Cumulative cultural evolution in a non-copying task in children and Guinea baboons

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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 be dependent 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 children where individuals observed and reproduced visual patterns 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 regarded for innovation rather than copying. Results nevertheless exhibited two fundamental properties of CCE: an increase over generations in task performance and the emergence of systematic structure. However, CCE arose from different mechanisms across species: children, unlike baboons, converged in behaviour over generations by copying specific patterns in a different location, thus introducing alternative copying mechanisms into the non-copying task. We conclude that CCE can result from non-copying tasks and that there is a broad spectrum of possible mechanisms that will lead to CCE aside from high-fidelity transmission.

Keywords: social learning; transmission chain; copying; cumulative cultural evolution; Guinea baboons; children;

Introduction

Human culture evolves over time with the gradual accumulation of modifications, from social norms (Nichols, 2002), to art (Morin, 2013), to language (Keller, 2005). In contrast, evidence for cumulative culture has been extremely difficult to find in other animal species (but see, e.g., Grant & Grant, 2010; Garland et al., 2011), and even difficult to induce through experimental manipulations (but see, e.g., Sasaki & Biro, 2017; Fehér, Wang, Saar, Mitra, & Tchernichovski, 2009). It has been proposed that this sharp contrast between human and non-human animal cultures can be explained by the lack of copying fidelity in the social learning of non-human animals (Tomasello, Kruger, & Ratner, 1993; Kempe, Lycett, & Mesoudi, 2014; Lewis & Laland, 2012). Faithful transmission can prevent the loss of cultural modifications and consequently result in cultural accumulation (Tomasello et al., 1993); therefore, the ability to faithfully transmit information through high-fidelity social learning has been taken as a requirement for cumulative culture. However, it is unclear whether there is a critical level of fidelity required to observe cumulative cultural evolution (CCE) and whether that required level of fidelity can ever actually be achieved by social learning mechanisms (Claidière & Sperber, 2009).

Transmission chain experiments have further shown that CCE can occur with learning mechanisms that exist in non-human animals, suggesting that cumulative culture is not after all dependent on special cognitive capacities found only in humans (Caldwell & Millen, 2008; Claidière, Smith, Kirby, & Fagot, 2014; Zwirner & Thornton, 2015). Claidière et al. (2014) for instance, performed a transmission chain study in which baboons observed and reproduced visual patterns on touch screen computers. Transmission led to the emergence of cumulative culture, as indicated by fundamental aspects of human cultural evolution such as (i) a progressive increase in performance and (ii) the emergence of systematic structure. Surprisingly, these results were achieved with an extremely low fidelity of pattern reproduction during the first generations of transmission, suggesting that high-fidelity copying 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. Claidière et al. (2014)'s study therefore shows that cultural transmission may give a misleading impression of high-fidelity transmission when in fact cultural evolution tends to produce variants that become more faithfully transmitted. 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. Beckner, Pierrehumbert, & Hay, 2017; Kirby, Cornish, & Smith, 2008).

Can we observe CCE in a non-copying task?

Most experiments on social learning and cultural transmission focus on copying tasks in which the individuals goal is to reproduce the input behaviour (for a thorough review, see Mesoudi & Whiten, 2008). However, other mechanisms through which humans and other animals learn, use and transmit information remain under-explored. Encouraged by the results of Claidière et al. (2014) 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 require direct copying. If high-fidelity copying is essential to CCE, we might not observe it in a task that does not involve copying.

To test this hypothesis, we performed an experiment with baboons and human children using the same protocol as in Claidière et al. (2014) but with a "non-copying" task in which the individuals were trained to avoid directly reproducing the patterns touched by a previous individual. In Claidière et al. (2014)'s original task participants were presented with a grid of 16 squares, four of which were briefly highlighted, and the task was to touch the squares that had been highlighted. The squares touched by one individual then became the highlighted squares for the next individual in the chain of transmission. In our new version of the task, the highlighted squares were instead to be avoided; the squares that one individual touched were the ones the next individual needed to avoid in order to be rewarded.

