Exploring the Emergence of Organized Colouration in Paintings Through Cultural Transmission

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Abstract.

Painting and drawing are symbolic representations that visually transform natural scenes into line and colour expressions. These artworks undergo a series of modifications when transmitted between individuals/communities, known as *cultural transmission*. The dynamics of cultural transmissions has been investigated experimentally, revealing structured linguistic and musical expressions as their outcomes. Cultural transmissions have also been modelled mathematically, proving a strong influence from a prior knowledge of transmitters. Here, we investigate an emergence of structured colour expression in painting via cultural transmission. We experimentally transmitted colouring books, wherein the participants memorised and reproduced the colour patterns of the book they saw; then, their response was presented as the memorization target for other participants. We expected the outcome of these transmissions represents the prior knowledge about the colour perception of the objects of the colouring books. Our results revealed a certain type of structuring in the last generation of the transmissions, indicated by the consistent use of fewer colours for recognizable segments/objects, compared to the random patterns in the first generation. However, naturalistic colour patterns (e.g. green for leaves) were observed only in some of the transmission chains. These results suggest that, like language and music, colour representations become structured during cultural transmission.

Keywords: paintings; cultural transmission; cultural evolution;

1. Introduction

Painting and drawing are products of higher cognitive functions that are unique to humans [1] and have been attested cross-culturally, just like language and music. Psychologically, painting and drawing represent humans' cognitive properties regarding visual-information processing and their symbolization of the visual world [2]. That is, a painting is not a simple reproduction of the visually perceived world—recovering features such as colours, luminance, or structural patterns—but is rather influenced by symbolic/categorical perceptions of objects and/or backgrounds. Moreover, paintings have been utilized as a means of conveying information across generations and between cultures in a symbolic way, similarly to written languages. For example, the paintings left by early human, possibly including Neanderthals, are considered to be a trace of primitive symbolic communication in cognitive archaeology [3,4]; they utilized colours and line patterns to symbolize observed information and communicate it among individuals.

Accordingly, unveiling how symbolic communication emerged in a particular culture and also finding cross-culturally general patterns in such emergence is of a major interest in the study of cultural evolution [5,6]. In the past two decades, researchers have explored possible accounts for the emergence of such symbolic communication systems under the experimental paradigm of *cultural transmission* [7–10]. In the experiment, participants play "the game of telephone"; they are ordered sequentially and instructed to memorize what their preceding participant say/show and convey it to the next participant as it is heard/seen. For example, participants may be asked to pass on some random text words/sentences via its reading and writing [7–10], or some rhythmic sound pattern by hearing and tapping [11–14]. The key idea behind this experimental design is that the carried signal is transformed through the transmissions between the participants, and this transformation has mathematically proved to be directed to cognitive biases of participants, or what they believed to be likely prior to observing the presented signal (under the assumption of Bayesian inference model [15]). Thus, the transmission of initially random texts and rhythms can result in an organized artificial language and musical pattern, respectively [7,12]. This offers a possible account for the emergence of symbolic communication systems; even a highly descriptive observation of a world, exemplified by a realistic painting, is eventually formatted into a symbolic representation by cultural transmission together with the underlying cognitive bias towards categorical perception.

As already reviewed, paintings and drawings, like language and music, serve as a means of symbolic communication. Accordingly, we would expect that some structured patterns could emerge in the process of visual perception, reproduction, and transmission of paintings/drawings between individuals, reflecting their prior knowledge or bias. For instance, humans are supposed to share some belief about the canonical colours on the objects drawn in a painting—like "a rose is red" and "a leaf is green"—based on their previous experiences. Such prior knowledge about objects' colour can override or complement our physical sensing and modify our recognition of the colour [16–20]. For instance, a banana drawn in grayscale is perceived slightly yellowish by an observer (called *memory colour effect* [16,19]).

