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Original Article

Convergent transformation and selection in cultural evolution

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ABSTRACT

In biology, natural selection is the main explanation of adaptations and it is an attractive idea to think that an analogous force could have the same role in cultural evolution. In support of this idea, all the main ingredients for natural selection have been documented in the cultural domain. However, the changes that occur during cultural transmission typically result in convergent transformation, non-random cultural modifications, casting some doubts on the importance of natural selection in the cultural domain. To progress on this issue more empirical research is needed. Here, using nearly half a million experimental trials performed by a group of baboons (*Papio papio*), we simulate cultural evolution under various conditions of natural selection and do an additional experiment to tease apart the role of convergent transformation and selection. Our results confirm that transformation strongly constrain the variation available to selection and therefore strongly limit its impact on cultural evolution. Surprisingly, in our study, transformation also enhances the effect of selection by stabilising cultural variation. We conclude that, in culture, selection can change the evolutionary trajectory substantially in some cases, but can only act on the variation provided by (typically biased) transformation.

1. Introduction

How similar is cultural evolution to biological evolution? And to what extent is cultural evolution Darwinian? These questions have been subject to much recent debate, and it has become clear that the answer crucially depends on the role that natural selection plays in cultural evolution (Acerbi & Mesoudi, 2015; Claidière, Scott-Phillips, & Sperber, 2014; Claidière & Sperber, 2007; Dennett, 1995; Henrich & Boyd, 2002; Kronfeldner, 2007; Mesoudi, Whiten, & Laland, 2004, 2006; Sperber & Claidière, 2008). In biology, natural selection[1] is the main explanation of adaptations and it is an attractive idea to think that an analogous force could have the same role in cultural evolution (Boyd & Richerson, 1985; Cavalli-Sforza, 1971; Dawkins, 1976; Dennett, 1995). Support for this idea comes from the fact that all three main ingredients for natural selection, phenotypic variation, differential fitness and heritability (Lewontin, 1970), exist in the cultural domain (Gerard, Kluckhohn, & Rapoport, 1956; Mesoudi et al., 2004). Furthermore, given the fact that Darwinian selection can be described in quite abstract terms (Price, 1971/1995), without reference to specifically biological properties, cultural and biological evolution may, in principle, differ in many ways and still both give a central role to selection. Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) were among the firsts to apply population genetics models to cultural evolution using culture-specific rules of transmission (such as one to many, conformity, prestige, etc.), later giving rise to the notion of social learning strategies (Laland, 2004; Rendell et al., 2011).

However, there is little agreement on how important cultural selection is for cultural evolution (Acerbi & Mesoudi, 2015; Claidière, Kirby, & Sperber, 2012). For some researchers, cultural selection could be the main factor explaining cultural traits (in particular technological ones) and therefore how modern humans adapted to widely different environments (Henrich, 2001). According to this view, cumulative cultural evolution (the gradual accumulation of cultural modifications over time) results from faithful transmission (through e.g. imitation, communication and teaching) and the generation of variation through innovation and random modifications (Tennie, Call, & Tomasello, 2009). This creates competition between cultural variants which in turn results in cultural selection and ultimately in a runaway process that gave rise to our modern culture. Under this hypothesis, the concrete mechanisms

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[1] For clarity, we will draw the distinction between the abstract process of natural selection and its implementation in different domains such as in biology (biological selection) and culture (cultural selection).

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through which biological evolution and cultural evolution operate are very different but they both instantiate the same underlying process that gives rise to biological and cultural adaptations: natural selection.

In contrast, other researchers have argued that the role of cultural selection is probably limited, mainly for two related reasons. Firstly, social learning mechanisms underlying cultural transmission may give a misleading impression of guaranteeing high fidelity when in fact cultural evolution tends to *produce* variants that become more faithfully transmitted (Claidière, Smith, Kirby, & Fagot, 2014; Kirby, Cornish, & Smith, 2008). Although there are important limitations to comparing fidelity across domains (Charbonneau, Submitted), the fidelity of social learning mechanisms, when it can be evaluated, is generally orders of magnitude lower than that of biological replication (Claidière & Sperber, 2010a; although not always, e.g. Pagel, Atkinson, S. Calude, & Meade, 2013) and would therefore require much stronger selection pressures to produce adaptations (a phenomenon known as the error threshold in evolutionary biology; Eigen, 1971; Eigen & Schuster, 1979; Nowak & Schuster, 1989; Williams, 1966). For instance, Eerkens (2000) tried to estimate the maximum fidelity with which humans could copy the production of a stone tool by measuring perceptual accuracy and found that errors were at a minimum between 3 and 5%.

Secondly, and most importantly, changes during transmission tend to produce convergent transformation[2] (Claidière, Scott-Phillips, et al., 2014), i.e. non-random cultural modifications, as has been shown repeatedly in cultural evolution experiments (e.g. Claidière, Smith, et al., 2014; Kalish, Griffiths, & Lewandowsky, 2007; Kirby et al., 2008). The cognitive mechanisms of attention, memory and inference involved in social learning transform cultural variants in particular directions (Sperber, 1996). When, within a social group, the direction of these transformations converges, cultural traits may emerge and stabilize despite low fidelity in transmission. Cultural traits that owe their evolution and relative stability to convergent transformation have been described as “cultural attractors” and the resulting evolutionary process as one of “cultural attraction” (Sperber, 1996). This possibility raises the question of the relative role of convergent transformation and selection in explaining cultural evolution.

The debate surrounding the relative role of natural selection and of convergent transformation in cultural evolution (Acerbi & Mesoudi, 2015) has remained mostly theoretical and although theoretical analyses can tell us much about the formal interaction between selection and convergent transformations, they cannot provide information regarding the occurrence of selection and convergent transformations in nature. Some researchers emphasise the role of transformations in explaining cultural evolution, others emphasise the role played by selection. Unfortunately, fieldwork and experimental evidence aimed at teasing apart the role of selection vs. transformations in explaining cultural change are crucially lacking.

Here, we used cultural transmission experiments together with computer simulations to tease apart the role of convergent transformation and selection in an experimental situation. Briefly, as in Claidière, Smith, et al. (2014), we used transmission chains (Bartlett, 1932), in which the behavioral output of one individual becomes the target behaviour for the next individual in the chain, to study the evolution of visual patterns in a group of baboons. The baboons were shown a 4 by 4 grid with 4 red squares and 12 white ones. After a very short time (400 ms) the red squares became white and the baboons' task was to touch the squares that had just turned white on the touchscreen (see Methods for further details). Claidière et al. showed that across time the initially random patterns became systematically structured, the patterns gradually transformed into mathematically rare configurations known as tetromino (four connected squares), leading to an increase in performance. In this initial work, there was no selection among patterns (because each occurrence of a pattern gave rise to just one new occurrence) and the results therefore reflect the effect that successive transformations can have on cultural evolution, in the absence of selection.

To study the combined effects of selection and transformation among patterns we used a three-step procedure. Firstly, we used data that were collected but not analysed in Claidière, Smith, et al. (2014) to create simulations of cultural transmission chains. We validate our approach by comparing results of the simulations to the experimental outcome of Claidière, Smith, et al. (2014). Secondly, using the validated simulation procedure, we proceed to introduce selection among patterns in our simulations and study a wide variety of parameter combinations. Finally, we used the simulations to generate predictions on the interaction between convergent transformations and selection and test these predictions experimentally.

2. Methods

2.1. General experimental principles

2.1.1. Participants

Guinea baboons (*Papio papio*) belonging to a large social group of the CNRS Primate Center in Rousset-sur-Arc (France) participated in Claidière, Smith, et al. (2014) and in this study. The baboons were all marked by two biocompatible 1.2 by 0.2 cm RFID microchips injected into each forearm and lived in an outdoor enclosure (700 m^2) connected to an indoor area which provided shelter when necessary. The outside enclosure was connected to 10 testing workstations that the animals could use freely at any time to participate in experiments. This procedure aimed at preventing adverse effects that capture and social isolation may entail. The voluntary participation of the subjects reduces stress levels, as inferred from the significant decrease in salivary cortisol levels as well as the frequency of stereotypies (Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014). Baboons were neither water- nor food-deprived during the research. Water was provided ad-libitum within the enclosure. Monkeys received their normal ration of food (fruits, vegetables and monkey chows) every day around 5 pm. The baboons were all born within the primate centre.

