High-fidelity copying is not necessarily the key to cumulative cultural evolution

High-fidelity copying is not the key to cumulative cultural evolution: a study in monkeys and children

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Abstract

The unique cumulative nature of human culture has often been explained by high-fidelity copying mechanisms found only in human social learning. However, transmission chain experiments in human and non-human primates suggest that cumulative cultural evolution (CCE) might not necessarily depend on high-fidelity copying after all. In this study we test whether CCE is possible even with a non-copying task. We performed transmission chain experiments in Guinea baboons and human children where individuals observed and produced visual patterns composed of four squares on touch screen devices. In order to be rewarded, participants had to avoid touching squares that were touched by a previous participant. In other words, they were rewarded for innovation rather than copying. Results

nevertheless exhibited three fundamental properties of CCE: an increase over generations in task performance, the emergence of systematic structure and the presence of lineage specificity. However, CCE arose from different mechanisms across species: children, unlike baboons, converged in behaviour over generations by copying specific patterns but in a different location, thus introducing alternative copying mechanisms into the non-copying task. We conclude that CCE can result from mechanisms with varying degrees of fidelity in transmission and thus that high-fidelity copying is not the key to the build-up of CCE.

Keywords: social learning; iterated learning; transmission chain; cumulative cultural evolution; primate behaviour; comparative cognition;

1. Introduction

Almost every aspect of human culture evolves through time with the gradual accumulation of modifications, from stories [1], to paintings [2], to social norms [3] and language [4]. In sharp contrast, it has proved extremely difficult to find evidence of cumulative culture in other animals [but see 5, 6, 7 for potential examples, 8, 9] or to induce cumulative culture in other species through experimental manipulations [10, 11 for potential examples, but see 12]. One of the main reasons invoked to explain this sharp contrast between human and non-human animal cultures is the low copying fidelity in non-human animals' social learning [13-19]; faithful transmission can prevent the loss of cultural modifications and therefore result in cultural accumulation [14], and the ability to faithfully transmit information through high-fidelity social learning has therefore been taken as a requirement for cumulative cultural evolution (CCE).

However, there are theoretical and empirical arguments suggesting that this view might be mistaken. Firstly, the notion of fidelity in cultural transmission is highly problematic [20]; it is

unclear whether there is a critical level of fidelity required to the build-up of CCE and whether that required level of fidelity can ever be achieved [20]. Secondly, when fidelity can be measured, it is generally low and unlikely to sustain long lasting cultural traditions [21, although not always, e.g. 22]. These results suggest that, even in humans, social learning is not of sufficiently high fidelity to prevent the loss of cultural modifications; nonetheless, cumulative culture is possible.

Furthermore, transmission chain studies in humans have shown that CCE can occur with social learning mechanisms that exist in non-human animals, suggesting that cumulative culture is not dependent on special cognitive capacities unique to humans [23-25]. [25], for instance, performed a transmission chain study in which baboons observed and reproduced visual patterns on touch screen computers. The baboons were organised into chains of transmission, where each baboon was provided with the patterns produced by the previous individual in their chain; as in some human transmission chain experiments [26 for instance], the baboons had no visual access to the behaviour of other individuals, simply the products of those behaviours. With this procedure, transmission led to the emergence of cumulative culture, as indicated by three fundamental aspects of human cultural evolution: (i) a progressive increase in performance, (ii) the emergence of systematic structure and (iii) the presence of lineage specificity [25]. Surprisingly, these results were achieved with an extremely low fidelity of pattern reproduction during the first generation of transmission (only 37% of the patterns were reproduced without errors). This initially low level of fidelity did not prevent the accumulation of modifications, and we observed a sharp increase in fidelity as patterns were passed on from generation to generation (reaching 72% in the 12th generation). Similar results have been found in transmission experiments with human participants, for example where the transmission of miniature languages results in the

emergence of languages which can be easily learned, even if the initial languages in each chain of transmission are transmitted only with very low fidelity [e.g. 27, 28]. Together, these results suggest that high-fidelity transmission may not always be the cause of cumulative culture and may in fact itself be a product of CCE. Individuals may transform input variants in accordance to their prior biases, and if those biases are shared at the population level, we expect transformations in the same direction to accumulate at each transmission step. This could thus lead to the evolution of variants which are more faithfully transmitted because they match the prior biases more and more closely over generations giving a misleading impression of high-fidelity transmission.

