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

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12 **Abstract**

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

22 copying. Results nevertheless exhibited fundamental properties of CCE: an increase over
23 generations in task performance and the emergence of systematic structure. However,
24 these properties arose from different mechanisms across species: children, unlike baboons,
25 converged in behaviour over generations by copying specific patterns in a different location,
26 thus introducing alternative copying mechanisms into the non-copying task. In children prior
27 biases towards specific shapes lead to convergence in behaviour across chains, while
28 baboon chains showed signs of lineage specificity. We conclude that CCE can result from
29 mechanisms with varying degrees of fidelity in transmission and thus that high-fidelity
30 copying is not necessarily the key to CCE.

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

33 **1. Introduction**

34 Almost every aspect of human culture evolves through time with the gradual accumulation
35 of modifications, from stories [1], to paintings [2], to social norms [3] and language [4]. In
36 sharp contrast, it has proved extremely difficult to find evidence of cumulative culture in
37 other animals [but see 5, 6, 7 for potential examples, 8, 9] or to induce cumulative culture in
38 other species through experimental manipulations [10, 11 for potential examples, but see
39 12]. One of the main reasons invoked to explain this sharp contrast between human and
40 non-human animal cultures is the low copying fidelity in non-human animals' social learning
41 [13-19]; faithful transmission can prevent the loss of cultural modifications and therefore
42 result in cultural accumulation [14], and the ability to faithfully transmit information
43 through high-fidelity social learning has therefore been taken as a requirement for
44 cumulative cultural evolution (CCE).

45 However, there are theoretical and empirical arguments suggesting that this view might be
46 mistaken. Firstly, the notion of fidelity in cultural transmission is highly problematic [20]; it is
47 unclear whether there is a critical level of fidelity required to the build-up of CCE and
48 whether that required level of fidelity can ever be achieved [20]. Secondly, when fidelity can
49 be measured, it is generally low and unlikely to sustain long lasting cultural traditions [21,
50 although not always, e.g. 22]. These results suggest that, even in humans, social learning is
51 not in itself of sufficiently high fidelity to prevent the loss of cultural modifications; other
52 mechanisms such as trial and error learning for instance can have a stabilising role [23].

53 Furthermore, transmission chain studies in humans have shown that fundamental
54 properties of CCE can be reproduced with social learning mechanisms that exist in non-
55 human animals, suggesting that CCE is not dependent on special cognitive capacities unique
56 to humans [24-26]. Claidière et al. [26], for instance, performed a transmission chain study
57 in which baboons observed and reproduced visual patterns on touch screen computers. The
58 baboons were organised into chains of transmission, where each baboon was provided with
59 the patterns produced by the previous individual in their chain; as in some human
60 transmission chain experiments [27 for instance], the baboons had no visual access to the
61 behaviour of other individuals, simply the products of those behaviours. With this
62 procedure, transmission led to the emergence of cumulative culture, as indicated by three
63 fundamental aspects of human cultural evolution: (i) a progressive increase in performance,
64 (ii) the emergence of systematic structure and (iii) the presence of lineage specificity [26].
65 Surprisingly, these results were achieved with an extremely low fidelity of pattern
66 reproduction during the first generation of transmission (only 37% of the patterns were
67 reproduced without errors). This initially low level of fidelity did not prevent the

68 accumulation of modifications, and we observed a sharp increase in fidelity as patterns
69 were passed on from generation to generation (reaching 72% in the 12th generation).
70 Similar results have been found in transmission experiments with human participants, for
71 example where the transmission of miniature languages results in the emergence of
72 languages which can be easily learned, even if the initial languages in each chain of
73 transmission are transmitted only with very low fidelity [e.g. 28, 29]. Together, these results
74 suggest that high-fidelity transmission may not always be the cause of cumulative culture
75 and may in fact itself be a product of CCE. Individuals may transform input variants in
76 accordance to their prior biases, and if those biases are shared at the population level, we
77 expect transformations in the same direction to accumulate at each transmission step. This
78 could thus lead to the evolution of variants which are more faithfully transmitted because
79 they match the prior biases more and more closely over generations giving a misleading
80 impression of high-fidelity transmission.

81 The vast majority of experiments on social learning and cultural transmission in humans and
82 non-human animals focus on copying tasks [see 30, 31 for reviews, 32]. In our opinion, this
83 almost exclusive interest in copying has prevented a more neutral exploration of the
84 mechanisms through which humans, and probably other animals, use and transmit the
85 information gained from other individuals and whether these other forms of social learning
86 and transmission may result in cumulative culture [see also 33].

87 Encouraged by the results of [26] showing that crucial properties of CCE can also result from
88 initially low transmission fidelity, we decided to test whether CCE could occur in a
89 transmission task that did not require copying. We performed an experiment with baboons
90 and children using the same protocol as [26] but with an “anti-copying” task in which the

91 individuals were trained to avoid directly reproducing the patterns produced by a previous
92 individual.

93 **2. Methods**

94 **2.1 Methods for baboons**

95 2.1.1 Participants and testing facility

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

100 The study was conducted in a facility developed by J.F., where baboons have free access to
101 computerized testing booths that are installed in trailers next to their outdoor enclosure [for
102 further information see 34, 35-37].

103 2.1.2 Computer-based tasks

104 Each trial began with the display of a grid made of 16 squares, 12 white and 4 green (see
105 ESM video 1). Touching the display triggered the immediate abortion of the trial and the
106 display of a green screen for 3 s (time-out). After 400 ms all the green squares became white
107 and, in order to obtain a food reward, the monkey had to select and touch four squares in
108 this matrix which had not previously been highlighted in green. Touching these four squares
109 could be done in any order and with less than 5 s between touches. Squares became black
110 when touched to avoid being touched again and did not respond to subsequent touches. A
111 trial was completed when 4 different squares had been touched. If four correct squares
112 were touched, the trial was considered a success and the computer triggered the delivery of

113 3-4 wheat grains; otherwise, the trial was considered a failure and a green time-out screen
114 appeared for 3 s.

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

119 2.1.3 Training to criterion

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

127 2.1.4 Between-individuals transmission procedure

128 We followed the transmission procedure described in [26] and therefore only report the
129 main elements here. Testing began when all 12 monkeys reached the learning criterion with
130 4 green squares and 12 white squares randomly placed on the grid. For each transmission
131 chain, a first baboon was randomly selected, and this subject received a first block of 50
132 transmission trials consisting of randomly-generated patterns. The squares touched by the
133 first individual in responding on a given trial, whether they were correct or not, were then
134 used as green squares on that trial for the next individual in the chain. The 50 transmission

135 trials were randomly reordered in a new block of 50 trials that became the set of patterns
136 shown to the next individual in that chain.