There are grounds for expecting this change in the pay-off structure of the task would prevent CCE from happening. In every trial, 495 different possible responses lead to a reward (a 27% likelihood of being correct by chance), creating a vast space of "correct" responses in every generation that are all different from the previous individual's response but which all will be rewarded. As well as directly penalising copying behaviour, the fact that the space of possible correct responses is so large and rather unconstrained by the input pattern suggests that any early accumulation of modifications (e.g., incipient structure in the system of patterns produced) could easily be wiped out by any individual in a chain of transmission, preventing cultural accumulation. However, participants could use non-copying alternative strategies that would result in convergent behaviour over generations. For instance, if participants try to minimise the effort of retaining and/or producing non-overlapping patterns, this might progressively cluster the responses on patterns of four connected squares (i.e., tetrominoes, which are easier to retain in memory and produce). This in turn might lead to increased performance over generations because such structured input patterns will be easier to avoid. Thus, if the search in the large evolutionary space is biased and there are alternative strategies which will lead to convergent behavioural output over generations, it might be possible to observe cumulative effects in transmission chains with a non-copying task.

Methods

Guinea baboons

Participants and testing facility Twelve Guinea baboons (Papio papio) belonging to a large social group of 25 from the CNRS Primate Center 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).

The study was conducted in a facility developed by J.F. (for further information, see Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014).The baboons live in an outdoor enclosure ($700m^2$) connected to an indoor area which provides shelter when necessary. The outside enclosure is connected to 10 testing booths each equipped with a touchscreen. The key feature of this facility is that baboons have free access to computerised testing booths that are installed in trailers next to their enclosure. 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's forearm. The baboon can thus participate in an experiment whenever they choose, and do not need to be captured to participate. The test program allows an independent test regime for each baboon, irrespective of the test booth it is using. Grains of dry wheat are used as reward. Baboons were neither water- nor food-deprived during the research. Water was provided *ad libitum* within the enclosure. Baboons received their normal ratio of food (fruits, vegetables and monkey chow) every day in the afternoon. The baboons were all born within the primate centre.

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.

Computer-based task Each trial began with the display of a grid made of 16 squares, 12 white and four green. 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 baboon had to select and touch four squares in this matrix which were not previously shown in green colour. Touching these four square could be done in any order. Squares became black when touched to avoid being touched again and did not respond to subsequent touches. A trial was completed when four different squares had been touched with less than 5 s between touches. If four correct squares were touched, then the trial was considered a success and the computer triggered the delivery of 3-4 wheat grains. If less than four correct squares were touched (i.e. at least one previously green square was touched), then 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 600×600 pixel grid and were displayed on a black background on a 1024×768 pixels screen. The inter-trial interval was at least 3 s, but could be much longer since baboons chose when to initiate a trial.

Training to criterion Twenty-five members of the colony underwent a training procedure to enable them to participate in the transmission chain experiment: only those animals who reached our final criterion (N=12) were admitted to the transmission chain study described below. 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 six, one green and 2-5 white), 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% for the 25 baboons included in the training). Progress through training was conditioned on performing above a criterion of 80% success on a block of 50 random trials (excluding aborted trials).

Transmission procedure We followed the transmission procedure described in (Claidière et al., 2014) and therefore only report the main elements here. Testing began when all 12 baboons reached the learning criterion with four 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 became the set of target patterns (randomly reordered) 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 nine such chains each with 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.

Children

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

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 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 carried out in accordance with the research ethics procedures of the Edinburgh Zoo's Bundongo Trail and of the department of Linguistics and English Language at The University of Edinburgh (Ref # 325-1718).

The experiment was conducted on iPads using the iOS application Pythonista 3, in a single session of approximately three minutes. The experiment took place in the hall of the the Edinburgh Zoo's Budongo Trail, with the child seated on a chair and the experimenter beside them throughout, providing all instructions verbally. The experimenter also provided encouragement to the child but no informative feedback during critical trials. All participants were rewarded with stickers at the end of the experiment.

iPad-based task 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. We excluded participants who failed to produce a minimum of two successful trials during the last two training blocks (grids of four and 16). 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 with a reward sound effect. Otherwise, the face of the monkey emoji was displayed with both hands covering the mouth along with 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 participants performance, the display filled with animated stars while a reward melody was played.