The vast majority of experiments on social learning and cultural transmission in humans and non-human animals focus on copying tasks in which the individual is rewarded for doing the same thing as another individual [see 29, 30 for reviews, 31]. In our opinion, this almost exclusive interest in copying has prevented a more neutral exploration of the mechanisms through which humans, and probably other animals, use and transmit the information gained from other individuals and whether these other forms of social learning and transmission may result in cumulative culture [see also 32].

Encouraged by the results of [25] showing that CCE can also result from initially low transmission fidelity, we decided to test whether CCE could occur in a transmission task that did not involve copying. We performed an experiment with baboons and children using the same protocol as [25] but with an "anti-copying" task in which the individuals were trained to avoid directly reproducing the patterns produced by a previous individual.

2. Methods

2.1 Methods for baboons

2.1.1 Participants and testing facility

Twelve Guinea baboons (*Papio papio*) belonging to a large social group of 25 from the CNRS Primate Centre in Rousset-sur-Arc (France) participated in this study. They were 6 males (median age 8 years, min = 5, max = 11) and 6 females (median age 8 years, min = 5, max = 12), all born within the primate centre.

The study was conducted in a facility developed by J.F. [for further information see 33, 34-36]. The key feature of this facility is that baboons have free access to computerized testing booths that are installed in trailers next to their outdoor enclosure (700m^2). Identification of the subjects within each test booth is made possible thanks to two biocompatible 1.2 by 0.2 cm RFID microchips injected into each baboon forearm. The test program allows an independent test regimen for each baboon, irrespective of the test booth it is using, and grains of dry wheat are used as reward. Baboons were neither water- nor food-deprived during the research.

2.1.2 Computer-based tasks

Each trial began with the display of a grid made of 16 squares, 12 white and 4 green (see ESM video 1). Touching this stimulus triggered the immediate abortion of the trial and the display of a green screen for 3 s (time-out). After 400 ms all the green squares became white and, in order to obtain a food reward, the monkey had to select and touch four squares in this matrix which had not previously been highlighted in green. Touching these four squares could be done 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. A trial was completed when 4 different squares had been touched. If four correct squares

were touched, the trial was considered a success and the computer triggered the delivery of 3-4 wheat grains; otherwise, the trial was considered a failure and a green time-out screen appeared for 3 s.

The stimuli consisted of 80x80 pixel squares (white or green) equally spaced on a 600x600 pixel grid and were displayed on a black background on a 1024x768 pixels screen. The inter-trial interval was at least 3 s but could be much longer since the baboons chose when to initiate a trial.

2.1.3 Training to criterion

Training followed a progressive increase in the complexity of the task, starting with one white square and one green square, followed by a stage with an increasing number of white squares (up to 6), then by a progressively increasing number of white and green squares up to 12. Training blocks consisted of 50 non-aborted trials (aborted trials were immediately re-presented, and the abortion rate was very low: Mean = 2.2%, Min = 0.23% and Max = 4.6%). Progress through training was conditioned on performing above criteria (80% success on a block of 50 random trials, excluding aborted trials).

2.1.4 Between-individuals transmission procedure

We followed the transmission procedure described in [25] and therefore only report the main elements here. Testing began when all 12 monkeys reached the learning criterion with 4 targets (green squares) and 12 distractors (white squares) randomly placed on the grid. For each transmission chain, a first baboon was randomly selected, and this subject received a first block of 50 transmission trials consisting of randomly-generated patterns. Once the first subject had been tested, its behavioural output (the actual pattern of squares touched)

on these 50 transmission trials was randomly reordered in a new block of 50 trials that became the set of target patterns shown to the next individual in that chain.

When the individuals were not involved in the transmission chain, they could perform random trials that were generated automatically by the computer and were not part of the transmission process. We ran 9 such chains with a total of 10 generations (i.e., 10 individuals in each chain), each initialised with a different set of randomly-generated trials. We also made sure that each baboon did not appear more than once in each chain and performed at least 500 random trials between sets of transmission trials to avoid interference between chains. In our analyses, the responses recorded in these random trials were compared to those obtained in the transmission chain, to infer the effects of cumulative culture.