137 When the individuals were not involved in the transmission chain, they could perform
138 random trials that were generated automatically by the computer and were not part of the
139 transmission process. We ran 9 such chains with a total of 10 generations (i.e., 10 individuals
140 in each chain), each initialised with a different set of randomly-generated trials. We also
141 made sure that each baboon did not appear more than once in each chain and performed at
142 least 500 random trials between sets of transmission trials to avoid interference between
143 chains (the order of the baboons in each chain was determined opportunistically). In our
144 analyses, the last 50 responses recorded in this set of 500 random trials were compared to
145 those obtained in the transmission chain, to infer the effects of cumulative culture. A
146 minimum of 450 random trials therefore separated the responses to transmission trials
147 from the responses to the random trials used in our analysis.

148 2.2 **Methods specific to children**

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

151 2.2.1 Participants and materials

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

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

159 2.2.2 Procedure: iPad-based tasks

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

173 2.2.3 Between-individuals transmission procedure

174 The transmission procedure was exactly as described in section 2.1.4 for the baboon's
175 version, with the only difference being the size of the testing/transmission set, which is 20

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.

176 trials in this version instead of 50. We ran nine transmission chains with a total of 10
177 generations each chain was initialised with a different set of randomly-generated trials.

178 **2.3 Ethics statement**

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

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

187 **2.4 Statistical analysis**

188 The aim of our analysis was to evaluate the strength of the evidence for cumulative culture
189 considering the three criteria highlighted in [26], that is, to test (i) a progressive increase in
190 performance, (ii) the emergence of systematic structure, and (iii) the presence of lineage
191 specificity. To this aim, we first analysed the data from baboons comparing transmission
192 versus random trials and later we analysed the data from transmission trials in children and
193 baboons.

194 **2.4.1 Analysis restricted to the baboon data**

195 We followed the procedure used in [26] to analyse the results and ran mixed-effects
196 regression models using the lme4 package developed in R [38, 39] The type of model (linear

197 or logistic) will vary according to the dependent variable². All models contain a fixed effect
198 of Generation (continuous variable with the 10 generations, ranging from 0 to 9) and a fixed
199 effect for Trial Type (two levels: transmission as the baseline, and random trials; 50 trials
200 each)³ with an interaction term between them. To control for the non-independence within
201 a given chain, models contain random intercepts for Subjects and Chain as well as by-
202 Subject random slopes for the effect of trial type, and by-Chain slopes for the effect of
203 Generation.

204 2.4.2 Cross-species analysis between baboons and children

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

211 3. Results

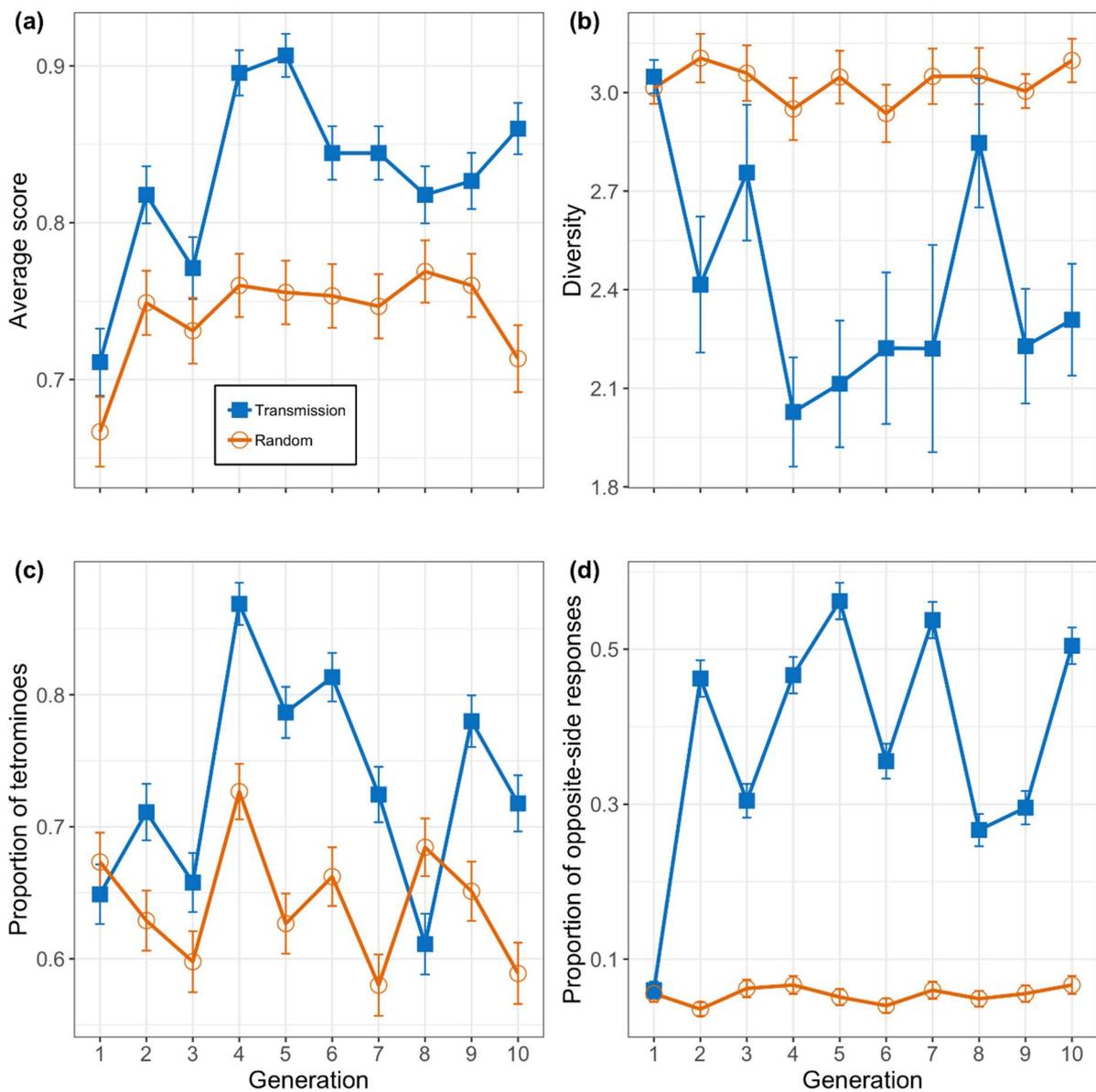
212 3.1 Is cumulative cultural evolution possible without copying in baboons?

213 **Increase in performance.** We found a progressive increase in performance over generations
214 in transmission chains with baboons (see Figure 1a). Using a dependent binary variable
215 determining the success or failure for each trial, the results of the logistic regression model

² For linear regression models, we obtained p-values using the lmerTest package where p-values are calculated based on Satterthwaite's approximation for degrees of freedom. For logistic models, we followed the standard practice and obtained p-values based on asymptotic Wald tests.