In the previous studies of cultural transmission, researchers have focused on the development of *shapes* in drawings. Indeed, the first experimental study dates back to 1932, when Frederick Bartlett [21] demonstrated an emergence of drawing. Just as in the modern paradigm, he initially prepared an "unrecognizable" instance of an Egyptian Hieroglyph, and then instructed the participants to memorize and reproduce it, serially serving the stimulus for the next generation. Consequently, the drawing by the participants "evolved" to an owl or a black cat. Moreover, Bartlett also shared the modern interpretation of this result; humans are strongly biased towards their own cultural expectations when reconstructing information from memory, and this memory or cognitive bias emerged in drawings due to the exaggerated consequences of serial reproduction. Consistent results were reported in recent studies as well [22]; transmission of drawings converged to simplified/structured patterns, presumably reflecting the prior knowledge or belief of participants. These findings support the argument that symbolic systems can emerge in transmission of paintings under a perceptual bias of humans.

Despite the rich history of investigation on the emergence of *shape* patterns in the literature, however, little exploration was made into cultural transmission of *colours* as a pictorial expression. Here, we experimentally investigated whether the structured colouration could emerge in a cultural transmission of paintings. Specifically, we utilized a "colouring book", containing line drawings with multiple colour-fillable areas, and instructed participants to memorize a sample colouring pattern and reproduce that pattern as precisely as possible in a limited time. The reproduced paintings were transmitted to other participants (in the next generation) following the paradigm of the previous cultural transmission experiments. We recorded and analysed the evolution of the colours used in the participants' paintings.

Prior to the conduction of the experiment, we expected three main results. First, due to the memory colour effect, naturalistic colouring patterns, seen on real objects, were thought to emerge in the consequence of the transmission. Second, each categorically recognized segment of objects in the drawings—such as petals and leaves of flowers—would be painted with a single or few, consistent colour(s); consequently, we expected uneven use of colour types (i.e. dominance of a few colours in the entire colouring book). Finally, fewer transmission errors would occur in later iterations, due to the emergence of organized—thus more easily memorable—patterns as expected in the second.

2. Materials and methods

2.1 Participants

We recruited 117 university students (age range 18-31, mean age 20.64) as participants in the experiment. Seventeen of them did not follow the instruction of the experiment (specifically, they put more than one colour within a single colouring area), and accordingly, they were excluded from the analysis. This left the data from 100 participants, who were grouped and ordered into ten chains, each consisting of ten participants. The ten chains were further categorized into two groups and presented with different stimuli as will be explained in the next section (i.e. 2 groups × 5 chains × 10 participants).

2.2 Stimuli and response format

We used two types of colouring books as the experimental stimuli: roses are drawn in one and animals of four species in the other (Figure 1A and B). The rose colouring book included seven flowers consisting of petals, leaves, stems, and sepals; there were 213 line-distinguished areas. The animal painting included two rabbits, one parrot, one dog, and one cat, having 186 colourable areas. The drawings were approximately of size 15 × 15 cm, and were printed on a A4 paper with grey background. Participants were provided with pens in six colours: black, red, blue, green, yellow, and brown.

2.3 Procedures

In the experiment, participants were presented with a sample painting (either of roses or of animals) and asked to memorize and reproduce it by filling a blank colouring book. The initial stimuli used for the first-generation participants (called the "generation 0" painting, and listed in Figure 1C) were constructed by assigning a random colour to each line-distinct area of the colouring book. These random colours were sampled uniformly and independently from the six options (black, red, blue, green, yellow, and brown; using the RANDOMBETWEEN(1,6) function in Microsoft Excel), and the resulting paintings were colour-printed on a A4-sized paper. It is noteworthy that the colours used in the initial stimuli did not perfectly match those of the pens used by the participants, due to the technical limitations.

Five different colourations were built to initiate the transmission chains of each type of the colouring books ("rose" and "animal"). Then, the reconstruction of these initial colouring patterns by the participants of generation 1 yielded the stimuli for those of generation 2, and so on (Figure 1D). After ten iterations of this transmission process, we obtained the responses from 100 participants in total (2 stimulus types × 5 chains × 10 generations).

The detailed procedure for each participant's trial is as follows. First, they were presented with a sample painting (either the initial stimuli or response from the previous generation) and asked to memorize its colouring pattern as precisely as possible within a minute. After this memorization phase, the participants were instructed to flip the sample painting, so that it was no longer visible to them, and they immediately started filling the blank book to recover the observed pattern. Specifically, the participants were instructed to paint all the white areas in twenty minutes by choosing one of the six colours—and not two or more—for each. This time limit was only intended to pace the participants, and the actual trials lasted until everyone completed the task.