Transmission procedure

The transmission procedure was exactly as described for the baboons' version, with the only difference being the size of the testing/transmission set, which was 20 trials in the child version instead of 50. We ran nine transmission chains with

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

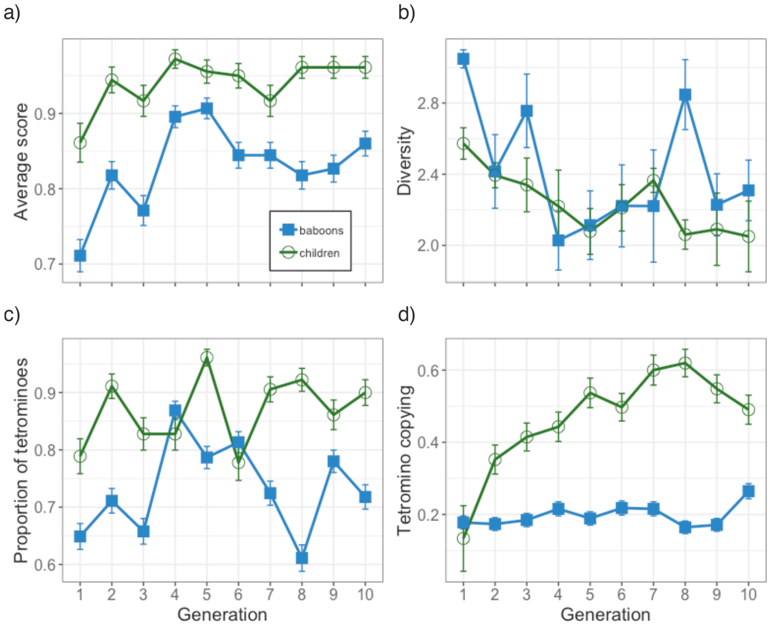

Figure 1: Blue squares and green circles illustrate the results for baboons and children respectively. (a) Average score, defined by the proportion of successful trials. (b) Average Shannon's diversity index within the set of responses. (c) Average proportion of tetrominoes produced. (d) Average proportion of observed tetrominoes which are copied.

a total of 10 generations (i.e., 10 children); each chain was initialised with a different set of randomly-generated trials.

Statistical analyses

The aim of our analyses is to evaluate the strength of the evidence for cumulative culture in baboons and children considering the two criteria highlighted in the introduction, that is, to test (i) a progressive increase in task performance over generations, and (ii) the emergence of systematic structure.

To analyse the results we used mixed-effects Growth Curve Analysis (GCA); the type of model, logistic or linear, will vary according to the dependent variable. All models contain three fixed effects: Generation, a quadratic polynomial for Generation (Generation^2), and Experiment (baboons as the baseline, and children). They also contain two interaction terms, between Generation and Experiment, and between Generation^2 and Experiment. To control for the non-independence within a given transmission chain, all models also contain random intercepts for Chain as well as by-Chain random slopes for the effects of Generation and Generation^2.

Results

Increase in task performance The average score was high across children and baboons, and we found a progressive increase in performance over generations of transmission across children and baboons (see Figure 1a). Using a dependent binary variable (success or failure for each trial) to analyse the evolution of success over generations, the results of the logistic GCA model show a significant effect of Generation ($\beta = 0.307, SE = 0.054, z = 5.700, p < 0.001$) and no significant interaction with Experiment ($z = 0.006, p = 0.995$), suggesting that task performance increases over generations of participants across children and baboons. We also found a significant effect of Generation^2 ($\beta = -0.027, SE = 0.005, z = -4.911, p < 0.001$) and no significant interaction with Experiment ($z = 0.351, p = 0.726$), suggesting that the increase in performance abates as we move along generations of participants. There was a further significant effect of Experiment ($\beta = 1.043, SE = 0.257, z = 4.062, p < 0.001$), suggesting that children generally scored higher in the task than baboons.

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 (Kirby et al., 2008). We observed a reduction of diversity among sets of grids during transmission (see Figure 1b). Using the same model structure as previously specified, and the Shannon's diversity index of the systems of responses (equal to Shannon entropy: Shannon, 1948) as the dependent variable, a linear GCA model reveals a significant effect of Generation ($\beta = -0.237, SE = 0.069, t = -3.535, p < 0.001$) and no significant interaction with Experiment ($t = 1.467, p = 0.144$), suggesting that the diversity of the systems decreased over generations of participants across children and baboons. We also found a significant effect of Generation^2 ($\beta = 0.022, SE = 0.007, t = 2.982, p = 0.003$) and no significant interaction with Experiment ($t = -1.597, p = 0.112$), suggesting that the decrease in diversity deflates as we move along generations of participants (across species). Moreover, the marginal effect of Experiment ($\beta = -0.356, SE = 0.19, t = -1.853, p = 0.068$) does not provide strong evidence to suggest a difference between children and baboons.