2.2 Methods specific to children

The experimental procedure for children was as similar as possible to the experimental procedure for baboons; in this section we detail the differences.

2.2.1 Participants and materials

Participants were 90 English-speaking children between the ages of 5 and 7 years old (42 female, mean age = 6 yo), recruited at the hall of the Edinburgh Zoo's Budongo Trail. Four further participants were excluded from the study because they failed the pre-established criterion to achieve at least 2/3 successful trials during training.

The experiment was conducted on iPads using iOS application Pythonista 3, in a single session of approximately three minutes. All participants were rewarded with stickers at the end of the experiment.

2.2.2 Procedure: iPad-based tasks

The experiment was divided into two phases, a training phase and a testing phase. The training phase followed a progressive increase in the complexity of the task over three blocks, starting with a grid of two squares (one white, one red[1]), then a grid of four (two red, two white) followed by the final grid of 16 (four red, 12 white). Training blocks consisted of three trials each. During testing, each trial (20 total) began with the display of a grid made of 16 squares as in the baboons' version, 12 white and four red. If four correct squares (any four of those which were not displayed in red) were touched the trial was considered a success and the smiley face of a monkey emoji was displayed along a reward sound effect. Otherwise, the face of the monkey emoji was displayed with both hands covering the mouth along a child-friendly incorrect answer sound effect. After the monkey emoji faded away, the screen remained black for 1 s before the next trial began. At the end of the experiment, irrespective of the participant's performance, the display filled with animated stars while a reward melody was played.

2.2.3 Between-individuals transmission procedure

The transmission procedure was exactly as described in section 2.1.5 for the baboon's version, with the only difference being the size of the testing/transmission set, which is 20 trials in this version instead of 50. We ran nine transmission chains with a total of 10 generations. Each chain was initialised with a different set of randomly-generated trials.

2.3 Ethics statement

The research with baboons 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

[1] We decided to change the colour of the squares in the input patterns to follow the (human) western colour conventions in which red is associated with prohibition.

(approval # APAFIS-2717-2015111708173794-V3). Procedures were also consistent with the guidelines of the Association for the Study of Animal Behaviour.

The experiment with children was carried out in accordance with the research ethics procedures of the Edinburgh Zoo's Bundongo Trail and approved by the ethics committee of the School of Philosophy, Psychology and Language Sciences at The University of Edinburgh (Ref # 325-1718).

2.4 Statistical analysis

The aim of our analysis was to evaluate the strength of the evidence for cumulative culture considering the three criteria highlighted in [25], that is, to test (i) a progressive increase in performance, (ii) the emergence of systematic structure, and (iii) the presence of lineage specificity. To this aim, we first analysed the data from baboons comparing transmission versus random trials and later we analysed the data from transmission trails in children and baboons.

2.4.1 Analysis restricted to the baboon data

We followed the procedure used in [25] to analyse the results and ran mixed-effects regression models using the lme4 package developed in R [37, 38] and calculated p-values using lmerTest [39][2]. The type of model (linear or logistic) will vary according to the dependent variable. All models contain a fixed effect of Generation and a fixed effect for Trial Type (two levels: transmission as the baseline, and random trials)[3] with an interaction term between them. To control for the non-independence within a given chain, models

[2] The library *lmerTest* calculates p-values of fixed effects from F statistics based on Satterthwate's approximation for denominator degrees of freedom, and it tests random effects using likelihood ratio

[3] Transmission trials were the test trials in which the baboons' input was the output of the previous baboon in the transmission chain, and the random trials were those 50 trials that the same baboons produced before the transmission trials.

contain the following random effects: intercepts for Subjects and Chain as well as by-Subject slopes for the effect of Trial Type, and by-Chain slopes for the effect of Generation.

2.4.2 Cross-species analysis

The models used for the cross-species analysis have a very similar structure to those described above. The only difference is that they do not contain a fixed effect for Trial Type, but they do contain a fixed effect for Primate Species (two levels: children as the baseline, and baboons) and its interaction with Generation. The random-effects structure is consequently reduced to only include random intercepts for Chain as well as by-Chain random slopes for the effect of Generation.