It is of note that the experimental instruction did not mention the treatment of the background. Consequently, one participant (chain A, generation 4; see Figure 2) painted the background, contrary to our intension. Due to the limited availability of the participants, we continued the experiment on that chain and also included the results in the analysis.

2.4 Re-identification of colours

The paintings collected from the participants were scanned into digital images (in the JPEG format), and the colour of each line-distinct area of the colouring books was re-identified systematically in the Hue- Saturation-Value (HSV) feature space. We first manually sampled three representative pixels within that area. Then, the RGB values of these pixels were extracted using the "cv2.imread" function of OpenCV (wrapped as a Python module [23]). We also used the OpenCV function, "cv2.cvtColor", for the RGB-to-HSV conversion.

Each representative pixels of the paintings were then classified into one of the six colour categories, or identified as "NULL" (i.e. colourless), based on their HSV values in the following procedure.

- The pixel was identified as "NULL" when its saturation was under 20 ($S \leq 20$) whereas the value was greater than 200 ($V \geq 200$).
- The pixel was categorized into "black" when its saturation and value were both under 100 ($S \leq 100$ and $V \leq 100$).
- Otherwise ($S \geq 20$), the pixel was classified by their hue into the nearest neighbour of the following category means:
    - Red: 0 or 180 ($0 \leq H < 4$ or $145 \leq H < 180$)
    - Brown: 8 ($4 \leq H < 19$)
    - Yellow: 30 ($19 \leq H < 55$)
    - Green: 80 ($55 \leq H < 95$)
    - Blue: 110 ($95 \leq H < 145$)

The colour category of the line-distinct area was then defined by the majority of the three-pixel colours. Although it was theoretically possible that all the three pixels were identified as having different colours—in such cases, we planned manually colour identification—there was no such complete disagreement in practice.

2.5 Analysis

The data collected from the transmission were analysed from three perspectives: 1) transmission accuracy, 2) randomness of colour use, and 3) local consistency of the colouration.

Transmission Accuracy

We first evaluated the transmission accuracy between successive generations, assessing whether each area of the colouring books was painted with the same colour as in the previous generation (coded as "1") or not (coded as "0"). Specifically, we investigated if this accuracy was influenced by the number of transmissions performed on the paintings, estimating its statistical significance by the generalized linear model (GLMM) that predicts the binary accuracy values from the generation. We built distinct linear models for each type of the colouring book (rose or animals). The statistical test was implemented in R [24], using the "glmer" function in the "lme4" package [25]. The generation effect was categorically represented in the reverse Helmert coding—which contrasts each generation with the mean of the previous generations—and treated as fixed effect terms. The transmission chains were used as a random effect, and the error distribution was binomial (formulated in R as glmer(correct ~ generation + (1 | chain)).

Randomness of colour use

Second, we assessed the degree of randomness in the colour assignments by utilizing the perplexity statistic. Formally, the perplexity $\mathcal{P}$ was defined by two to the exponent of the colour-proportion entropy:

$$\mathcal{P} = 2^{-\sum_{i=1}^{6}(p_i \log_2 p_i)},$$

where the integer $i \in \{1, \ldots, 6\}$) indexes the six colours (black, red, blue, yellow, green, and brown), and p_i denotes the relative frequency of each colour, normalized s.t. $\sum_{i=1}^{6} p_i = 1$. The perplexity offers an intuitive interpretation of the colour proportions by associating their dispersion with the uniform distribution over $\mathcal{P}$ (e.g. the uniform distribution over six categories has the perplexity of $\mathcal{P} = 6$).

The perplexity estimated from the empirical frequencies was evaluated against the random baseline built as follows. First, random probabilities of occurrence (π) over six colours were sampled from the Dirichlet distribution with a concentration parameter of 1 ($\alpha = \mathbf{1}$; i.e. uniform distribution over the simplex of $6 - 1$ dimensions), and the numbers of occurrences of six colours in the 213 areas of the rose painting and 186 areas of the animal painting were sampled from the multinomial distribution parameterized by π. Then, the perplexity of the random colouration was calculated from the relative frequencies of these colour samples. We collected 10,000 random perplexities in this procedure, and the statistical significance of the experimental result was assessed by the proportion of the random perplexities smaller than that of the experiment (i.e. the p-value was estimated in a Monte Carlo manner). The random sampling from the Dirichlet and multinomial distributions were implemented by the "rdirichlet" and "rmultinom" functions of R respectively (the former is available in the package "MCMCpack" [26]).