To explore the type of structures that emerged during transmission which might guide the observed decrease in diversity, we looked at the main structures found in Claidière et al. (2014), 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 GCA model with a binary dependent variable representing the presence or absence of a tetromino suggest that children and baboons have a significant tendency to produce tetrominoes ($\beta = 0.688, SE = 0.225, z = 3.058, p = 0.002$) and that children produced them significantly more than baboons ($\beta = 1.046, SE = 0.353, z = 2.961, p = 0.003$). We also found a weak effect of Generation ($\beta = 0.252, SE = 0.112, z = 2.263, p = 0.024$) and no effect of its interaction with Experiment ($\beta = -0.214, SE = 0.177, z = -1.206, p = 0.228$), suggesting that the proportion of tetrominoes produced slightly increase with generation in baboons as well as in children. However, the significant effect of Generation^2 ($\beta = -0.026, SE = 0.012, z = -2.080, p = 0.038$) and the non-significance of its interaction with Experiment ($\beta = 0.030, SE = 0.020, z = 1.517, p = 0.129$) suggest that such increase in the production of tetrominoes reduces with generation.

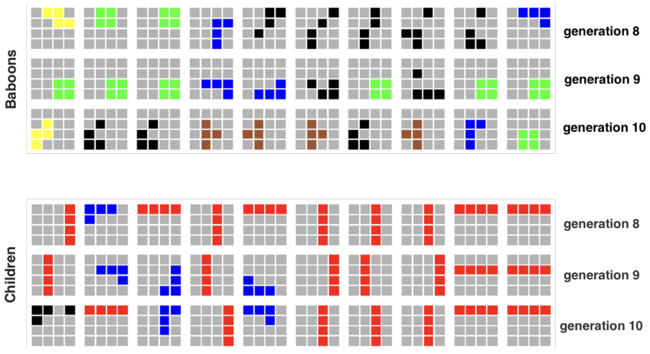

Figure 2: Baboons' and children's example responses, rows correspond to 10 example grids in generations 8-10 of a given chain (from top to bottom). Colouring of each grid reflects the tetromino class each pattern belongs to (green for squares, blue for L-shapes, brown for T-shapes, yellow for S-shapes, and black for non-tetrominoes).

Copying in a non-copying task So far, the general tendencies in the results found in children are very similar to those found in baboons—the only difference so far is that children score higher and produce more tetrominoes than baboons on average. However, an inspection of 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). Figure 1d indicates 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 GCA model confirms that while baboons copy input tetrominoes significantly below chance ($\beta = -1.27, SE = 0.174, z = -7.336, p < 0.001$) constantly across generations (Generation, $z = -1.416, p = 0.157$; Generation^2, $z = 0.012, p = 0.100$) , children increasingly copy input tetrominoes over generations ($\beta = 0.559, SE = 0.121, z = 4.602, p < 0.001$) and more so initially than later on, where the increase abates (as indicated by the interaction between Generation^2 and Experiment, $\beta = -0.048, SE = 0.012, z = -4.620, p < 0.001$).

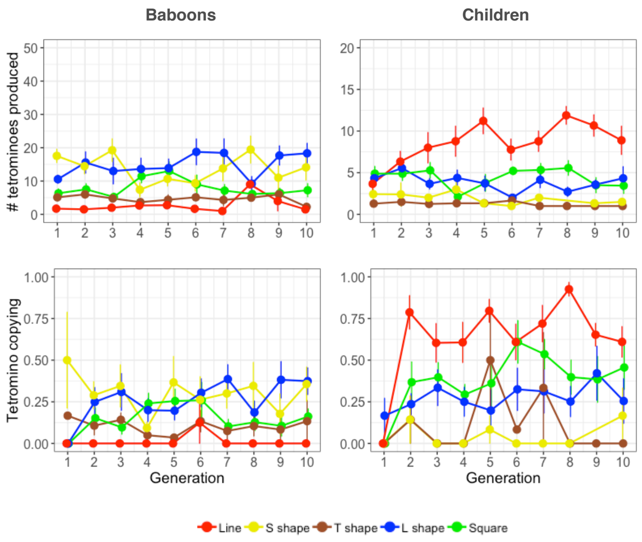

Figure 3: Top row: Average number of tetromino shapes produced by baboons (left) and children (right) for each of the five tetromino classes (over 20 and 50 trials respectively). Bottom row: Average proportion of tetrominoes that are copied from one generation to the next for baboons (left) and children (right).