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.

216 suggest that the proportion of successful trials increases significantly with generation in
 217 transmission trials ($\beta = 0.0654$, $SE = 0.026$, $z = 2.466$, $p = 0.014$) and that it does so
 218 significantly less in random trials ($\beta = -0.05$, $SE = 0.019$, $z = -2.580$, $p = 0.01$). This difference
 219 in the increase in performance over time between trial types reveals a clear benefit of
 220 cultural transmission.



221

222 Figure 1: Results from transmission and random trials in baboons, depicted by blue squares and orange circles

223 respectively. (a) Average score defined by the proportion of successful trials; (b) average Shannon's diversity

224 index within the set of responses; (c) average proportion of tetrominoes produced; and (d) average increase in
225 opposite-side responses. Error bars represent standard errors.

226

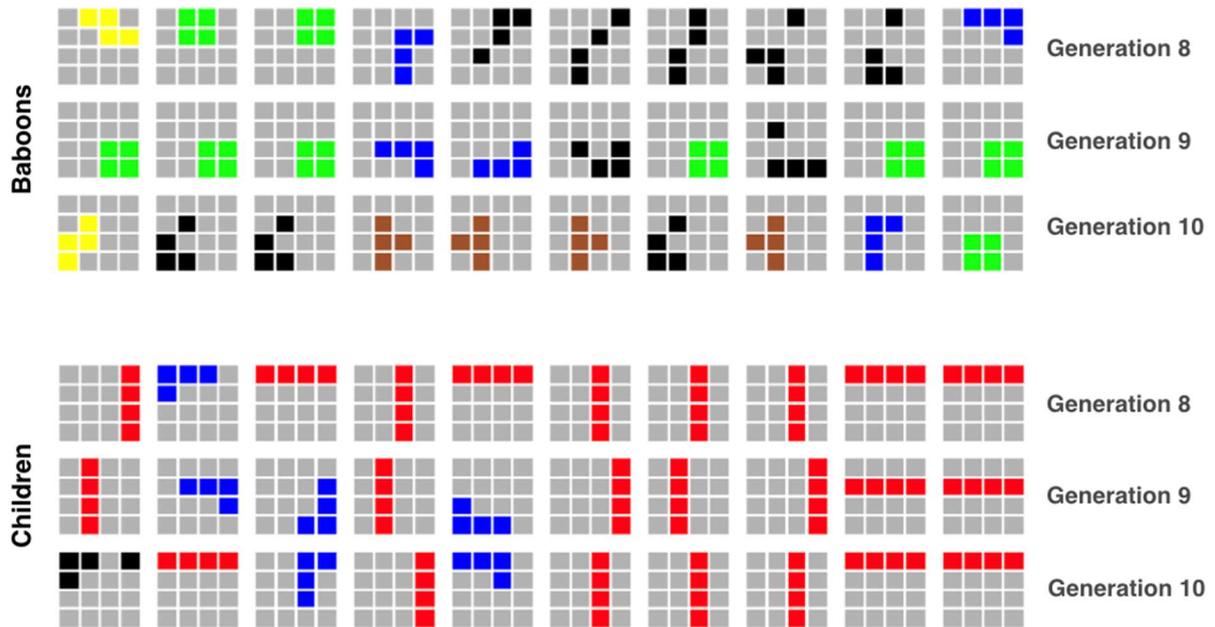
227 **Emergence of systematic structure.** One indicator of the emergence of structure is a
228 progressive decrease in response diversity due to a focus on a subset of responses. We
229 observed a reduction of diversity among sets of grids during transmission trials compared to
230 random trials (Figure 1b). A linear mixed effects model with the Shannon diversity index
231 (equal to Shannon entropy, [40]) as the dependent variable suggests marginally significant
232 reduction in diversity over generations in transmission trials ($\beta = -0.036$, $SE = 0.018$, $t =$
233 -2.031 , $p = 0.047$) and no strong evidence for a different trajectory in random trials ($\beta =$
234 0.038 , $SE = 0.022$, $t = 1.679$, $p = 0.095$). This linear model fails to capture the sharp decrease
235 in diversity between generations 1 and 2 and predicts a much lower diversity value for
236 generation 1 in transmission trials ($\beta = 2.64$) than the one observed in Fig 1b (>3).
237 Consequently, the difference in the overall diversity observed in Fig 1b from generation 2
238 onwards is captured by the effect of Trial Type ($\beta = 0.394$, $SE = 0.136$, $t = 2.890$, $p = 0.006$),
239 suggesting that diversity is significantly higher in random trials than in transmission trials
240 overall.

241 To explore the type of structures that emerged during transmission and which might guide
242 the observed decrease in diversity, we looked at the main structures found in [26], that is,
243 tetrominoes (grids where all four squares are connected—lines, squares, L-shapes, T-shapes,
244 S-shapes; tetrominoes will be familiar to anyone who has played Tetris). Figure 1c shows the
245 proportion of tetrominoes produced over generations. The results from a logistic mixed
246 regression model with a binary dependent variable representing the presence or absence of

247 a tetromino suggest that baboons have a significant tendency to produce tetrominoes,
248 similar across random and transmission trials (intercept, $\beta = 1.01$, $SE = 0.217$, $z = 4.675$, $p <$
249 0.001 ; trial type, $\beta = -0.308$, $SE = 0.194$, $z = -1.59$, $p = 0.112$). However, we found that the
250 proportion of tetrominoes did not change over generations in either random ($\beta = 0.014$, $SE =$
251 0.018 , $z = 0.817$, $p = 0.414$) or transmission trials ($\beta = -0.027$, $SE = 0.017$, $z = -1.586$,
252 $p=0.113$).

253 Further inspection of the response strategies suggested a spatial alternation of the
254 responses (from one side of the response grid to the opposite side) between subsequent
255 generations in transmission chains (see Figure 2). To quantify this, we created a binary
256 variable that indicated if the position of the response was in a part of the screen that was
257 opposite to that of the stimulus. We divided the screen into four quadrants: right half, left
258 half, top half and bottom half. If the stimulus and the response were in different quadrants
259 (left vs right or top vs bottom), we coded them as opposite-side responses (only responses
260 that were entirely in one quadrant were considered). Figure 1d shows the number of
261 opposite-side responses increases sharply during the first generation and remains high
262 compared to random trials. Results from the logistic regression model suggest that the
263 percentage of opposite-side responses marginally increases over generations in
264 transmission trials ($\beta = 0.068$, $SE = 0.037$, $z = 1.826$, $p = 0.069$) and not in random trials ($\beta =$
265 -0.071 , $SE = 0.027$, $z = -2.648$, $p = 0.008$). Thus although the linear model fails to capture
266 the sharp increase in the first generation and provides weak evidence of an increase in the
267 proportion of opposite-side responses over generations in transmission trials, it provides
268 stronger evidence against such increase in random trials. Moreover, the model captures a
269 significantly lower proportion of opposite-side responses in random trials than in

270 transmission trials ($\beta = -2.034$, $SE = 0.22$, $z = -9.238$, $p < 0.001$), further confirming the
 271 difference observed in Figure 1d from generation 2 onwards.