Local consistency of colouration

In addition, we evaluated the spatial distributions of the colour use. Specifically, we examined if neighbouring blocks in the colouring book were painted in the same colour, resulting in a stronger local colour consistency compared to the global ratio. We formalized this test by counting the number of pairs of adjacent colouring areas that were assigned the same colour (the rose and animal colouring books included 504 and 339 pairs of neighbouring areas in total). Then, the statistical significance of these counts was estimated by comparing them with 10,000 random re-assignments of the colours used in each participant's response (i.e. colour shuffling within the colouring books). Specifically, the p-value was defined by the proportion of the random re-assignments that resulted in a greater number of neighbour colour match than the experimental result.

3. Results

3.1 Qualitative overview

Figure 2 presents examples of the transmission trajectories. Overall, we observed a tendency that distinct flower parts (e.g. leaves and petals) and individual animals were painted with a few consistent colours. Most remarkably, one of the transmission chains achieved a surprisingly naturalistic colour patterns (the top row of the figure).

3.2 Transmission accuracy

Figure 3 illustrates the transmission accuracy between each successive generation. Overall, the accuracy increased along with the cumulative number of transmissions (i.e. fewer errors were made in the later generations). The GLMM analysis revealed the statistically significant improvements at 3rd and 5-10th generations of the "rose" chains ($p < 0.001$) and 2-10th generation of the "animal" chains ($p = 0.0014$ at 3rd generation and $p < 0.001$ elsewhere; see also the Supplementary Table S1, S2).

3.3 Randomness of colour use

Figure 4 shows the proportion of the six colours used in each generation. The use of certain colours became dominant in the later generations (e.g. red and brown in the rose paintings, and brown and green in the animal paintings), in the compensation for the fewer occurrences of others (e.g. yellow and blue in the rose paintings, and red and black in the animal paintings). We quantitatively evaluated these uneven frequencies by the perplexity statistic.

Figure 5A presents the global colour perplexities—based on the colour proportions in the entire colouring books—over generations together with the top 95 percent range of the random perplexities estimated by the Monte Carlo method (shaded areas). We identified roughly two trends in the ten chains. On the one hand, three of the five "rose" chains (A, H, J) and a single "animal" chain (E) achieved small perplexities of 1.75–3.21 at generation 10. On the other hand, the chains stayed around the perplexities of 4.33–5.65, indicating the preservation of colour diversities. The overall statistical significance of the "rose" chain was $p = 0.2956$ and that of the "animal" chains was $p = 0.6841$; thus, the global perplexities are not significantly smaller than those of random colour ratios.

By contrast, when we segmented the rose paintings into eight parts—distinguishing seven flowers and grouping all the leaves and stems into one—their geometric-average perplexity within the paintings ranged between 1.3066–3.1203 at generation 10 (Figure 5B). Similarly, the geometric-average perplexity over the five individual animals was 1.4500–3.3388. The overall statistical significance of the "rose" chain was $p = 0.0264$ and that of the "animal" chains was $p = 0.0433$.

These results indicate that the distinct segments/objects were painted only with a few primary colours.

3.4 Local consistency of colouration

Figure 6A presents the counts of colour match between neighbouring areas per generation and chain. In addition, Figure 6B plots the proportion of the random colour re-assignments that resulted in greater match counts than the observed values. As expected from the analysis of perplexities in the previous section, we observed an increasing trend over generations, and the colour-matched neighbours at generation 10 amounted 41.07-80.16% in the "rose" chains and 50.44-84.96% in the "animal" chains. The overall statistical significance of the "rose" chain was $p = 0.1193$ (not significant mainly due to the chain labelled as J) and that of the "animal" chains was $p < 0.001$ (no random colour permutation yielded greater counts than any of the observed counts).

4. Discussion

This study explored an emergence of organized and systematic painting patterns using the experimental paradigm of cultural transmission. Consequently, on the one hand, we found simple and consistent colouring patterns in the last few generations of the transmission chains, with each segment (rose petals vs. leaves) and object (individual animals) painted with only two or three colours. On the other hand, the natural and plausible colours of petals, leaves or animals were not always observed, contrary to our pre-experimental predictions. We quantitatively confirmed this high-level generalization through the analysis of the colour perplexities and colour match between neighbouring areas. In addition, we also showed that fewer transmission errors were made in the later generations of the transmission, which indicates an emergence of easily communicable patterns.