We further explored the difference in copying in children and baboons by examining specific tetromino shapes because the inspection of the patterns produced (Figure 2) also suggested that children tended to produce many lines and that they copied them more so than any other pattern. Figure 3 shows the average number of tetrominoes produced as well as the proportion of tetromino copying subset by each of the five possible tetromino shapes. A visual inspection of Figure 3 reveals a clear preference for lines over other tetrominoes in children. Moreover, lines are the only pattern that shows an increase in production over time in children. We thus ran a logistic mixed-effects regression model (without the quadratic term, and with an added fixed effect for Tetromino Type with an interaction term) to test whether this observed increase in the production of lines over generations in children could be accompanied by an increase in tetromino copying specific to lines. Results suggest that children copy lines significantly more than baboons ($\beta = 5.055, SE = 2.075, z = 2.436, p = 0.015$), who in contrast produce lines below chance ($\beta = -4.24, SE = 2.065, z = -2.052, p = 0.040$) equally across generations ($\beta = 0.001, SE = 0.356, z = 0.004, p = 0.997$). Results further suggest that lines are the most copied tetrominoes in children ($\beta = -0.048, SE = 0.012, z = -4.620, p < 0.001$; the smallest difference is shown with square tetrominoes: $\beta = -4.105, SE = 2.096, z = -1.958, p = 0.05$) but that this tendency to copy lines does not change over time ($\beta = -0.017, SE = 0.358, z = -0.047, p = 0.962$). We did not find a single significant interaction of Generation in the model (biggest effect: $z = 0.343, p = 0.732$). Altogether, these results suggest that children have a constant tendency to copy lines (above other tetrominoes), and once lines are introduced in the system, they are maintained. This in turn results in their accumulation and increase in number over time as new lines are introduced.

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 generations of individuals and will therefore be lost (Tomasello et al., 1993). In a process closely similar to biological replication, faithful copying could guarantee the transmission of modifications and therefore naturally lead to CCE. However, cultural evolution is much broader than biological evolution because it does not fundamentally derive from a process akin to replication and is therefore not constrained to certain modes of transmission (Claidière & André, 2012): several studies illustrate the fact that transmission can be of low fidelity and still lead to CCE (Caldwell & Millen, 2008; Claidière et al., 2014; Kirby et al., 2008; Claidière & Sperber, 2009).

The purpose of this study was to add to this research by examining the possibility of finding CCE with a non-copying task across human and non-human primate species. Results from children and baboons exhibited the two properties of CCE examined: (i) an increase in task performance linked to (ii) the emergence of some type of systematic structure. Despite the presence of a large evolutionary space (1820 possible responses for any single grid) and a very lenient reward function (27% chance of being correct by chance on any trial), we found the emergence of structure. This pattern probably emerged because the participants tended to cluster their responses in tetrominoes.

Although results from children and baboons were strikingly similar we found that, unlike the baboons, children introduced alternative 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 (at least partially) their higher scores and tetromino production in comparison to baboons.

This observed copying strategy could be in line with children's tendency to high-fidelity copy even when not required in the task (Lyons, Young, & Keil, 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). 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 (stronger than in baboons; on average, almost 80% of responses are tetrominoes in childrens first generations), which results in high-fidelity copying once these patterns are introduced. Further inspection of the results showed that children tended to produce many line tetrominoes as well as to copy them from the input (more so than any other pattern), altogether suggesting that the bias towards tetromino shapes could be particularly strong for line tetrominoes. This bias towards copying and producing lines could be cognitive or task-specific (i.e., lines could potentially be easier and faster to produce altogether or in the context of an iPad game where one finger instead of two is mostly used), or it could simply reflect that lines are particularly salient to children (e.g., because of drawing or colouring).

Conclusion

Our study demonstrates that CCE can be observed in a non-copying task in baboons and children. Results across species exhibited two crucial properties of CCE: (i) an increase in task performance over generations and (ii) the emergence of systematic structure. However, these seemingly similar properties of CCE across species arose from different mechanisms: children, unlike baboons, converged in behaviour across generations by copying specific patterns (i.e., tetrominoes, and in particular lines) in a different location thus introducing biased copying into what was set up as a non-copying task. Together, our results suggest that CCE does not necessarily depend on (at least unbiased) 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 high-fidelity copying remain to be further explored.

Data accessibility

The data that support the findings of this study are openly available in the Open Science Foundation repository at https://doi.org/10.17605/OSF.IO/ZA265.

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