272
 273 Figure 2: Baboon's and children's example responses (extracted from their corresponding Chain 5). Rows
 274 correspond to generations 8 to 10 (from top to bottom), each row contains 10 example grids. Colouring of
 275 each grid reflects the tetromino class each pattern comes from (red for lines, green for squares, blue for L-
 276 shapes, brown for t-shapes, yellow for s-shapes, black for non-tetrominoes).

277 **Presence of lineage specificity.** If responses are indeed dependent on those of previous
 278 generations within a given chain and independent between chains, we expect different
 279 transmission chains, or lineages, to develop different responses. For instance, one chain
 280 might converge on alternating between top and bottom responses when another might use
 281 left vs. right, or one chain might contain more S-shapes and another more T-shapes. In order
 282 to assess the presence of lineage-specific systems and its potential effect on the baboons'
 283 performance, we conducted a follow up study in which we tested baboons' performance on
 284 trials from the 10th generations of the nine chains (this additional experiment is presented in

285 detail in the ESM). In one condition the test sets were unmodified (all the trials within a set
286 belonged to the same chain), in another condition they were randomly pooled from
287 different chains. If there is lineage specificity, we expect the baboons to perform better on
288 the unmodified sets than the randomly pooled sets.

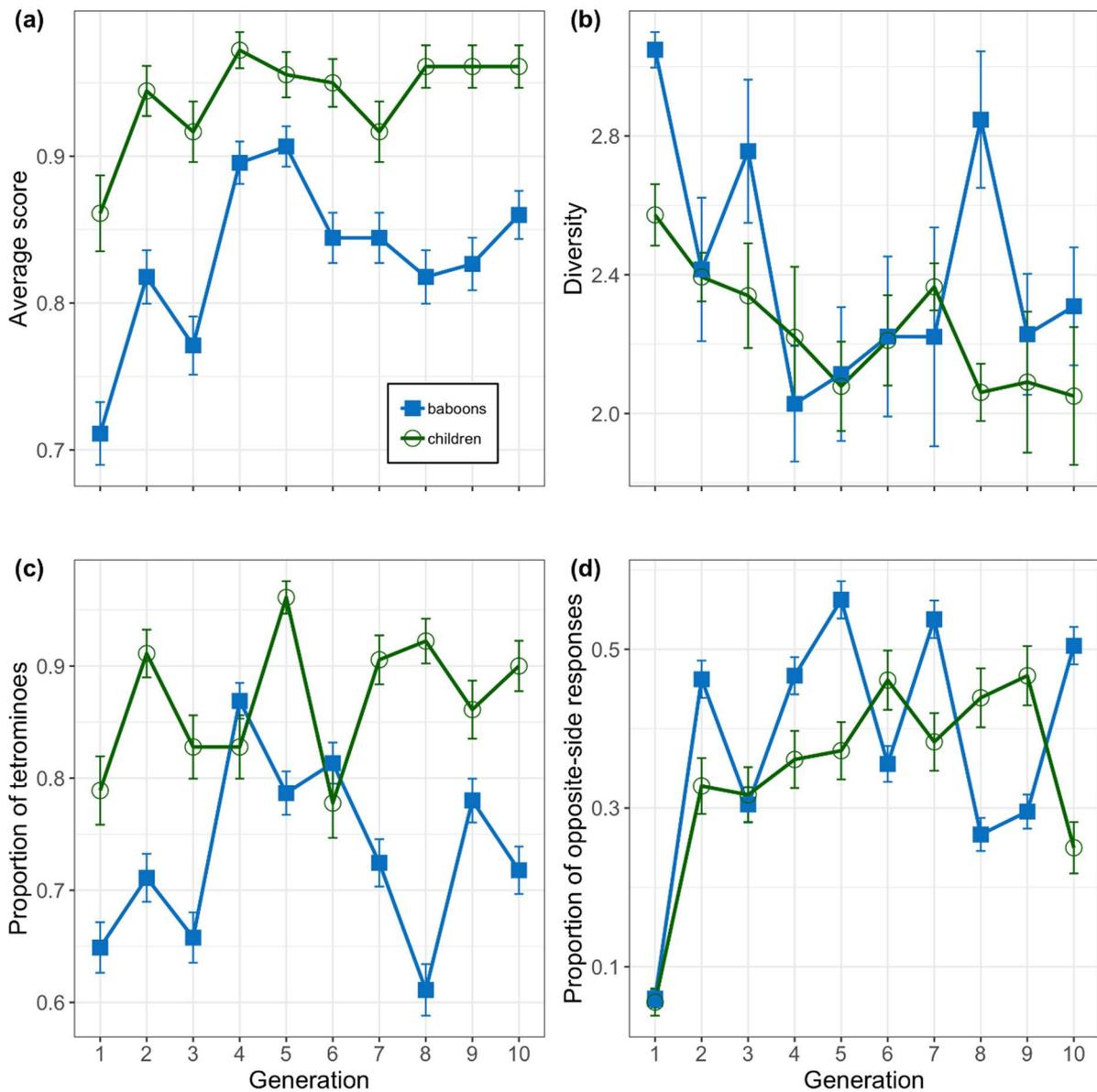
289 As expected, baboons were more successful in the unmodified set condition ($\beta = 0.18$, SE =
290 0.79, $z = 2.28$, $p = 0.022$; details provided in the ESM). Importantly, the divergence between
291 lineages is not solely due to differences in response position but also to differences in shape
292 distributions (see ESM).

293 To summarise the baboons' results, we found the three distinctive properties of CCE
294 outlined above: an increase in score, the emergence of systematic structure in the response
295 set and the presence of lineage specificity. These results are also in line with the core
296 criteria for CCE outlined by [32]; in this non-copying task, we observe a repeated cycle of
297 changes in behaviour that improve performance as they are transmitted to other
298 individuals. We now turn to compare these results with those obtained in the experimental
299 version with children.

