reinitialized every time a mutation occurs-, and we did not consider the effect of population size on evolutionary dynamics. We had run some exploratory simulations to test the effects of the variation of these parameters (not reported in the results section). Varying population size (n=200; n=500) and changing the way mutations were implemented (α each time modified by a value randomly selected between -0.1 and +0.1) did not seem to change qualitatively our main results. Selection pressure, however, had some impact on the results. Interestingly, *less* selection pressure ("reproducing" individuals randomly chosen among the twenty, or fifty, individuals with the highest average payoffs) favored the evolution of social learning when costs were high, at least in peaked and rugged search spaces, and for large behavioral repertoires (S=100; S=200). We interpret this result as meaning that, with high selection pressures, "lucky" individuals that found optimal behaviors without using costly social learning were highly favored by the evolutionary algorithm, making populations of social learners unstable. The interactions between population size and selection pressure are anyhow inherently complex, and we plan to explore their effect on the evolution of faithful social learning in scenarios like ours in future works.

We also assumed that individuals were randomly paired in their interactions, a part from the fact that only individuals with proportionally high payoffs were targeted as possible demonstrators. Starting from the same set-up, one could certainly include more realistic rules of interactions, considering for example individuals being in different ways selective in their decisions about when and from who to copy (for the importance of these and other social learning "strategies" see Laland, 2004; Rendell et al. 2011), or explicitly consider a spatial dimension in the model, with individuals having different movement "rules" and interactions constrained by physical proximity.

As a final remark, we initialized our populations with random behaviors, chosen among all the possible alter-

natives of their potential behavioral repertoire. This is possibly an unrealistic situation (real populations do not show highly diverse - and certainly not random - behaviors) but we believe such a simplification to be useful as a "starting point" for the evolutionary algorithm. Again, future work could analyze how behavioral constraints impact on the evolution of social learning, starting from homogeneous populations that behave suboptimally or already optimally, in which case social learning would be necessary to maintain the correct behavior through time.

3.3   General considerations and implications for modern human culture

We conclude with some general considerations derived from our results. In social learning research, the complexity of a task is often considered suggestive of the presence of social learning - with "easy" tasks being solved with individual learning and "difficult" tasks needing social transmission (see also Acerbi et al., 2011). Especially in laboratory tasks, experimenters try to propose "difficult" tasks to animals to encourage the use of social information to solve them (Day et al., 2003, Baron et al., 1996, Laland, 2004, Tennie et al., 2009). While this is probably a good rule of thumb, our model suggests that what makes faithful social learning useful is not the difficulty of a task *per se* (see also Tennie and Hedwig, 2009) but the fact that relatively unconstrained behavioral alternatives are potentially involved in that task (or, if you prefer, a task is "difficult" when this happens). A spider's web may or may not be less complex than potato washing, what is different is that, in the former case, natural selection, working on the genetic level, highly constrained the behavioral repertoire, narrowing down the possible alternatives.

Within this perspective, even very complex human "cultural" behaviors may be a result of a combination of a genetically/ecologically narrowed behavioral repertoire, constrained search spaces, and some form of social learning (Sperber, 1996). One might consider, for example, cookery traditions. The impressive variability of foods consumed in different cultures is the outcome of various forms of cultural transmission (between and within societies) that nonetheless act on a "constrained space": ecologically constrained (local availability of products), genetically constrained (only some products are edible; some taste preferences are at least partly innate, Rozin, 1990), and technologically constrained (many products have to be processed in a specific way to became edible; the technologies available in a group limit the choice of processing food techniques). On the

other side, some cultural behaviors are relatively less constrained. Many fashions and fads, for example, result from pure transmission processes (see e.g. Bentley et al., 2007, Acerbi et al., 2012): the fashion of, say, "wearing green" one year but not the next has not much to do with behavioral constraints as we intended them in this paper. Analogously, if we take into consideration highly complex technological tasks, products of human cumulative culture (Richerson and Boyd, 2005), behavioral constraints become less and less important. Building a kayak – or an airplane – is certainly subject to constraints (all in all airplanes need to fly and kayaks need to float) but their guidance is so loose that only high fidelity copying mechanisms can allow an individual to acquire the necessary skills to produce them. Humans, nevertheless, also excel in a parallel strategy to solve those problems: cultural "epistemic engineering" (Sterelny, 2003) is, according to the view presented here, a matter of narrowing the alternative solutions to a problem, and artificially build highly informative search spaces so as to reduce the need of costly social learning.

In conclusion, we believe that an explicit attention towards what is learned, and towards the potential alternatives and constraints, may enrich the theoretical toolbox of social learning modeling, and possibly our understanding of humans and other species' culture.

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