2.1.2. Self-testing procedure and computer-based tasks

Experiments were conducted in a unique testing facility developed by J.F. The key feature of this facility is that baboons have free access to computerized testing booths that are installed in trailers next to their enclosure. They can thus participate in experiments whenever they choose, and do not need to be captured (more details can be found in Fagot & Bonté, 2010; Fagot, Marzouki, Huguet, Gullstrand, & Claidière, 2015; Fagot & Paleressompoulle, 2009).

During the experiment, each computerized trial began with the display of a grid made of 16 squares, 12 white and 4 red (Claidière, Smith, et al., 2014). Touching this stimulus display triggered the immediate abortion of the trial and the display of a green screen for 3 s (timeout). After 400 ms all the red squares became white and, in order to obtain a food reward, the monkey had to touch the previously red squares, in any order and with less than 5 s between touches. Squares became black when touched to avoid being touched again, and did not respond to subsequent touches. The trial was completed when 4 different squares had been touched. If three or four correct squares were touched the trial was considered a success and the computer triggered the

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[2] Different terms have been used in the literature to emphasise the fact that changes in cultural transmission are neither random nor blind with respect to their consequences, unlike biological mutations. For instance, Boyd and Richerson (1985) use the terms “guided variation” to emphasise the fact that in cultural transmission, variants can be generated which are reliably *improvements* on the culturally-inherited behaviour, rather than random changes. Sperber and colleagues highlight that many modifications of the input in cultural transmission are not errors of copying but transformations aimed at a cognitive or practical goal; they argue that learning in general, and cultural transmission in particular, involve both preservative and constructive mechanisms (Claidière, Scott-Phillips, et al., 2014; Sperber, 2000; Sperber & Claidière, 2006). Here we use “convergent transformations” (or just “transformations” for short when there is no ambiguity) to describe modifications in transmission that are not random.

delivery of a reward. If less than 3 correct squares were touched the trial was considered a failure and a green time out screen appeared for 3 s.

2.1.3. Training

All members of the colony underwent a training procedure to enable them to participate in the experiment: only those animals who reached our final criterion were admitted into the experiments. Training followed a progressive increase in the complexity of the task, starting with only one target (red square), followed by a stage with one target and one distractor (white square), then by an increase in targets up to four and finally by an increase in the number of distractors up to 12. Training blocks consisted of 50 trials and progress through training was conditioned on performing above criteria (80% success on a block of 50 random trials, excluding aborted trials (on average 1.7% (SD = 0.98%) of trials), which were re-presented).

2.1.4. Transmission procedure

For each transmission chain, a first baboon was selected according to a pre-defined order (different in each chain) and this subject received a first block of 50 transmission trials, consisting of randomly-generated patterns. Once the first subject had been tested, its behavioral output (the actual pattern of squares touched while attempting to reproduce the observed patterns) was used to generate the set of target patterns shown to the next individual in that chain. This procedure was repeated for the remaining individuals of the chain. Once an individual had completed the set of 50 transmission trials, it was allowed to continue with the task, but was now presented exclusively with random trials, which were generated automatically and were not part of the transmission process. For convenience, and in accordance with previous studies (e.g. Horner, Whiten, Flynn, & de Waal, 2006; Kirby et al., 2008), we will use the term generation (or "cultural generation") to describe the number of transmission steps in each chain.

To minimise any effects of transmission trials in chain n on transmission trials in chain n + 1, each monkey received a large number of random trials. Therefore, the total number of random trials performed during each experiment was extremely high (24,620 random trials on average for each monkey in Claidière, Smith, et al., 2014, SD = 14,923; 17,983 random trials for the present experiment, SD = 6833).

2.2. Methods specific to the experiments with selection

2.2.1. Participants

Fifteen baboons participated in Claidière, Smith, et al. (2014), 8 males (mean [range] age 5.3 [2.1; 8.1] years) and 7 females (5.5 [2.7; 8.9] years). Fourteen baboons took part in the present study, 5 males (7.2 [4.69, 10.70] years) and 9 females (6.5 [3.29, 10.54] years). Eleven baboons participated in both studies.

2.2.2. Selection procedure

In order to evaluate the effect of selection on cultural evolution, we implemented a procedure to produce a differential reproduction of the grids according to the geometric distance between the squares, a parameter we call *selection direction*. Initially, we used two selection directions. In one condition, we selected grids with the *minimum* inter-square distance (selection *aligned* with transformations). In another condition the grids with *maximum* inter-square distance were selected (selection *opposite* transformations). Finally, in our last studies we selected grids according to intermediary distances (neither the most compact, nor the most spread out).

A subset of the top-ranked grids (1, 5, 10 or 25 grids among the set of 50, a parameter we call *selection pressure*) were then selected and all equally reproduced without variation to make a new set of 50 grids. When grids with the same distance had to be selected between, we chose randomly. The order of the resulting set of 50 grids was then randomly shuffled to break any sequential order effects, and the set of grids was passed on as stimuli to the next individual in the chain.

Note that variation in the procedure only comes from the transformations that the baboons spontaneously apply to the grid. There is no added "noise" or randomness introduced by the selection process. This is essential because the aim of the study was to explore the interaction between realistically generated variation and artificially simulated selection. Also note that in our procedure, selection is not a consequence of the baboon's behaviour (such as a choice to copy certain grids compared to others) but the result of external factors (imposed by the experimenter). This is justified by the fact that we wanted to clearly contrast the effect of selection and transformation and also by the fact that in general there is no relationship between the ease with which something is learned and transmitted and its efficacy (in the technological domain for instance the most efficient techniques are often difficult to acquire).

2.3. Ethics statement

This research was carried out in accordance with French and EU standards and received approval from the French Ministère de l'Education Nationale et de la Recherche (approval # APAFIS-2717-2015111708173794-V3). Procedures were also consistent with the guidelines of the Association for the Study of Animal Behaviour.

2.4. Methods for the simulations

As a first approximation, transformations in transmission chains can be simulated by a Markov process in which the state of the chain at a certain generation is solely determined by the state of the chain at the preceding generation, and a transition matrix that represents the likelihood of all possible transformations (e.g. Kalish et al., 2007; Nowak, Komarova, & Niyogi, 2001). Consequently, to simulate transmission chains we used the data that were collected but not analysed during the experiment performed by Claidière, Smith, et al. (2014) to generate a transition matrix between grids. We exploited the 492,409 random trials, i.e. trials in which the grid presented to the baboons were randomly picked from the set of possible grids, performed by the 15 baboons during this experiment (on average each monkey completed about 24,620 random trials, SD = 14,923) to calculate, for every possible grid (N = 1820), the probability that this grid would be changed into any other possible grid (including itself). Importantly, given the size of the transition matrix it was not possible to calculate a transition matrix for each individual that took part in the experiment. Therefore, we had to pool together trials from the entire baboon group. This gave us an experimentally based transition matrix (1820 × 1820) representative of the behaviour of an average baboon. Note that this transition matrix assumes that successive trials performed by the baboons are completely independent (this is discussed further below).

Once this transition matrix had been calculated we simulated transmission chains using the following procedure. Starting from a set of 50 randomly selected grids as inputs, we used the transition matrix to generate likely output grids, we then selected those grids according to the procedure described above, randomly shuffled the order of the selected grids and presented them as input to the next generation. This procedure was repeated to simulate the same number of generations (n = 12) as in Claidière, Smith, et al. (2014). Finally, we performed Monte-Carlo simulations with 500 replications of this procedure in order to generate distribution of relevant coefficients.