300 **3.2 Are the trends in CCE without copying similar across children and baboons?**

301 A visual inspection of the data obtained from the transmission chain experiments with
302 children reveals strikingly similar tendencies to those found in baboons (see Figure 3). Using
303 the analyses described in section 2.4.2, we found a clear increase in task performance over
304 generations ($\beta = 0.124$, SE = 0.045, $z = 2.719$, $p = 0.007$), a significant decrease in the
305 diversity of the sets of responses ($\beta = -0.046$, SE = 0.019, $t = -2.433$, $p = 0.016$), a stable high
306 proportion of tetrominoes over generations (intercept: $\beta = 1.717$, SE = 0.246, $z = 6.979$, $p <$
307 0.001; generation: $\beta = 0.059$, SE = 0.048, $z = 1.249$, $p = 0.212$) and a significant increase in

308 the (overall high) proportion of opposite-side responses (intercept, $\beta = -1.149$, $SE = 0.225$, z
309 $= -5.117$, $p < 0.001$; generation, $\beta = 0.102$, $SE = 0.04$, $z = 2.538$, $p = 0.011$). The analyses
310 further suggest no difference in the effect of Generation across species in all these
311 tendencies; we did not find a single significant interaction between Generation and Primate
312 Species (score, $z = -0.924$, $p = 0.355$; diversity, $t = 0.186$, $p = 0.853$; tetrominoes, $z = -0.636$,
313 $p = 0.525$; opposite-side responses, $z = -0.565$, $p = 0.572$). However, we found differences
314 across species in overall score as well as in the overall production of tetrominoes: baboons
315 scored lower ($\beta = -0.962$, $SE = 0.250$, $z = -3.844$, $p < 0.001$) and produced less tetrominoes
316 than children ($\beta = -0.748$, $SE = 0.328$, $z = -2.277$, $p = 0.023$), confirming the differences
317 observed in Figures 3a and 3c respectively. Results therefore suggest that the general
318 tendencies found in children are very similar to those found in baboons.



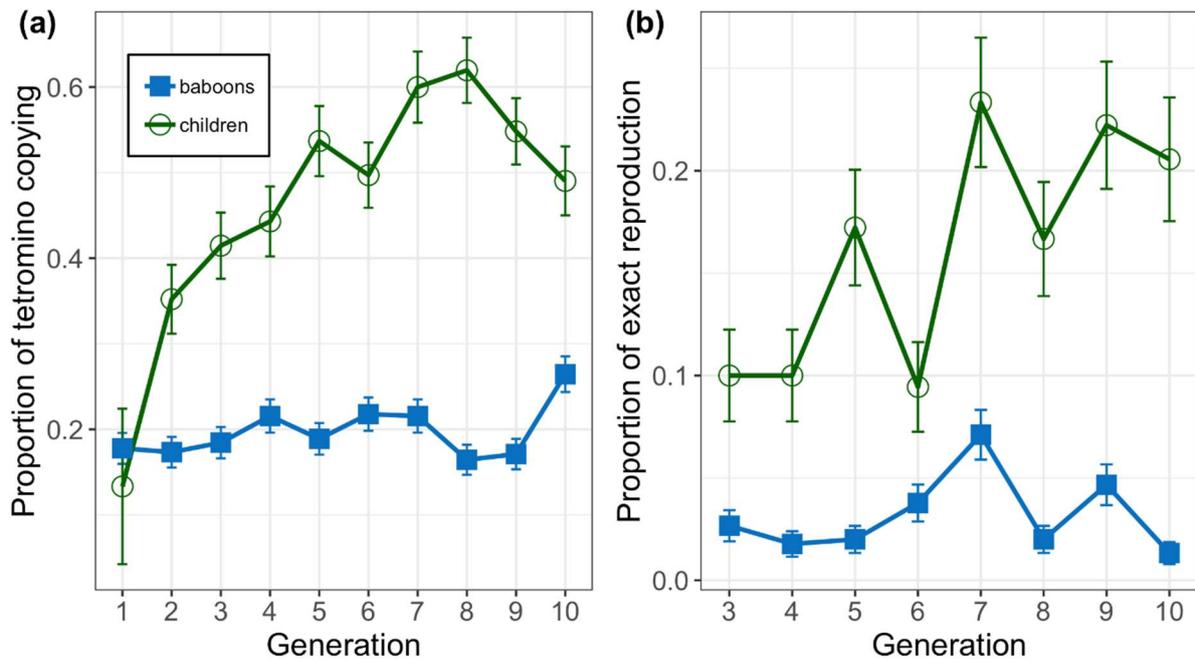
319

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

324 However, the inspection of the specific patterns produced (see e.g. Figure 2) suggested that
 325 children tended to copy the overall shape of the response of the previous individual but
 326 shifted its position to avoid direct copying of the observed pattern—which was possible
 327 because the non-copying task only prevented them from copying both shape and location of

328 the input patterns. Figure 4a shows the proportion of input tetrominoes whose shape was
329 copied (in a different location) in the response, and Figure 4b shows the proportion of trials
330 in which the tetromino produced at a given generation is the exact re-production (shares
331 the same shape and location) of the one produced two generations ago in the same chain.
332 We observe that while baboons tend not to copy the overall shape of input tetrominoes in
333 their responses, children seem to do so increasingly over generations. A logistic mixed-
334 effects model confirms that children copy input tetrominoes increasingly over generations
335 ($\beta = 0.099$, $SE = 0.025$, $z = 3.923$, $p < 0.001$) and significantly more than baboons (as
336 suggested by the interaction between Generation and Primate Species, $\beta = -0.082$, $SE =$
337 0.034 , $z = -2.374$, $p = 0.018$). Another model further confirms that the proportion of re-
338 production of the exact same response as the one produced two generation ago also
339 increased in children ($\beta = 0.099$, $SE = 0.030$, $z = 3.282$, $p = 0.001$), and significantly more than
340 in baboons ($\beta = -0.042$, $SE = 0.035$, $z = -2.371$, $p = 0.018$).

341



342

343 Figure 4. (a) Average proportion of tetriminoes that are copied from one generation to the next. (b)

344 proportion of responses that are identical between every other generation.

345 We further explored the difference in tetrimino copying between children and baboons by

346 examining specific tetrimino shapes, because the inspection of the patterns produced also

347 suggested that children tended to produce many lines and that they copied them more so

348 than any other pattern. An inspection of the average number of tetriminoes produced as

349 well as the proportion of tetrimino-copying subset by each of the five possible tetrimino

350 shapes (see ESM) reveals a clear preference for lines over other tetriminoes in children. A

351 logistic mixed-effects regression model (detailed in the ESM) show that lines are the most

352 copied tetriminoes ($\beta = 0.803$, $SE = 0.206$, $z = 3.905$, $p < 0.001$; the smallest difference is

353 shown with square tetriminoes: $\beta = -1.342$, $SE = 0.316$, $z = -4.250$, $p < 0.001$) but that this

354 tendency to copy lines does not increase over time ($\beta = -0.012$, $SE = 0.036$, $z = 0.324$, $p <$

355 0.001). Nonetheless, a further logistic mixed-effects model excluding line tetriminoes (see

356 ESM) suggests that this constant tendency to copy lines is not the sole driver of the effect of

357 generation on the overall proportion of copied tetrominoes; children still copy the shape of
358 other input tetrominoes increasingly over generations

359 **4. Discussion**

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

365 The purpose of this study was to test this fundamental hypothesis by examining the
366 possibility of finding essential properties of CCE with what was set up as a non-copying task.
367 We used a cultural transmission task similar to the copying task used in [26] but in which the
368 participants had to avoid what was produced by the previous individual in the chain. The
369 results from the transmission chain experiments with baboons exhibited all three
370 fundamental properties of CCE examined: (i) an increase in score linked to (ii) the
371 emergence of some type of systematic structure, and (iii) lineage specificity. Despite the
372 presence of a large evolutionary space (1820 possible responses) and a 27% chance of being
373 correct by chance, we found the emergence of systematic responses alternating in position
374 from one side of the response grid to another. The results from baboons thus show that the
375 three fundamental properties of CCE examined are possible without copying.