3. Results

3.1 Is cumulative cultural evolution possible without copying in baboons?

Increase in performance. We found a progressive increase in performance over generations in transmission chains with baboons (see Figure 1a). Using a dependent binary variable determining the success or failure for each trial, the results of the logistic regression model show a significant effect of generation (β = 0.064, SE = 0.026, z = 2.466, p = 0.014) as well as a significant interaction between generation and trial type (β = −0.05, SE = 0.019, z = −2.580, p = 0.01), suggesting that the proportion of successful trials increases significantly with generation in transmission trials and that it does so significantly less in random trials. This increase in performance over time during transmission trials significantly above random trials reveals a clear benefit of cultural transmission.

Emergence of systematic structure. One indicator of the emergence of structure is a progressive decrease in response diversity due to a focus on a subset of responses. We observed a reduction of diversity among sets of grids during transmission trials compared to

random trials (Figure 1b). A linear mixed effects model with the Shannon diversity index (equal to Shannon entropy, [40]) as the dependent variable suggests a significant effect of Generation (β = −0.036, SE = 0.018, t = −2.031, p = 0.047) thus confirming that the diversity of the set of responses decreases over generations in transmission trials. However, we found no strong evidence to support a significant difference in the effect of generation between random and transmission trials (β = 0.038, SE = 0.022, t = 1.679, p = 0.095), thus suggesting that the decrease in diversity over generations does not significantly differ between trial types. Nevertheless, we do find that diversity is significantly higher in random trials than in transmission trials (β = 0.394, SE = 0.136, t = 2.890, p = 0.006), altogether confirming the difference in the overall diversity observed in Figure 1b.

Figure 1: Results from transmission and random trials in baboons, depicted by blue squares and orange circles respectively. (a) Average score defined by the proportion of successful trials; (b) average Shannon's diversity index within the set of responses; (c) average proportion of tetrominoes produced; and (d) average increase in opposite-side responses. Error bars represent standard errors.

To explore the type of structures that emerged during transmission and which might guide the observed decrease in diversity, we looked at the main structures found in [25], that is, tetrominoes (grids where all four squares are connected—lines, squares, L-shapes, T-shapes, S-shapes; tetrominoes will be familiar to anyone who has played Tetris). Figure 1c shows the proportion of tetrominoes produced over generations. The results from a logistic mixed regression model with a binary dependent variable representing the presence or absence of a tetromino suggest that baboons have a significant tendency to produce tetrominoes, similar across random and transmission trials (intercept, β = 1.01, SE = 0.217, z = 4.675, p < 0.001; Trial Type, β = −0.308, SE = 0.194, z = −1.59, p = 0.112). However, we found no

effect of Generation (β = 0.014, SE = 0.018, z = 0.817, p = 0.414) and no significant interaction between Generation and Trial Type (β = −0.027, SE = 0.017, z = −1.586, p=0.113), suggesting that the proportion of tetrominoes did not change over generations in either random or transmission trials.