3. Results

3.1. Study 1: effect of convergent transformations on cultural evolution

Before simulating the effect of selection on cultural evolution, it is essential to compare the results of the simulations without selection to the results of the experiments, in order to validate the fact that the simulations correctly approximate the behaviour of the baboons. With nearly half a million random trials (each grid was presented as an input on average 270 times, SD = 17 times), the computation of the transition matrix from these trials gave rise to a matrix containing 96.2% of empty cells. This high proportion of transitions with null probabilities can have two different origins. Firstly, it may be due to the fact that just under half a million random trials was too few to provide an accurate estimate of the full matrix of transitions (the matrix contains more than 3 million transition probabilities). Secondly, the large number of null transitions could be a consequence of the high success rate of the baboons in the task, greatly limiting the number of realised transitions compared to possible ones. Thus, if the number of random trials is too low to provide an accurate estimate of the matrix, then we expect the simulations to differ substantially from the experimental results. Alternatively, if the sparseness of the matrix accurately reflects the baboons' behaviour, the simulations should produce results substantially similar to the experiments.

Accordingly, we first compared the results of Monte Carlo simulations without selections to the experimental results obtained by Claidière et al. (Fig. 1). We find that the evolution of the score (proportion of accurately-reproduced grids, i.e. where 3 or more squares from the presented pattern were also present in the reproduced pattern) and the evolution of the proportion of tetromino (a grid with four connected squares, a good indicator of the emergence of structure in Claidière, Smith, et al. (2014)) with generations in the simulations match the experimental results (Fig. 1A and B). The decrease in Shannon entropy, indicative of the grid set diversity, is also similar but remains higher in the simulations (Fig. 1C) – this likely indicates set effects driven by inter-grid interference in the experimental data (i.e. grids transmitted together in a set are non-independent and therefore resemble each other more than expected under an assumption of independence), a point which we return to below in Study 3. Finally, the grids produced from the simulations (Fig. 1D) and the experiment (Fig. 1E) are very similar. The proportion of the different tetromino types was also highly similar in the experimental results (Fig. 2, "Experimental" bar) and in the simulation (Fig. 2, "No selection" bar).

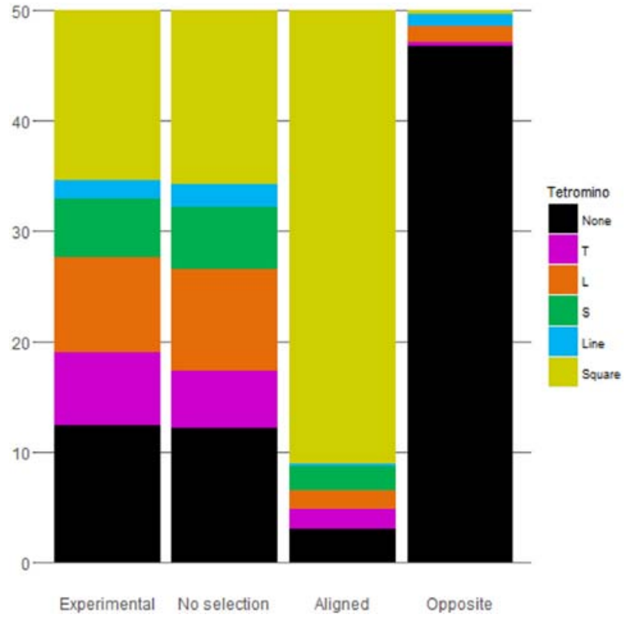

Fig. 2. Average number of tetromino and non-tetromino in the set of 50 grids at the 12th generation in four different conditions: 1) results from Claidière, Smith, et al. (2014). 2) Simulations without selection. 3) Simulations with aligned selection (selection pressure = 10 grids). 4) Simulations with opposite selection (selection pressure = 10 grids).

We conclude that the estimated transition matrix, despite its sparseness, correctly approximate the behaviour of the baboons, or at least enough to allow us to meaningfully explore the effect of selection with simulations.

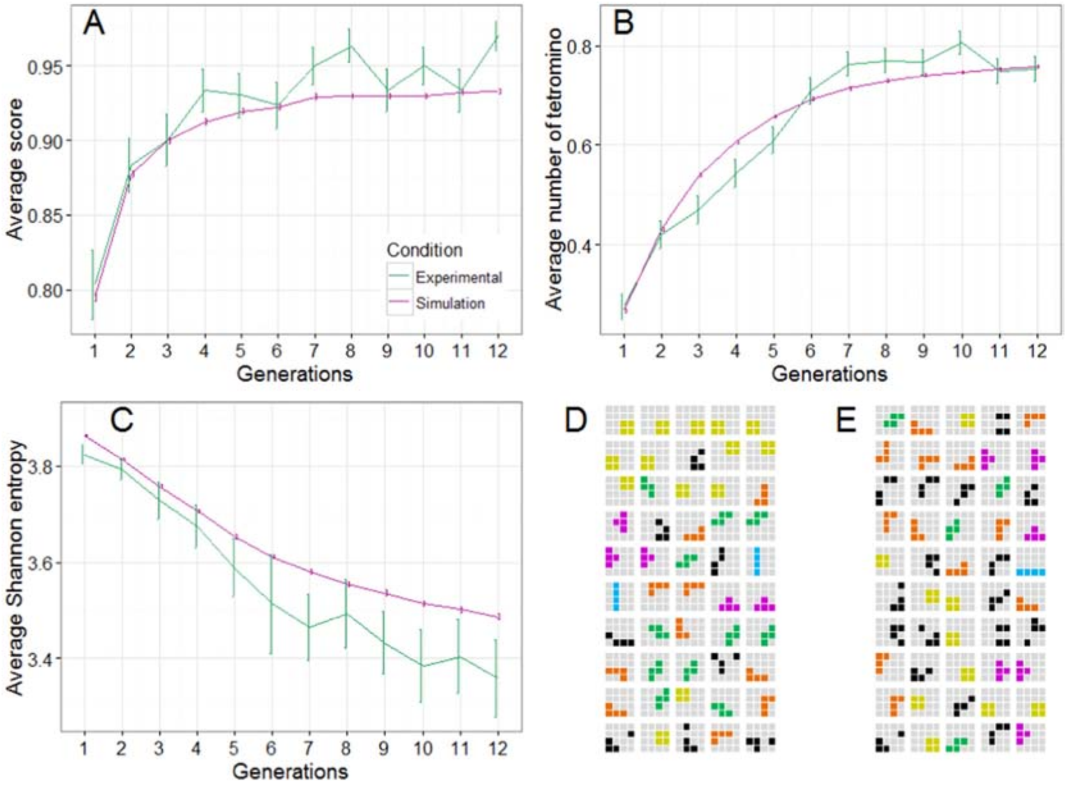

Fig. 1. Similarity between the simulations and the results of Claidière, Smith, et al. (2014). Evolution of the score (A), number of tetromino (B) and Shannon entropy (C) in the simulations and in Claidière, Smith, et al. (2014). Example of grid sets at the 12th generation for the simulations (D) and experiment (E). Error bars indicate standard error of the mean.

3.2. Study 2: effects of selection on cultural evolution

As shown in Fig. 2, transmission without selection (Experimental and No selection bar) favours the emergence of tetromino. Their compact shapes may facilitate detection memorization, and reproduction, explaining why baboons tend to transform other shapes into tetromino (Claidière, Smith, et al., 2014). Our second simulation (simulation 2) aimed at studying the effect of selection in two opposed situations, one in which selection was aligned with convergent transformations (Aligned condition) and one in which it was opposite to transformations (Opposite condition). In the *aligned* condition, we selected grids with the minimal distance between squares (maximally compact grids), whereas in the *opposite* condition, we selected grids with a maximal distance between squares (minimally compact grids, which cannot be tetromino). In both conditions, we performed simulations with different selection pressures (1, 5, 10, 25 grids selected in the set of 50) and analysed the results as previously.

The results (Figs. 2 & 3) show that when selection is aligned with convergent transformations, the effect of transformations is amplified, the increase in score is larger and faster, the proportion of tetromino grids is greater and the overall entropy of the set of grids decreases sharply, resulting in a homogeneous set of grids (Fig. 4). When the selection is opposite to the transformations, we find a strong decrease in score with an increase in selection pressure and, as expected, a large decrease in the number of tetromino. Interestingly however, the decrease in Shannon entropy suggests that the set of grids becomes more homogeneous through time, although less so than when the selection is aligned. The inspection of the sets of grids (Fig. 4) suggests that selection favours one particular type of grid in both conditions, tetromino in the aligned condition, domino (two connected squares) on opposite sides in the opposite condition.