Under the assumption of Bayesian inference, paintings of the last few generations of the transmission chains represent participants' prior beliefs on the plausible painting patterns [15]. In this view, the present results would reflect a high-level bias towards simpler and more consistent colouring patterns, rather than a bias towards the natural colour patterns recalled to us for specific objects (e.g. the belief that leaves are green). Intensive use of a few colours, quantitatively represented as the low colour perplexities, is likely to be strongly influenced by our way of looking at natural scenes; we tend to perceptually identify or segment objects by their consistent colours amongst diverse visual information. In addition, preference for simpler patterns is consistent with the previous attempts employed in Bayesian models of various cognitive domains, including language learning [27–30], categorization of visually perceived objects [31] and classification of natural numbers [32,33].

Prior to conducting the experiment, we expected an emergence of more realistic colouring patterns, such as red on the rose petals and green on the leaves, in the outcomes of the transmissions. Indeed, we observed such realistic colouration in some of the transmission chains, but they were not the majority (2 or 3 out of 10). Instead, the transmission results are best characterized by the slight dominance of brown and the relatively little use of blue in both the "rose" and "animal" paintings. Retaining the assumption of Bayesian inference, a possible account for this result is that the participants were not strongly guided on the specific contents of the line drawings (e.g. petal, leaf, dog, parrot, etc.). Instead, their bias might have followed more abstract, higher-level colouring pattern shared across general objects or their segments, only avoiding universally rare patterns with too many colours in segments.

Some readers may interpret our results as an outcome of each participant's memory limitations; that is, it may sound reasonable to think that more memorable patterns are more easily/precisely transmittable and thus could survive a long series of transmission. However, the emergence of simple and consistent colouring patterns we observed cannot be fully explained by their memorability, alone. First of all, our participants were not informed that their responses could be recycled as stimuli for other participants. Thus, they could not assist/ease the next participant's memorization task intentionally by generating simpler and more memorable patterns. In other words, the use of fewer and segment/object-consistent colours in the results cannot derive from strategic modifications of the paintings towards well-organized and easily memorable patterns for memorization efficiency [34]. Moreover, it has proven that greater memorability does not guarantee the preservation of certain patterns [35]. For example, a patch of an irregular colour, surrounded by a uniform pattern, would stand out and thus be memorable (the Von Restorff effect [36]), but such irregularity eventually disappears from the transmitted information, and most importantly, it would (almost) never revive due to the low probability of its spontaneous emergence. This also explains why naturalistic colouring patterns, which could be much more memorable, are not guaranteed to emerge.

Indeed, the deviation from the naturalistic colouration observed in this study may elucidate the emergence of more abstract, symbolic forms of artwork in the human history. Even when individuals strive to memorize and reproduce what they observe as precisely as possible, a chain of such replications can unveil their common, underlying bias towards simpler and more consistent patterns, which are consequently advantageous for communication purposes. Similar findings have been reported in the previous studies on artificial languages and rhythms, which demonstrate the emergence of morphologically systematic lexicons [7–10] and integer-rational rhythmic structures [11–14], respectively. Thus, cultural transmission offers a universal hypothesis for the origin of various organized artifacts and/or behaviours of humans.

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Conflict of Interest

The authors have no conflict of interests to disclose.

Ethics

Our experiment complied with the Guidelines for Research in Human Participants, and was approved by the Human Research Ethics Committee of Primate Research Institute, Kyoto University (Permit No. 2018-03). Note that three of the authors (MI, TM, and HK) are now affiliated with different institution; however, all data reported here were collected during their affiliation with Kyoto University.

Data Availability

All painting data were shown in supplementary materials as thumbnail (i.e. miniature images). The analysis code and original painting data would be available upon a reasonable request to authors.

Use of Artificial Intelligence (AI) and AI-assisted technologies

We have not used AI-assisted technologies in creating this article.