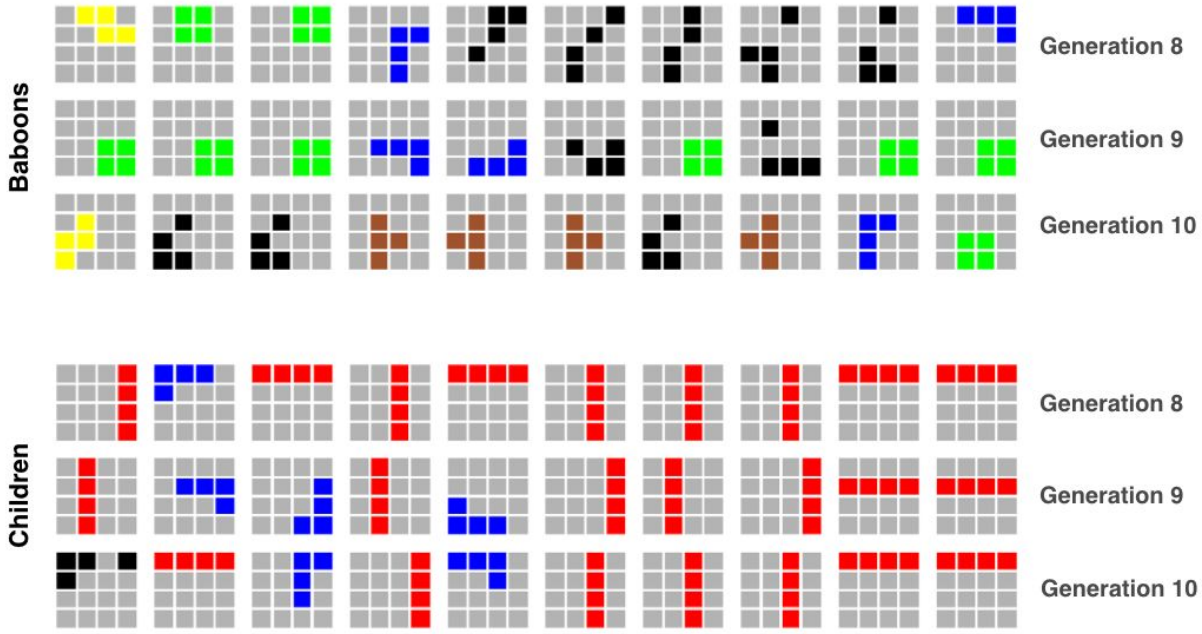

Figure 2: Baboons' and children's example responses (extracted from their corresponding Chain 5). Rows correspond to generations 8 to 10 (from top to bottom), each row contains 10 example grids. Colouring of each grid reflects the tetromino class each pattern comes from (red for lines, green for squares, blue for L-shapes, brown for t-shapes, yellow for s-shapes, black for non-tetrominoes).

Further inspection of the response strategies suggested a spatial alternation of the responses (from one side of the response grid to the opposite side) between subsequent generations in transmission chains (see Figure 2). To quantify this, we created a binary variable that indicated if the position of the response was in a part of the screen that was opposite to that of the stimulus. We divided the screen into four quadrants (top vs. bottom, right vs. left) and coded as opposite-side responses those that were on opposite sides of the

screen (only responses that were entirely in one quadrant were considered). Figure 1d shows the number of opposite-side responses increases sharply during the first generation and remains high compared to random trials. Results from the logistic regression model show a marginal effect of Generation (β = 0.068, SE = 0.037, z =1.826, p = 0.069) and a significant interaction between Generation and Trial Type (β = −0.071, SE = 0.027, z = −2.648, p = 0.008). Although the linear model fails to capture the sharp increase in the first generation and provides weak evidence of an increase in the proportion of opposite-side responses over generations in transmission trials, it provides stronger evidence against such increase in random trials. Moreover, we find that the proportion of opposite-side responses is significantly lower in random trials than in transmission trials (β = −2.034, SE = 0.22, z = −9.238, p < 0.001), confirming the difference observed in Figure 1d.

Presence of lineage specificity. If the responses tend to alternate, we then expect different transmission chains, or lineages, to result in different tendencies. For instance, one chain might converge on alternating between top and bottom responses when another might use left vs. right. In order to assess the presence of lineage specificity and its potential effect on the baboons' performance, we conducted a follow up study in which we tested the performance of the baboons on trials from the 10th generation of the nine chains (this additional experiment is presented in detail in the ESM). In one condition the sets were unmodified (all the trials within a set belonged to the same chain), in another condition they were randomly mixed sets of trials coming from different chains. If there is lineage specificity, we expect the baboons to perform better in the unmodified set condition compared to the randomly mixed sets.

As expected, baboons were more successful in the unmodified set condition compared to the randomly mixed set (β = 0.172, SE = 0.079, z = 2.161 p = 0.031; details provided in the ESM); this seems to be the case at the group and individual levels for all but one baboon.

To summarise the baboons' results, we found the three distinctive properties of CCE outlined above: an increase in score, the emergence of systematic structure in the response set and the presence of lineage specificity. These results are also in line with the core criteria for CCE outlined by [31]; in this non-copying task, we observe a repeated cycle of changes in behaviour that improve performance as they are transmitted to other individuals. We now turn to compare these results with those obtained in the experimental version with children.