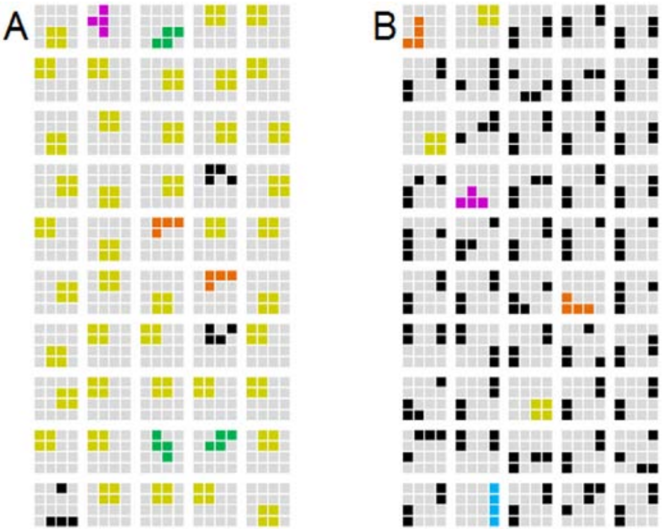

Fig. 4. Example of grid sets at the 12th generation when the selection is aligned with the transformations (A) and when it is opposite to it (B). Selection pressure is set at 10 grids.

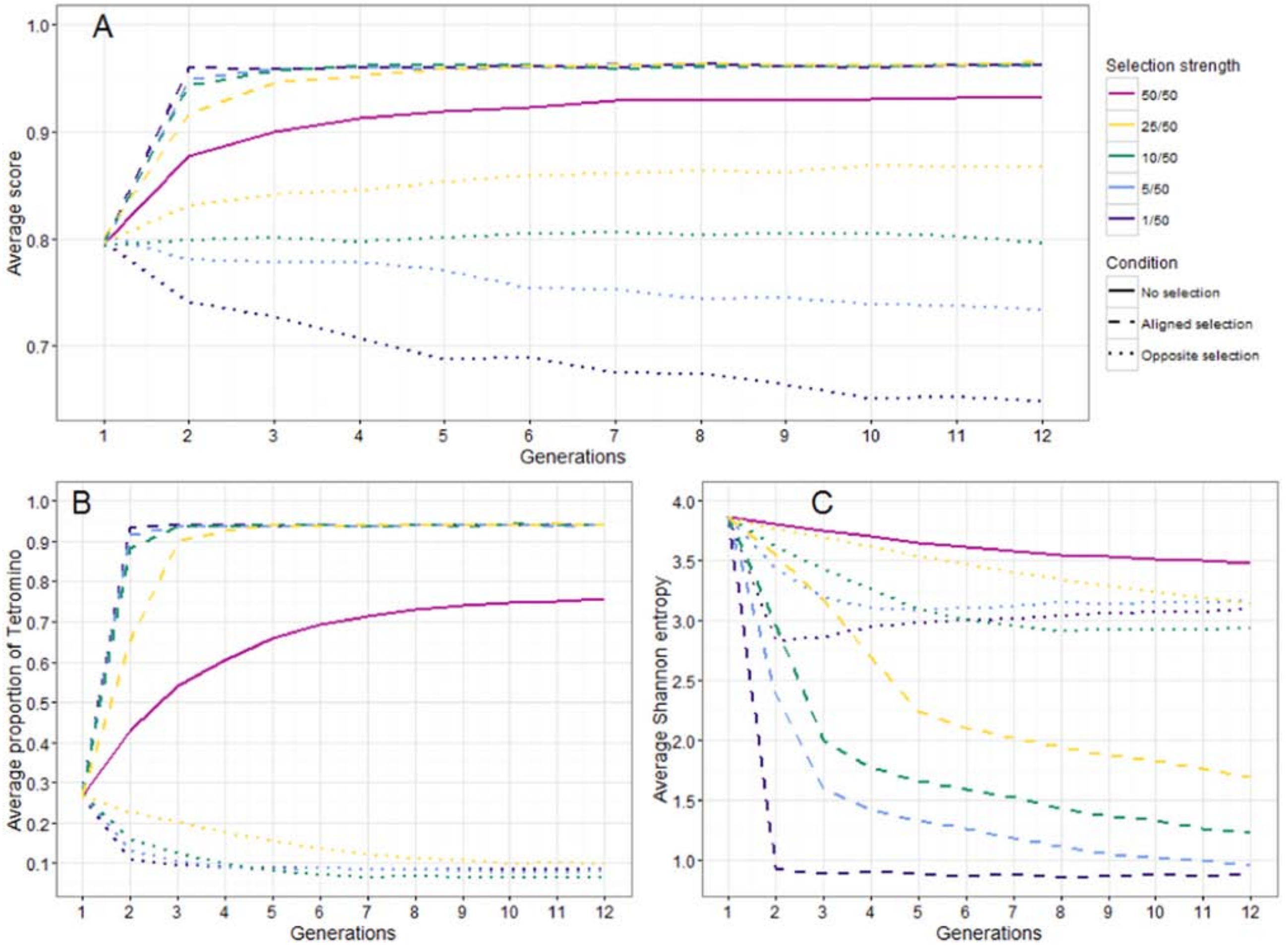

Fig. 3. Effect of selection on cultural evolution. Evolution of the score (A), number of tetrominos (B) and Shannon entropy (C) in the absence of selection (solid line), with aligned selection (dashed lines) and with opposite selection (dotted lines). The colours represent variations in selection pressure, from 50 grids selected in the set of 50 (i.e. no selection) to 1 grid selected in the set (i.e. maximal selection).

This is further confirmed by examining the number of clusters within a grid (the number of groups of squares, a grid with a tetromino contains for instance only one cluster) present in the different conditions. Fig. 5 shows that selection acts to shift the distribution obtained without selection: selection makes the compact forms more frequent when it is aligned with transformations and the less compact ones more frequent when it is opposite to transformations.

In summary, introducing selection within the experimental transmission chains shows that both selection and transformation contribute to explaining the evolutionary trajectory and outcome. Roughly speaking, selection acts to shift the distribution of the outcome in one direction or another but is constrained by the variation provided by convergent transformations (this is further discussed in the Discussion).

3.3. Study 3: balance between convergent transformation and selection in cultural evolution

The preceding simulations assumed that successive trials were completely independent (i.e. the likelihood of a grid changing into another grid does not depend on any other grid). However, during Claidière, Smith, et al. (2014) the grids were transmitted as a set of trials from one baboon to the next, and the results suggested that the likelihood of a grid transforming into another depended on other grids in the set, what we will call here *set effects*. Set effects come from the fact that the response of a baboon on a trial is influenced by preceding trials (previous experiments have shown such effects in other contexts; e.g. Huguet, Barbet, Belletier, Monteil, & Fagot, 2014). This inter-trial dependence is likely limited in the random condition because the trials are randomly generated, thereby preventing the reinforcement of expectations or biases across trials. However, during transmission chains the transmission of a set from one generation to the next creates an opportunity for the dependence between trials to build up with trials and with generations. In theory, set effects could change the conclusions of the preceding sections because they can affect the outcome of selection and attraction and their interaction.

To illustrate, imagine that all the baboons are biased towards producing a certain response (e.g. square). When the trials are random a small bias will produce a few more squares than expected by chance. During transmission trials the same bias will produce a few squares during the first generation, a few more during the second, still more on the third, and so on and so forth, leading to the progressive accumulation of squares in the set. Set effects exist when this accumulation reinforces the bias in favour of frequent grids, creating a positive feedback loop increasing the strength of the accumulation. In such a case, the likelihood of a grid changing into another (e.g. square) depends on other grids in the set (how many squares there are). Set effects will typically result in greater homogeneity of the set of grids than expected without such effects, and they will also create divergence between lineages (lineage specificity see Claidière, Smith, et al., 2014). Consequently, if set effects are important during transmission chains, we should expect more homogeneous sets in the experiments compared to sets from the simulations (since they do not include set effects). This seems validated by Fig. 1C in which the entropy of the sets produced during Claidière, Smith, et al. (2014) experiment is consistently lower than the entropy of the simulations of that experiment (Study 1).