376 Next, we aimed at testing the generalisability of our results to children. Interestingly,
377 children's results were very similar to the baboons' regarding CCE: we also found an
378 increase in score linked to the emergence of systematic structures. However, unlike the
379 baboons, children introduced copying mechanisms into the non-copying task by copying the

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

385 The observed copying strategy could be in line with children's tendency to high-fidelity copy
386 even when not required in the task [41, 42]. Complementarily, it could also be partly
387 explained by the fact that children, unlike baboons, only saw grids of two and four squares
388 during training before the target grid of 16, and in these grids, the rewarded output is
389 necessarily the mirror image of the input. However, we only observe high-fidelity copying of
390 specific shapes (i.e., tetrominoes), which are potentially already preferred by children
391 because they are easier to produce and/or remember than more scattered grid patterns
392 (80% of responses are tetrominoes the first generation of child chains). Once these
393 preferred shapes are in the system, they are maintained. Results thus suggest that the
394 observed bias is not solely a copying bias, but a bias towards tetromino shapes which results
395 in a behaviour that can appear as high-fidelity copying once these patterns are introduced.
396 Further support for this conclusion comes from the lack of lineage specificity in children's
397 results, which reveals a shared prior bias in children's performance: all transmission chains
398 converge on the same behaviour, constituted mainly of tetromino responses, and in
399 particular of lines.

400 However, in spite of the large number of lines, we also found evidence of an increase in a
401 general tendency to copy, suggesting that the more the systems became structured, the
402 more likely specific structures were to be copied (Figure 4a).

403 The fact that the children copied the pattern they saw while at the same trying to avoid its
404 location created a remarkable situation in which the responses of the individuals separated
405 by one generation became more likely to be exactly the same (both in shape and position;
406 Figure 4b). A tendency to avoid what the previous individual did may be conceived as a re-
407 production of behaviour over two steps when the number of possible behaviours is limited,
408 an interesting illustration of the theoretical example of re-construction given in [33].

409 Social learning is usually defined as a broad notion that encompasses any form of
410 transmission of information between individuals (Heyes 1994); however, studies of social
411 learning tend to focus on the observational learning of technological problems. Our study
412 broadens the experimental perspective on social learning and CCE in several ways. Firstly,
413 we focus on the tendency to avoid doing what others have done before, a clear but
414 understudied case of social learning. Furthermore, our experiment lacks observational
415 learning because it is based on the indirect transmission of visual patterns through a
416 network of computers, a common feature of human social learning. Lastly, individuals in our
417 task are trying to best respond to each other's inputs, rather than acting collectively improve
418 an artefact.. From that perspective our results also speak to the relationship between CCE
419 and collective intelligence, which also suggests that repeated interactions among individuals
420 can improve group performance without the need for copying [43].

421 Finally, the purpose of this experiment was to address a theoretical question concerning the
422 possibility of observing defining properties of CCE with a non-copying task, not to assess the
423 importance or relevance of this phenomenon in nature. Nevertheless, are there natural
424 examples of the type of transmission studied here? In animals, for example, when resources
425 are scarce, the observation of others going to a (e.g., food or nesting) patch could promote

426 the search of a different patch. In humans specifically, there is an often-explicit search for
427 innovation, for instance in art and science. In conclusion, our results suggest that CCE does
428 not necessarily depend on high-fidelity copying and that there is a broad spectrum of
429 possible transmission mechanisms that will lead to CCE; these mechanisms that are not
430 based solely, or even mainly, on indiscriminate high-fidelity copying remain to be further
431 explored.

432 **5. Data Accessibility**

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

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

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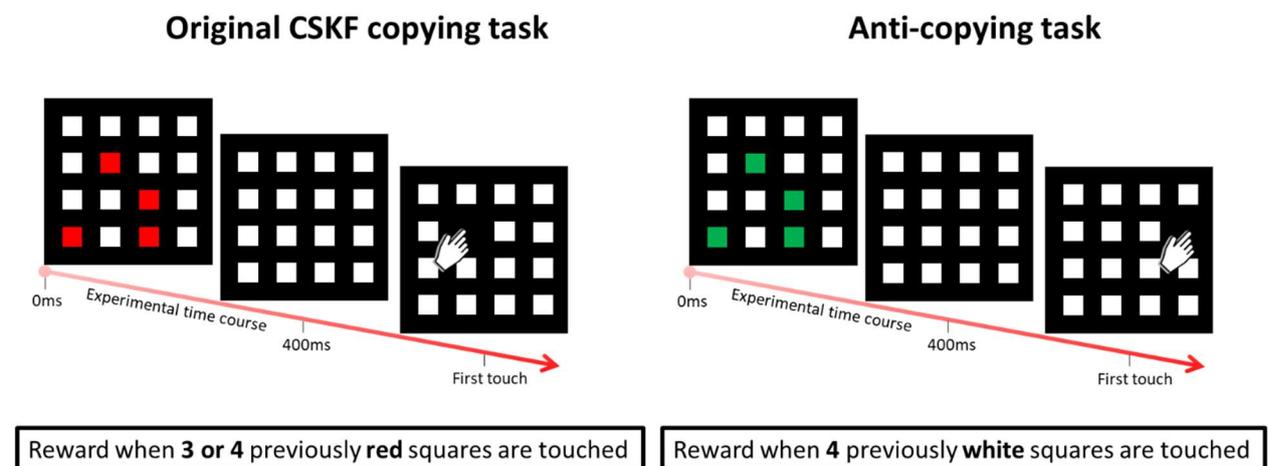
High-fidelity copying is not necessarily the key to cumulative cultural evolution: a study in monkeys and children

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Supplementary material A:

Comparison of the copying and anti-copying tasks

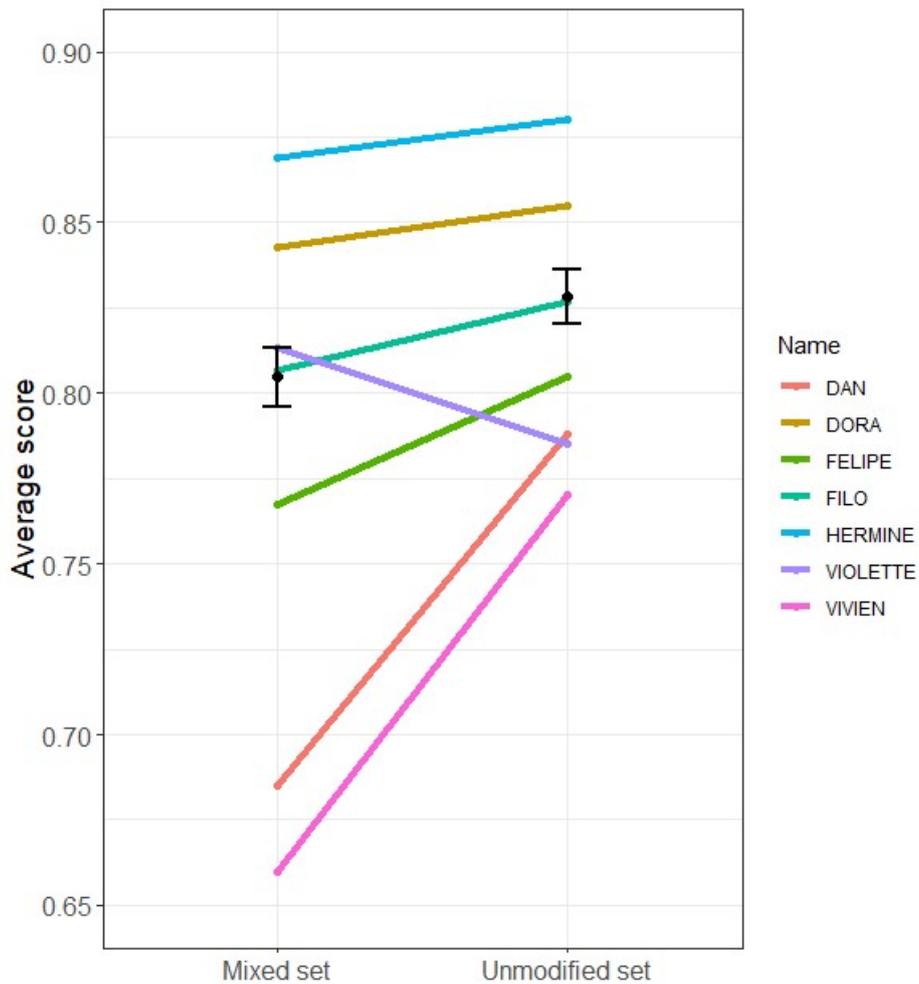


Supplementary Figure A1: From left to right: experimental designs of the copying task used in Claidière, Smith, Kirby, and Fagot (2014) and the non-copying task used here.

Supplementary material B:

Test of lineage specificity in baboons

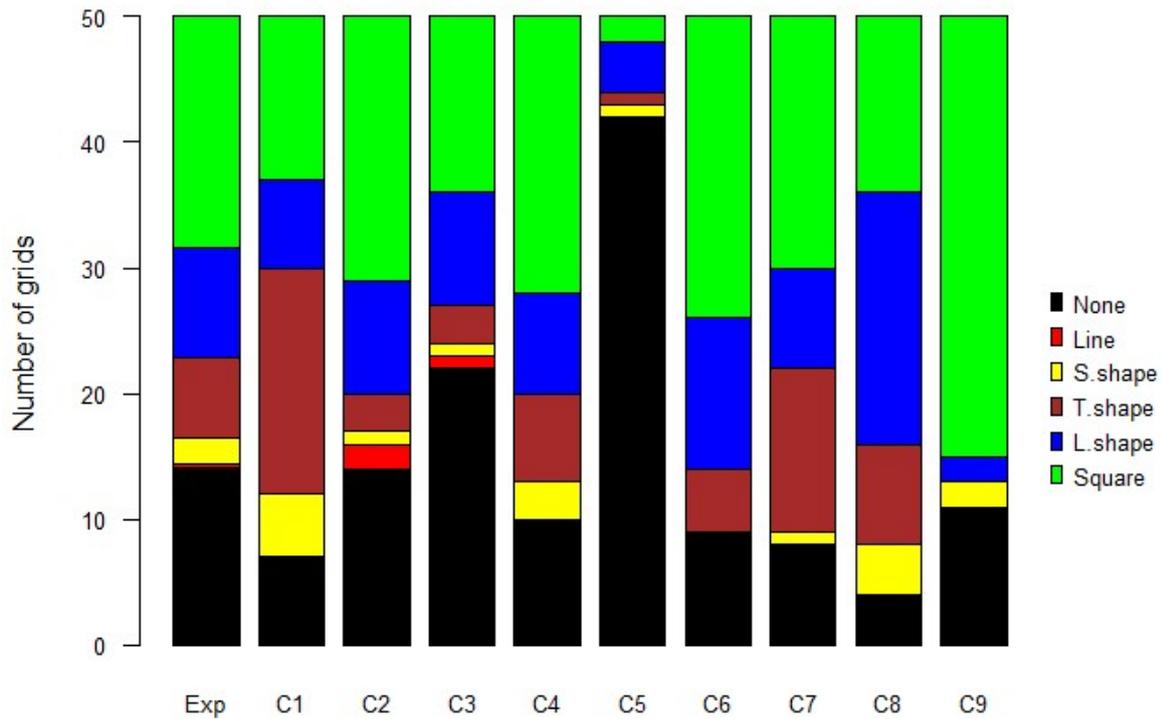
After having performed the nine transmission chains described in the main text, we conducted an experimental test of lineage specificity borrowed from Cornish, Smith & Kirby (2013) to assess the divergence between the transmission chains. Based on Claidière et al (2014), we expected that CCE would produce systematicity because the set of 50 grids that were transmitted together should tend to collectively adapt to the task (e.g. by exploiting similar patterns or using similar regions of the grid), but that independent chains should converge to different solutions (i.e. each chain will constitute an independent and distinct lineage). This allowed us to experimentally test for lineage-specificity and systematicity, by comparing the baboons' performance on sets of grids that evolved within a single chain of transmission to their performance on artificially-constructed sets of grids created by intermingling grids drawn from the last generation of several independent chains of transmission. Specifically, we used the test trials of the last generation of each chain to compare the baboons' performance when exposed to unmodified sets of test trials and sets made of a recombination of test trials from different chains. 'Natural' sets of grids which had evolved together should be systematically related and therefore easier for the baboons; artificial sets constructed by mixing grids from different chains should lack systematicity due to their independence from each other and therefore should be harder for the baboons.



Supplementary Figure B1: Test of lineage specificity with the results at the averaged group level (black dots) and at the level of the individuals. Error bars represent the standard error.