3.2 Are the trends in CCE without copying similar across children and baboons?

A visual inspection of the data obtained from the transmission chain experiments with children reveals strikingly similar tendencies to those found in baboons (see Figure 3). Using the analyses described in section 2.3.2, we found a clear increase in task performance over generations (β = 0.124, SE = 0.045, z = 2.719, p = 0.007), a significant decrease in the diversity of the sets of responses (β = −0.046, SE = 0.019, t = −2.433, p = 0.016), a stable high proportion of tetrominoes over generations (intercept: β = 1.717, SE = 0.246, z = 6.979, p < 0.001; Generation: β = 0.059, SE = 0.048, z = 1.249, p = 0.212) and a significant increase in the proportion of opposite-side responses generation (β = 0.102, SE = 0.04, z = 2.538, p = 0.011). The analyses further suggest no difference in the effect of generation across species in all these tendencies; we did not find a single significant interaction between Generation and Primate Species (score, z = −0.924, p = 0.355; diversity, t = 0.186, p = 0.853; tetrominoes, z = −0.636, p =0.525; opposite-side responses, z = −0.565, p =

0.572). However, we found differences across species in overall score as well as in the overall production of tetrominoes: baboons scored lower ($\beta = -0.962$, SE = 0.250, z = -3.844, $p < 0.001$) and produced less tetrominoes than children ($\beta = -0.748$, SE = 0.328, z = -2.277, p = 0.023), confirming the differences observed in Figures 3a and 3c respectively. Results therefore suggest that the general tendencies found in children are very similar to those found in baboons.

However, the inspection of the specific patterns produced (see e.g. Figure 2) suggested that children tended to copy the overall shape of the response of the previous individual but shifted its position to avoid direct copying of the observed pattern—which was possible because the non-copying task only prevented them from copying both shape and location of the input patterns. Figure 4a shows the proportion of input tetrominoes whose shape was copied (in a different location) in the response, and Figure 4b shows the proportion of trials in which the tetromino produced at a given generation is the exact re-production (shares the same shape and location) of the one produced two generations ago in the same chain. We observe that while baboons tend not to copy the overall shape of input tetrominoes in their responses, children seem to do so increasingly over generations. A logistic mixed-effects model confirms that children copy input tetrominoes increasingly over generations ($\beta = 0.099$, SE = 0.025, z = 3.923, $p < 0.001$) and significantly more than baboons (as suggested by the interaction between Generation and Primate Species, $\beta = -0.082$, SE = 0.034, z = -2.374, p = 0.018). Another model further confirms that the proportion of re-production of the exact same response as the one produced two generation ago also increased in children ($\beta = 0.099$, SE = 0.030, z =3.282, p = 0.001), and significantly more than in baboons ($\beta = -0.042$, SE = 0.035, z = -2.371, p = 0.018).