Crucially, set effects should also affect the outcome of experimental transmission chains with selection, because selection tends to increase the frequency of selected grids. If the baboons are sensitive to the frequency of the grids in the set, as proposed by Claidière, Smith, et al. (2014), they should produce more tetromino when they are frequent (selection for minimal distance), and fewer tetromino when they are less frequent (selection for maximal distance). However, when

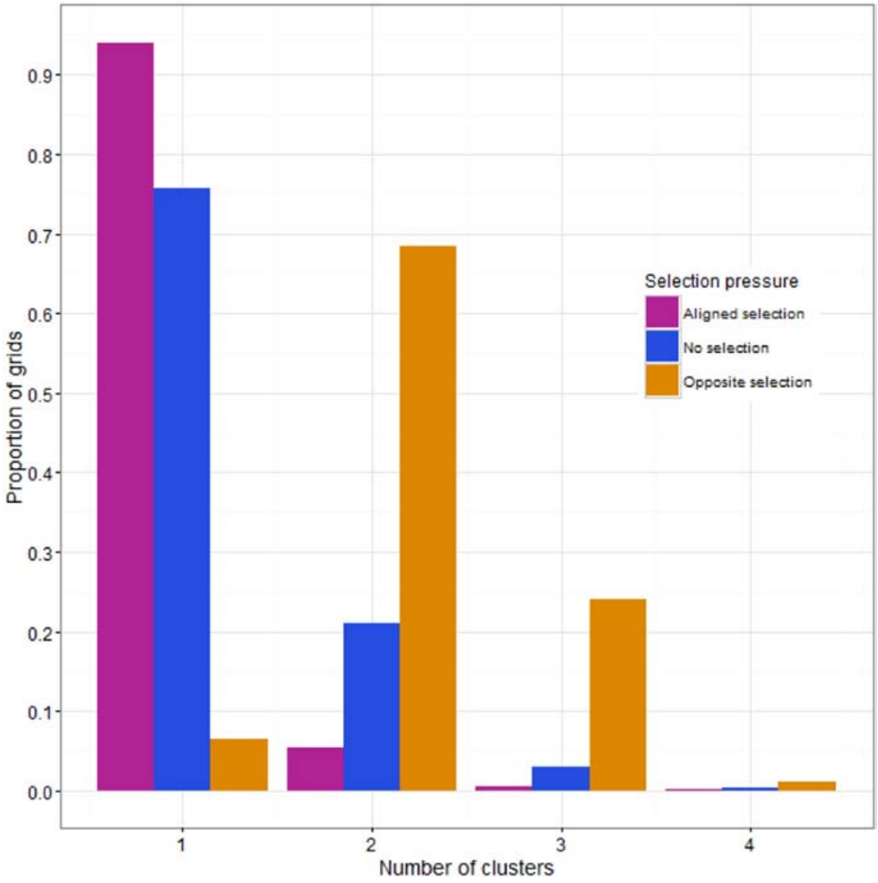

Fig. 5. Number of clusters at generation 12 in three conditions: no selection, aligned selection and opposite selection. Selection pressure is set at 10 grids.

selection is extreme, the effect might disappear due to ceiling and floor effects. In order to study the effect of selection on set effects, we paid particular attention to cases in which the selection process retains grids with intermediary distances among squares. To test the importance of set effects we used the same procedure as before, but since the results do not qualitatively differ for different selection pressure, we only discuss below the case in which selection pressure is set at 10 grids. We simulated each of the 41 possible selection directions between selection for the minimal distance (the first 10 most compact grids) and selection for the maximal distance (the 10 least compact grids). For convenience we will refer to these directions by the numbers 1 to 41 (1 referring to the minimal distance: selection of the grids 1 to 10 when ranked according to the distance from minimal to maximal; 41 referring to selection for the grids with maximal distance, from 41 to 50). The results of the simulations show that there is a smooth transition between selection for minimal distance and selection for maximal distance (see Fig. 6). As expected, the proportion of tetromino gradually decreased when the selection was directed towards less compact grids.

As explained above, we expected this transition to be more abrupt in an experiment with baboons, due to set effects favouring systematically-structured sets of grids. We therefore ran a new experiment to test this hypothesis. This experiment was in its general principles similar to Claidière, Smith, et al. (2014) except that the transmission procedure followed exactly the same procedure as the above simulations. The baboons (except for the first individual in the chain) were therefore exposed to a set of grids that had been produced by another baboon and then selected according to a certain selection pressure (this was fixed at 10 grids), and a certain selection direction. Six different chains were run, one with each of the following selection directions: 1, 12, 23, 28, 32 and 41.

As expected, we found that the transition from grids that are largely composed of tetromino vs. composed of non-tetromino was more abrupt in the experiment than in the simulations (Fig. 7). The point of equality (PE), corresponding to 50% of tetromino, was obtained with a selection of 23 in the case of the simulations, and with a selection of 29 for the experimental data. Moreover, at the PE an increase in position of one unit decreases the proportion of tetromino by 7% for the simulations and 33% for the experimental data (see Fig. 7). This step-like transition from sets where tetromino are common to sets where they are rare confirms the presence of set effects.

Furthermore, set effects can either be specific to certain grids, if the probability of a tetromino increases the probability of other tetromino but not of other grids (e.g. near-tetromino, for instance), or they can be general, if any frequent grid increases the probability of similar grids. If set effects were the same across all grids, irrespective of the presence or absence of tetromino, then only the slope of the curve should increase and the two curves should cross at PE. This is not what we found. Fig. 7 shows that the change in slope is largely a consequence of the fact that the baboons maintain a higher proportion of tetromino than expected from the simulations. This can be interpreted as stronger set effects for tetromino than other grids.

To further explore set effects, we examined the evolution of the proportion of tetromino in the set with the number of generations. Fig. 8 shows that when the direction of selection is 23 (panels A and B) and 28 (panels C and D), the simulations predict a majority of non-tetromino grids while in the experiment there is a large increase in the number of tetromino (note that these tetromino are mostly Ls and not squares as before, therefore showing the effect of selection). Set effects therefore drastically affect the outcome of the evolutionary process when the selection is neither perfectly aligned with convergent transformations, nor completely opposite to them. Furthermore, set effects are not independent of the grids in the set, they selectively reinforce the effect of transformations (i.e. they are stronger for tetromino).

4. Discussion

Understanding the interaction between the convergent transformations that occur during social transmission and cultural selection is fundamental to understanding the relationship between biological and cultural evolution and ultimately the origin of human culture. In biology, adaptations are largely the result of undirected mutations coupled with highly faithful transmission mechanisms (whose fidelity itself comes from the process of natural selection, Sturtevant, 1937). In contrast, there is no single or dominant transmission mode in culture (Claidière & André, 2012) but a variety of psychological mechanisms which have evolved to deal with short-term to lifelong challenges, not necessarily to transmit culture faithfully across generations (Claidière & Sperber, 2010b; Sperber, 1996). Learning typically involves transformations of the input; many of these transformations are not random but directional; many of these directional transformations converge across members of the same social group who live in the same environment and share background information. These facts have been repeatedly demonstrated in cultural evolution experiments (e.g. Claidière, Smith, et al., 2014; Kalish et al., 2007; Kirby et al., 2008). They are well captured by models which treat learning as an inductive process guided both by the evidence learners receive and by their priors regarding the