Supplementary Figure B1 shows that, as expected, baboons were more successful in the unmodified set condition compared to the randomly mixed set; this seems to be the case at the group and individual levels for all but one baboon (i.e., Violette). We used a logistic mixed-effects regression model with trial success as dependent variable to test the significance of the difference between these two conditions. The model included Condition (mixed vs. unmodified) as a fixed effect and random intercepts for Subject as well as by-Subject random slopes for the effect of condition order. Results from the model suggest a significant difference between conditions: the odds of success were an estimated 18.7%

higher in the unmodified sets compared to the mixed sets ($\beta = 0.172$, s.e. = 0.079, $z = 2.161$, $p = 0.031$).



Supplementary Figure B2: Lineage specific set of tetrominoes. Distribution of the different grid types in the 9 chains at generation 10 and expected distribution obtained by collapsing across chains at this generation (Exp).

To further test for the presence of lineage specificity, we explored the cross-lineage divergence between the systems with regard to the grid types they contained.

Supplementary Figure B2 shows a substantial diversity in the distribution of the different grid types between chains. We compared the distribution of the six grid types (T-shape, L-shape, S-shape, line and square tetrominoes as well as non-tetrominoes) at generation 10 in each chain to an expected distribution obtained by collapsing all the systems across all 9 chains at generation 10. Under the null hypothesis, we would expect individual chains to

look like draws from this expected distribution (Supplementary Figure 2B). Three chains showed a significant degree of lineage specificity (chain 1: $\chi^2=31.05$, $p=0.002$; chain 2: $\chi^2=11.07$, $p=0.14$; chain 3: $\chi^2=9.11$, $p=0.20$; chain 4: $\chi^2=2.88$, $p=0.71$; chain 5: $\chi^2=77.70$, $p<0.001$; chain 6: $\chi^2=7.44$, $p=0.23$; chain 7: $\chi^2=2.88$, $p=0.71$; chain 8: $\chi^2=77.70$, $p<0.001$; chain 9: $\chi^2=7.44$, $p=0.23$; all p-values calculated by simulation with Benjamini–Hochberg correction for multiple comparisons).

Supplementary materials C:

Tetromino copying by tetromino type

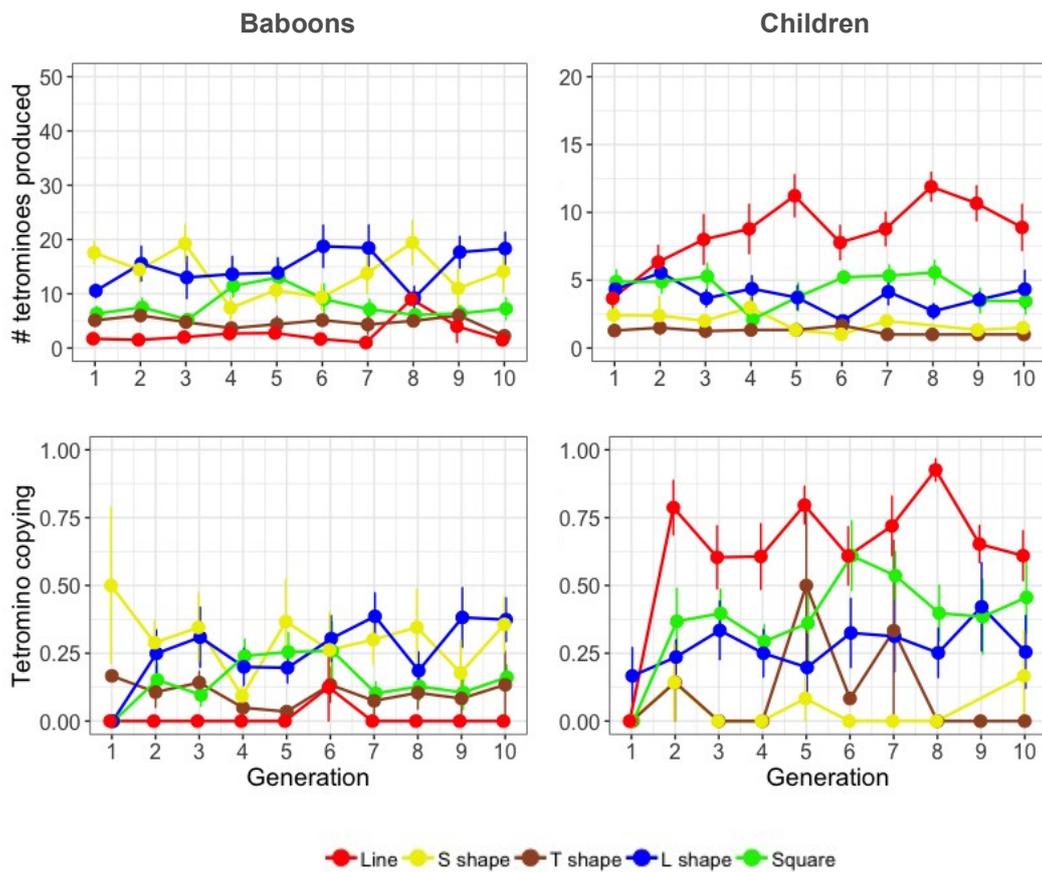


Figure C1: Top row: Average number of tetrominoes produced in children and baboons by tetromino shape (over 20 and 50 trials respectively). Bottom row: Average proportion of tetrominoes that are copied from one generation to the next by shape.

Supplementary Figure C1 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 Supplementary Figure C1 reveals a clear preference for lines over other tetrominoes in children but no specific preference in baboons. Moreover, lines are the only pattern that shows an increase in production over time in children. We ran a logistic mixed-effects regression model to test whether the observed increase in the production of lines over generations in children could be accompanied by an increase in tetromino-copying specific to lines. Our model's DV was whether or not the output tetromino type matched the input. We included fixed effects for Generation and Tetromino Type, random intercepts for Chain and by-Chain slopes for the effect of Generation. As reported in the main text, results show that lines are the most copied tetrominoes ($\beta = 0.803$, s.e. = 0.206, $z = 3.905$, $p < 0.001$; the smallest difference is shown with square tetrominoes: $\beta = -1.342$, s.e. = 0.316, $z = -4.250$, $p < 0.001$) but that this tendency to copy lines does not increase over time ($\beta = -0.012$, s.e. = 0.036, $z = -0.324$, $p = 0.746$). 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 of the number of lines over time as new ones are introduced. Nonetheless, a further logistic mixed-effects model excluding lines (and also excluding random slopes to avoid a singular model fit) 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 ($\beta = 0.009$, s.e. = 0.003, $z = 2.921$, $p = 0.003$), and marginally more so than baboons ($\beta = -0.007$, s.e. = 0.035, $z = -1.903$, $p = 0.057$).

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