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Figures

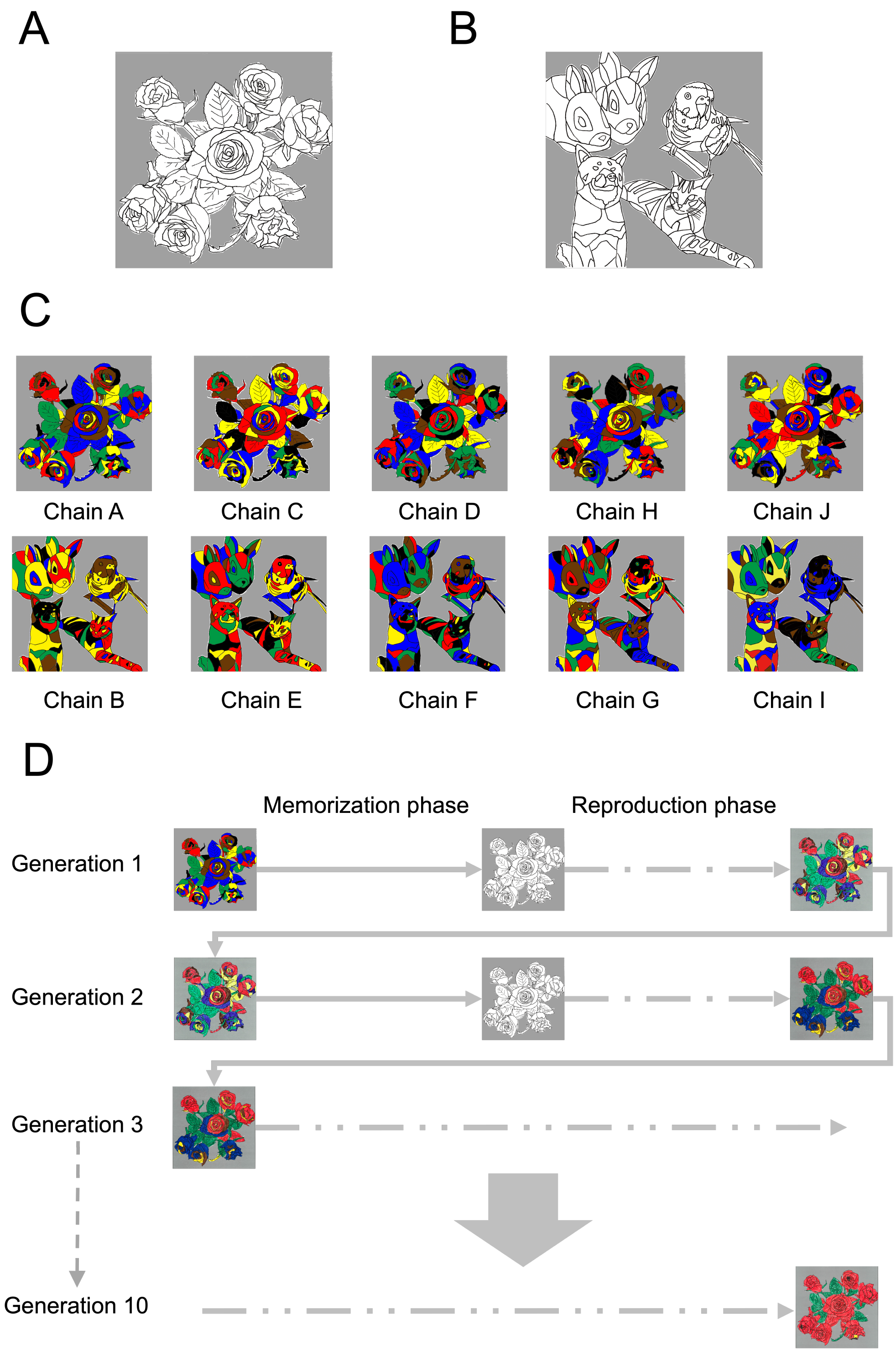

A
B
C
Chain A
Chain C
Chain D
Chain H
Chain J
Chain B
Chain E
Chain F
Chain G
Chain I
D
Memorization phase
Reproduction phase
Generation 1
Generation 2
Generation 3
Generation 10

Figure 1. Schematic diagram of the cultural transmission experiment using colouring books. (A) is a rose and (B) is an animal colouring book. (C) Generation 0 sample colouring books of 10 chains. (D) Flow of the cultural transmission experiment using a colouring book. First, participants viewed a sample colouring book for one minute and memorized its colour pattern (memorization phase). Then, the participants reproduced the colour pattern in twenty minutes (reproduction phase). All colouring areas should be painted. The resulting colouring book was used as a sample for the next generation of colouring books. This was repeated and transmitted up to generation 10.