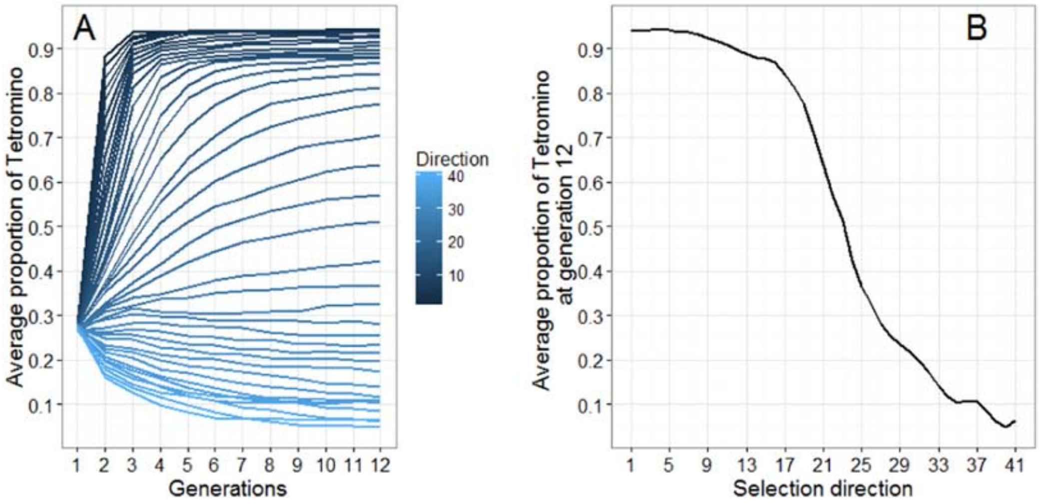

Fig. 6. Simulation results showing the effect of the direction of selection on the emergence of tetromino. A: Evolution of the proportion of tetromino with generations when the direction of selection changes from 1 to 41. B: Average proportion of tetromino at generation 12 for different selection directions. The results represent the average of 500 simulations in every condition.

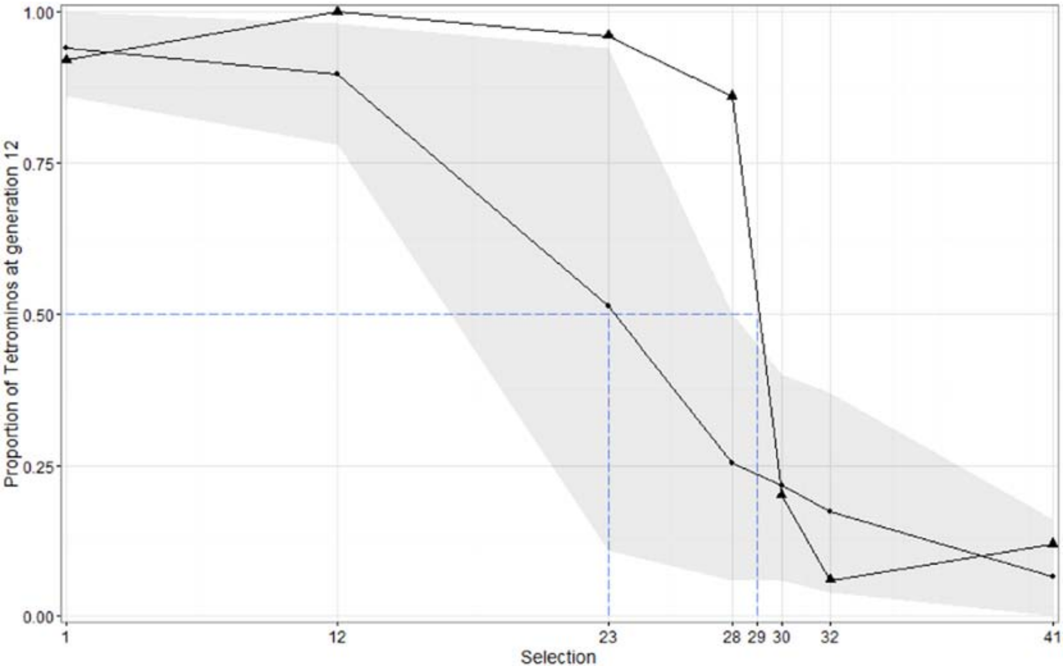

Fig. 7. Observed and simulated proportion of tetromino at generation 12. Dots represent the average proportion of tetromino obtained through simulations (the grey area represents the 95% confidence interval of the proportion) and triangles the results obtained during the experiment. The dotted blue lines show the selection values at PE.

knowledge or know-how to be acquired (e.g. Griffiths & Kalish, 2005; Kirby, Dowman, & Griffiths, 2007; Kirby, Tamariz, Cornish, & Smith, 2015). In such models, the inductive biases of learners determine the likely transformations that they make during learning, and are therefore one important source of convergent transformations that play a central role in shaping the products of cultural evolution. The inductive biases of learners may not be aligned with the variants favoured by selection, because cognitive mechanisms have evolved to help individuals maximise the benefit they can get from social information they process rather than maximise faithfulness and accuracy per se (Claidière & André, 2012; Claidière & Sperber, 2010b; Sperber, 1996).

This, it has been argued, has two different consequences: (i) we should expect changes to be much more frequent in the case of cultural transmission than in biological transmission (i.e. a higher "mutation rate" in biological terms with the qualification that what is involved in the cultural case is not properly described as a process of "mutation"; Claidière & Sperber, 2010a; Eerkens, 2000) and (ii) many if not most changes in cultural transmission, rather than being random failures of replication, should be adjustments to short-term goals (i.e. equivalent to "directed mutations" in biology or "guided variation"; Kronfeldner, 2007). Both effects will decrease the impact of selection on cultural evolution. Similar results have been demonstrated previously in simulation. For instance, Smith (2004) shows that the properties and functionality of culturally-transmitted signalling systems are largely determined by the biases of learners even when cultural selection is in play. Griffiths, Kalish, and Lewandowsky (2008) show for a very general model of cultural transmission (Bayesian iterated learning) that there are broad classes of cases in which selection cannot overcome the inductive biases shaping the transformations that occur during cultural transmission. Not all researchers agree however. Mesoudi et al. (2004) for instance argue that "Although this [cultural] variation may not be entirely random with respect to selection, ultimately it matters less to the Darwinian process how variation arises, than that variation exists and is exposed to selection" (see also Henrich, et al., 2008 for the same argument).

To progress on these questions more empirical research is needed, both in the laboratory and in the field, and recent studies have shown for instance the importance of transmission mechanisms (Morgan et al., 2015), group size (Derex, Beugin, Godelle, & Raymond, 2013) and psychological mechanisms (stereotypes, Martin et al., 2014; disgust, Miton, Claidière, & Mercier, 2015; facial recognition, Morin, 2013) in explaining cultural evolution. Our research adds to this literature by providing an empirically grounded study of the relationship between selection and convergent transformations. In this context, our first important result (Study 1) is that the transition matrix established from the baboon's behaviour has both extremely low fidelity of reproduction (the average of the coefficients on the diagonal of the transition matrix is only 20.4% [min = 0.7%; max = 88.8%], showing that on average the probability of a perfect reproduction of a grid is very low) and is strongly biased (96.2% of the probabilities in the transition matrix are null; note that if the transformation were random there would be far fewer null transition probability because all the errors would be equally likely). Under these circumstances, our results show that convergent transformations are essential in explaining the outcome of the evolutionary process (Study 2). To illustrate, imagine that we compare results in four conditions: (1) transmission with random mutation in the absence of selection (while still maintaining the same fidelity), (2) random mutation with selection, (3) convergent transformations in the absence of selection, and finally (4) convergent transformations and selection. Fig. 9 shows the result of this comparison in terms of proportion of grids with different number of clusters, when the strength of selection is 10 (as before) and the grids are selected for maximal distance (where we expect the contrast between the different conditions to be maximal). With the level of fidelity found in our experiments, selection has very little effect when variation is randomly generated, despite the huge selection pressures used in our simulations (in this example 40 grids in the set of 50 are eliminated every generation). This is because very few grids are selected every generation, but many will "mutate" into other grids, preventing the accumulation of structure, a problem known as the error threshold in biology (Eigen, 1971; Eigen & Schuster, 1979; Nowak & Schuster, 1989; Williams, 1966). On the contrary, when the variation results from convergent transformations, selection can have a stronger effect on the outcome (in Fig. 9 the effect of selection is maximal because selection goes against transformations).