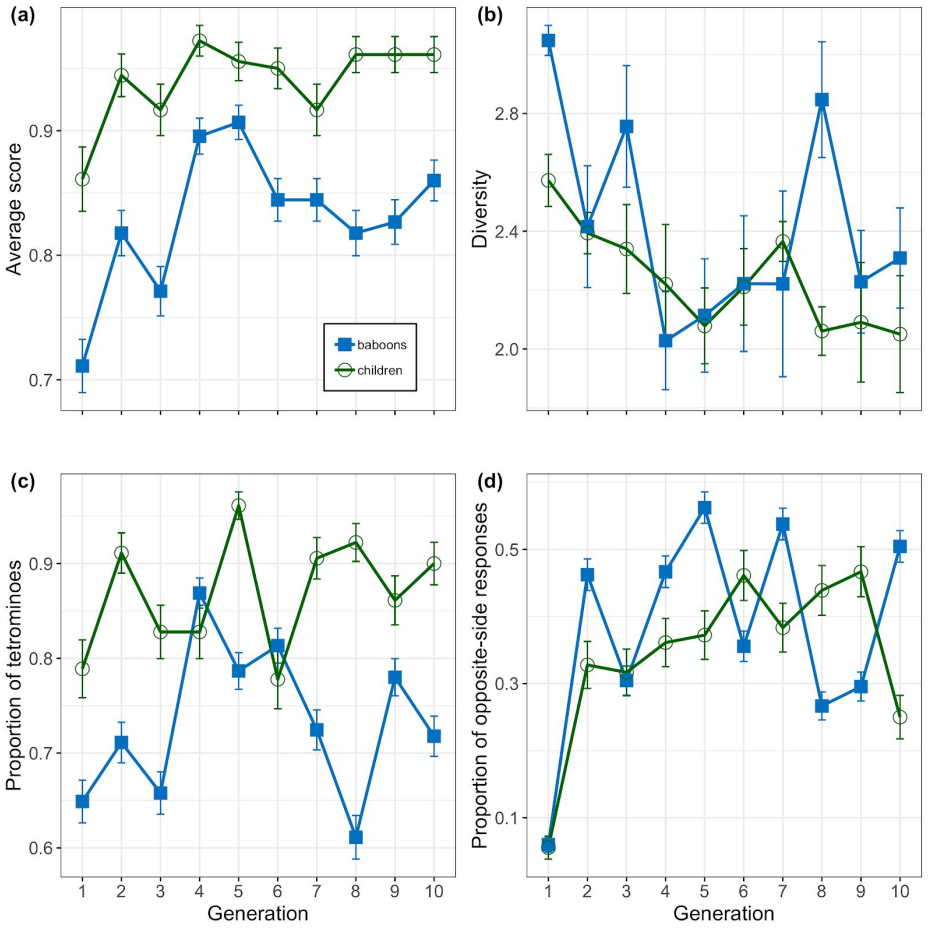

Figure 3: Results from the transmission chains with baboons (blue squares) and children (green circles): (a) average score defined by the proportion of successful trials; (b) average Shannon's diversity index within the set of responses; (c) average proportion of tetrominoes produced; and (d) average increase in opposite-side responses. Error bars represent standard errors.

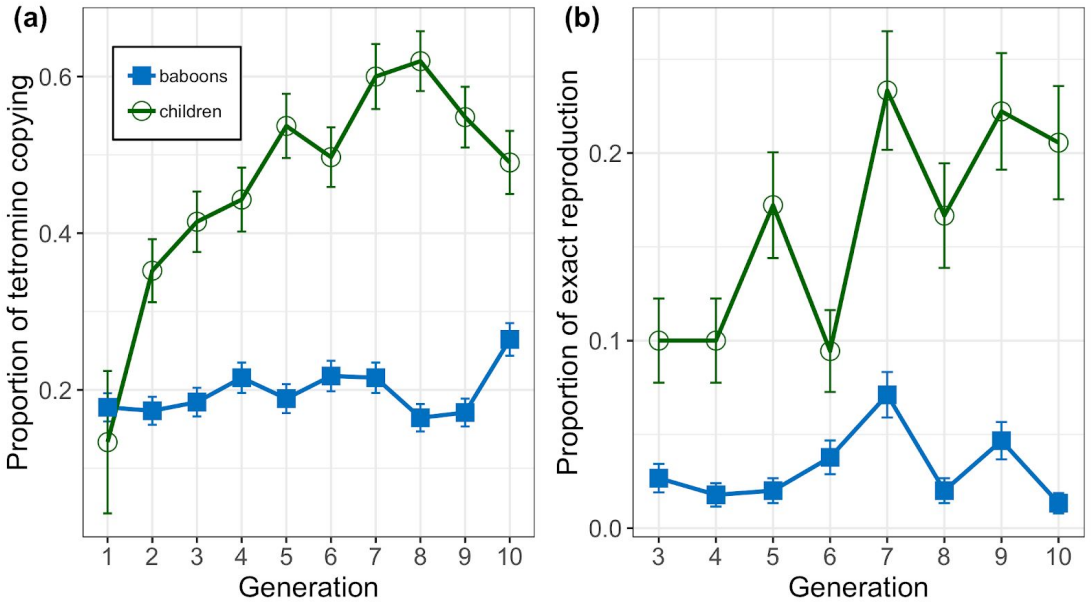

Figure 4: (a) Average proportion of tetrominoes that are copied from one generation to the next. (b) Proportion of responses that are identical between every other generation.