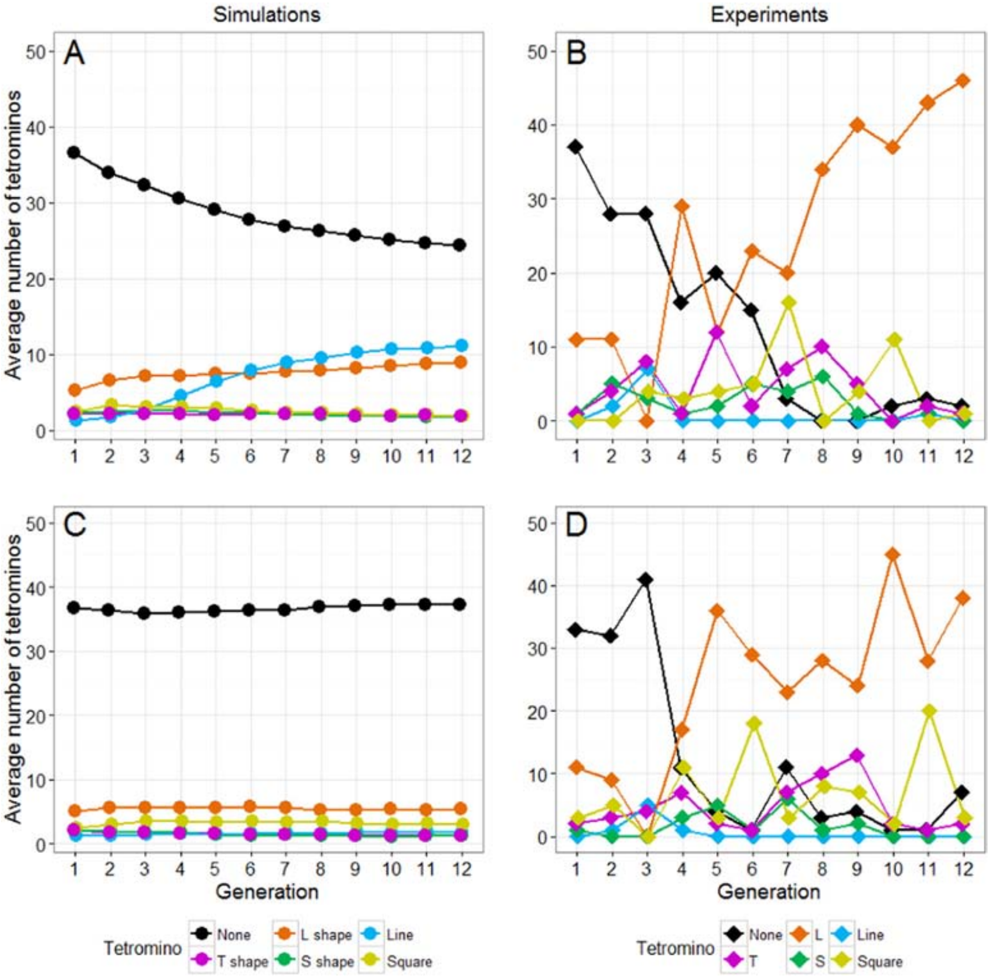

Fig. 8. Evolution of the number of the different tetromino with the number of generations when the direction of selection is 23 (A, B) and 28 (C, D). Dots represent the average proportion of tetromino obtained through simulations and lozenges the results obtained during the experiment. Colour codes as in Fig. 2.

The reason for this is simply that the few selected grids will be transformed into other grids that stay within the vicinity of the selected ones, allowing structure to accumulate.

Importantly, our results are in agreement with previous theoretical studies and complement earlier findings. Henrich and Boyd (2002) have developed a model of the interactions between transformation and selection. In this relatively simple model a continuous cultural trait (between 0 and 1) is transformed every time it is transmitted: transformations converge towards 0 when the value of the trait is under a certain threshold (m) and converge towards 1 otherwise. The authors further assume that selection is represented by a positive correlation between the trait value and the probability that an individual is selected as a model by the next generation (the entire population is replaced every generation). The authors concluded from their study that selection is the main driving force of cultural evolution when convergent transformations are sufficiently strong (i.e. lead to a few replicators). Claidière and Sperber (2007) further showed that this conclusion is not general but depends on particular features of Henrich and Boyd's model (such as the fact that selection peaks at an attractor; see also Acerbi & Mesoudi, 2015). Furthermore, Griffiths et al. (2008) also showed that under a broad range of conditions, selection cannot overcome the impact of convergent transformation.

In principle then, both convergent transformations and selection can be important factors influencing the evolutionary dynamic. Our present results agree with this general conclusion: the distribution of grids at equilibrium depends both on transformations and the strength and direction of selection (Fig. 9: difference between convergent transformation only and convergent transformation with selection). However, our results go even further by showing that under realistically low level of fidelity and hence high level of change during transmission, selection has, in fact, little effect unless transformations, rather than being random, are convergent. To illustrate this point we use Henrich and Boyd's model and show that in their original model, when convergent transformation is present, such transformation is the main contributing factor to the final evolutionary outcome (Fig. 10A & B; details of the model are presented in the electronic supplementary material). In the absence of convergent transformations, i.e. when the value of the trait changes randomly in any direction every generation, selection has almost no effect (Fig. 10C; see also Fig. 9 for a similar conclusion with experimental data: almost no difference between random mutation and random mutation with selection). This result can first seem paradoxical; transformations should decrease the effect of selection when both are not perfectly aligned, not enhance it. However, selection can only have a significant effect when the mutation rate is below a threshold (known as the error threshold see Eigen, 1971; Eigen & Schuster, 1979; Nowak & Schuster, 1989; Williams, 1966). Transformation therefore potentiates the effect of selection by bringing cultural items towards attractors, i.e. towards regions of the cultural trait space in which the mutation rate is sufficiently low for selection to operate efficiently. In other words, in these cases, it is convergence towards attractors, and not fidelity, that creates sufficient cultural stability for selection to operate.

Accordingly, it would be highly misleading to evaluate the role of selection from cultural items that have evolved because that would lead to

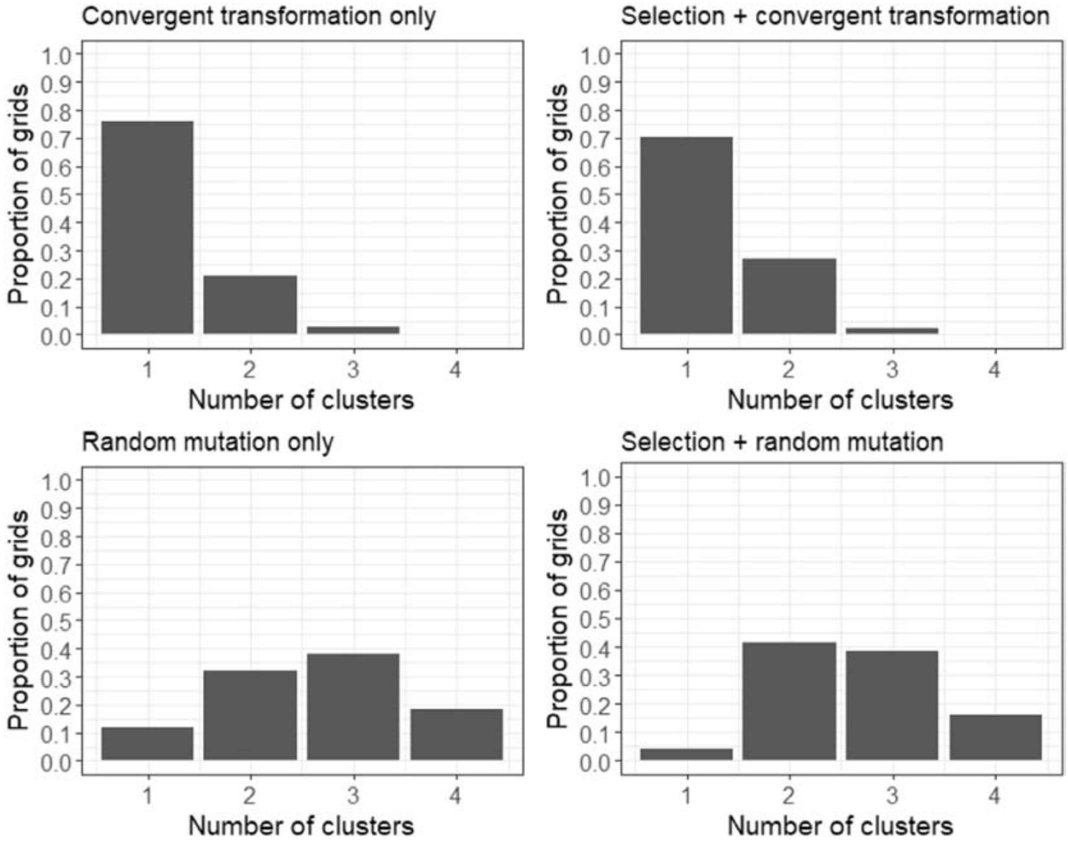

Fig. 9. Proportion of grids with different number of clusters inferred from simulations with convergent transformations or random mutations, and with or without selection. The selection pressure is set at 10 grids and the grids are selected for maximal distance.

a misinterpretation of the role of transformations. A good illustration of this is found in language evolution for instance. If we look at the world's languages today and in the past, some have survived, others have disappeared (which might reflect selection). Languages are quite faithfully transmitted from one speaker to another (inheritance) and they compete with each other (competition). On this basis, one might be tempted to conclude that languages gradually evolved from a simple form to become more complex and more expressive through a process similar to natural selection. However, we know that that's not the case. Studies of the evolution of creoles and sign languages show that groups of individuals can create a new language from scratch because individuals transform the language in just a few generations towards forms that are simpler, yet more expressive (Mufwene, 2008; Senghas, Kita, & Özyürek, 2004). This process, we think, is quite general. In more technological problem-solving experiments for instance, participants do not start to assemble random spaghetti towers or to randomly strike stones together to produce flints - they have insight, knowledge and experience that considerably constrains their behaviour. In our view, these constraints are essential in producing a limited number of forms that can then be selected: in other words, convergent transformations potentiate selection.

One limitation of our simulations of cultural evolution among baboons is that they underestimate the effect of transformations because they assume that the grids in a set evolve independently of each other. In Claidière, Smith, et al. (2014) and in Study 3 here, baboons are sensitive to the composition of the set and they tend to increase the proportion of the grids that are most frequent in the set. Study 3 shows however that set effects are stronger in the presence of tetromino than other grids, and therefore selectively reinforce the effect of transformations. Since selection increases the homogeneity of the set of grids, it also increases set effects and consequently amplifies the effect of transformations even further. Set effects therefore create an important difference between the simulations and the experimental results (Figs. 7 & 8).

Another limitation of the present study comes from the artificiality of the experimental method used. The computerized task proposed to the baboons bears little similarity with cultural evolution "in the wild." It is not intended to model any aspect of actual cultural transmission among baboons but rather to capture some essential aspects of cultural transmission in general. Our experiments and simulations allow us to investigate in great detail, in this admittedly artificial context, the two features that have been at the centre of discussions regarding the relative role of convergent transformations and selection in cultural evolution: low fidelity and biased transformations. While it is quite likely that both the strength and the effects of transformations and selection will vary substantially between cultural domains, between species, and so on, we believe that our experiments and simulations capture some essential aspects of cultural evolution.

By providing a realistic assessment of the transformations that occur during cultural transmission in a complex experimental paradigm, this study can serve to inform further theoretical work and simulations of cultural evolution. At the very least, our results clearly show that measuring the amplitude and directionality of transformations during cultural transmission is absolutely essential to understanding the effect of selection on cultural evolution. Selection can change the outcome of the evolutionary process substantially in some cases, but can only act on the variations provided by typically biased transformations.

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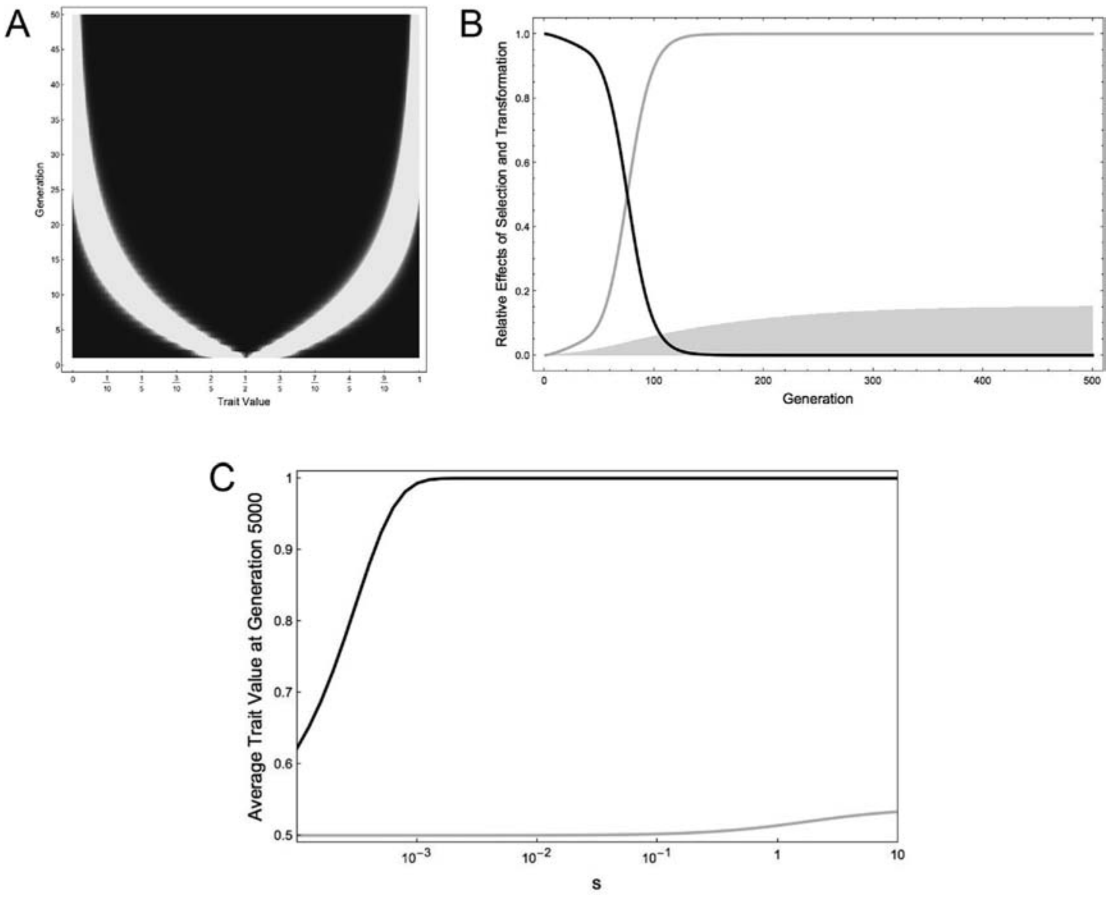

Fig. 10. Interaction between selection and convergent transformations in Henrich and Boyd's model: (A) Composition of the population of cultural items through time shown by a density plot where the frequency of each item type is proportional to light intensity. The population initially contains only individuals with intermediate trait value (0.5). Transformation towards the two attractors, 0 and 1, first causes a rapid branching into two types (low/high trait value). Selection then leads to the fixation of the high-value type only (not shown in panel A). (B) Relative contribution of selection (in gray) and transformation towards an attractor (in black) to cultural change. We show both the relative effect of each force at a given generation (lines), and the relative effect of selection cumulated since the first generation (gray surface). Because convergence to the attractor is faster than selection: (i) attraction plays a major role in the early generations, (ii) the cumulated contribution of attraction to cultural change is larger that the cumulated contribution of selection (gray surface is relatively small), but (iii) the instantaneous effect of attraction rapidly decreases. Once cultural items have converged toward attractors, then selection is the only force contributing to cultural change. (C) Distribution of trait values after 5000 generations of evolution as a function of the strength of selection, with or without convergent transformation (black or gray, respectively). In all three panels, the mutation rate is $\mu = 10^{-1}$, and the strength of selection is $s = 10^{-2}$.

Data availability

The data associated with this research is available at the Open Science Framework repository (DOI 10.17605/OSF.IO/H84Y6).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2017.12.007.

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