We further explored the difference in tetromino copying between children and baboons by examining specific tetromino shapes, because the inspection of the patterns produced also suggested that children tended to produce many lines and that they copied them more so than any other pattern. An inspection of the average number of tetrominoes produced as well as the proportion of tetromino-copying subset by each of the five possible tetromino shapes (see ESM) reveals a clear preference for lines over other tetrominoes in children. A logistic mixed-effects regression model (detailed in the ESM) show that lines are the most copied tetrominoes (β = 0.803, SE = 0.206, z = 3.905, $p < 0.001$; the smallest difference is shown with square tetrominoes: β = −1.342, SE = 0.316, z = −4.250, $p < 0.001$) but that this tendency to copy lines does not increase over time (β = −0.012, SE = 0.036, z = –0.324, $p < 0.746$). Nonetheless, a further logistic mixed-effects model excluding line tetrominoes (see ESM) suggests that this constant tendency to copy lines is not the sole driver of the effect of generation on the overall proportion of copied tetrominoes; children still copy the shape of

other input tetrominoes increasingly over generations (β = 0.009, SE = 0.003, z = 2.921, p = 0.003).

4. Discussion

The idea that faithful copying is essential to CCE is both intuitive and appealing: if socially learned behaviours are not faithfully transmitted, modifications to what is being transmitted will not be passed on to other individuals and will therefore be lost [14]. In a process closely similar to biological replication, faithful copying could guarantee the transmission of modifications and therefore naturally lead to CCE.

The purpose of this study was to test this fundamental hypothesis by examining the possibility of finding CCE with what was set up as a non-copying task. We used a cultural transmission task similar to the copying task used in [25] but in which the participants had to avoid what was produced by the previous individual in the chain. The results from the transmission chain experiments with baboons exhibited all three fundamental properties of CCE examined: (i) an increase in score linked to (ii) the emergence of some type of systematic structure, and (iii) lineage specificity. Despite the presence of a large evolutionary space (1820 possible responses) and a 27% chance of being correct by chance, we found the emergence of systematic responses alternating in position from one side of the response grid to another. The results from baboons thus show that CCE is possible without copying of any sort.

Next, we aimed at testing the generalisability of our results to children. Interestingly, children's results were very similar to the baboons' regarding CCE: we also found an increase in score linked to the emergence of systematic structures. However, unlike the

baboons, children introduced copying mechanisms into the non-copying task by copying the shape of the input pattern in a different location, which was not prevented in the task (the non-copying task only forbid them from copying the exact grid pattern in the input, which included both the shape and location of the stimulus). This strategy adopted by children might in turn potentially explain their higher scores and tetromino production in comparison to baboons.

The observed copying strategy could be in line with children's tendency to high-fidelity copy even when not required in the task [41, 42]. Complementarily, it could also be partly explained by the fact that children, unlike baboons, only saw grids of two and four squares during training before the target grid of 16, and in these grids, the rewarded output is necessarily the mirror image of the input. However, we only observe high-fidelity copying of specific shapes (i.e., tetrominoes), which are potentially already preferred by children. Once these preferred shapes are in the system, they are maintained. Results thus suggest that the observed bias is not a copying bias (at least uniquely), but a bias towards tetromino shapes which results in high-fidelity copying once these patterns are introduced.

Further inspection of the results showed this bias is significantly stronger for line tetrominoes: children tended to produce many line tetrominoes as well as to copy them from the input. This specific bias towards the production and copying of lines in particular could be cognitive or task-specific, or it could simply reflect that lines are particularly salient to children. However, in spite of the large number of lines, we also found evidence of an increase in a general tendency to copy, suggesting that the more the systems became structured, the more likely specific structures were to be copied (Figure 4a).

The fact that the children copied the pattern they saw while at the same trying to avoid its location created a remarkable situation in which the responses of the individuals separated by one generation became more likely to be exactly the same (both in shape and position; Figure 4b). A tendency to avoid what the previous individual did may be conceived as a re-production of behaviour over two steps when the number of possible behaviours is limited, an interesting illustration of the theoretical example of re-construction given in [32].

In conclusion, our results suggest that CCE does not necessarily depend on high-fidelity copying and that there is a broad spectrum of possible transmission mechanisms that will lead to CCE; these mechanisms that are not based solely, or even mainly, on indiscriminate high-fidelity copying remain to be further explored.

5. Data Accessibility

The data that support the findings of this study are openly available in the Open Science Foundation repository at https://osf.io/za265/, DOI 10.17605/OSF.IO/ZA265.

6. Acknowledgements

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test systems. C.S., J.F., S.K. and N.C. coded the software for the experiments. C.S., J.F. and N.C. collected the data. C.S. and N.C. analysed the results.

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