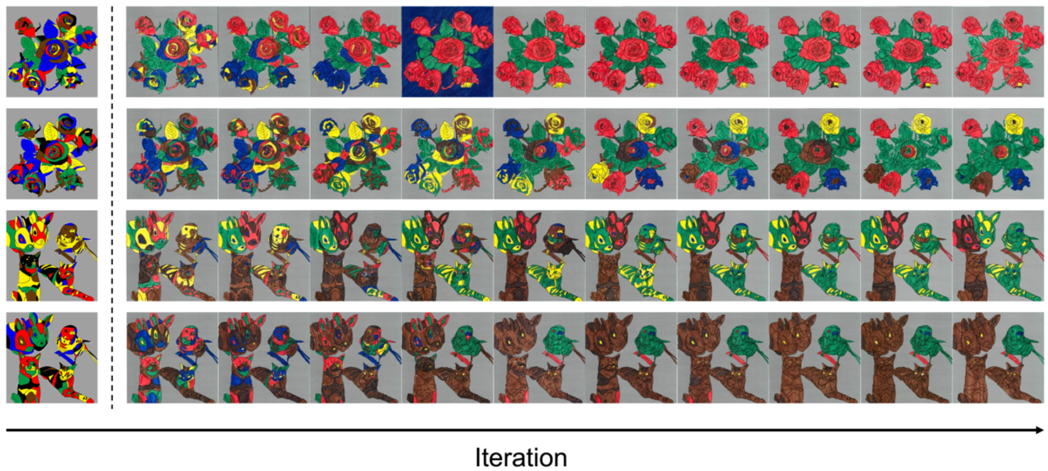


Figure 2. Example results of colour transmission process. (Top two rows) The most remarkable natural colour emerged in the rose colouring book. (Bottom two lines) Transmission results of animal colouring book.

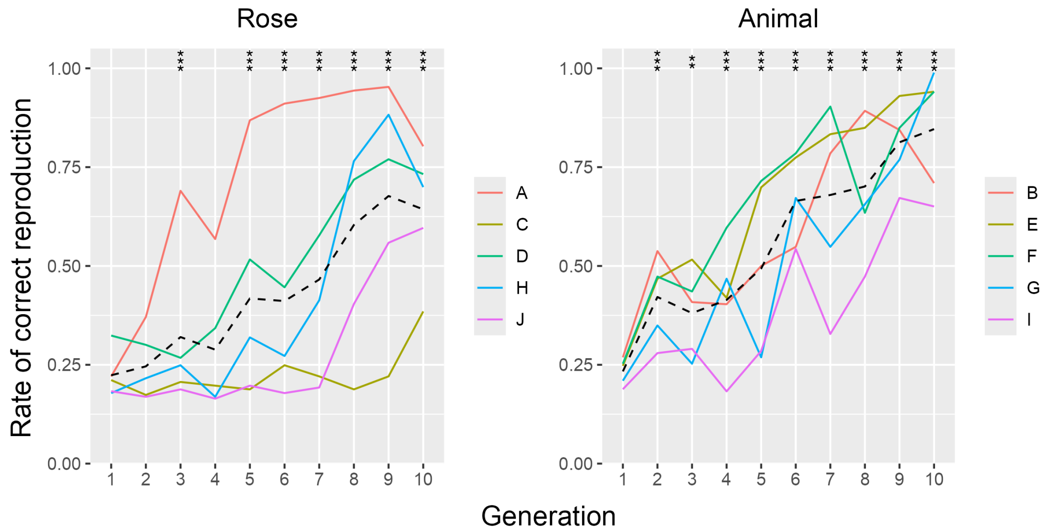


Figure 3. Line plots of the performances for each generation (Left: Rose type; Right: Animal type). Asterisks represent the significant improvements from the previous generations ($* : p < 0.05$; $** : p < 0.01$; $*** : p < 0.001$). The dashed line represented the mean values of 5 chains.

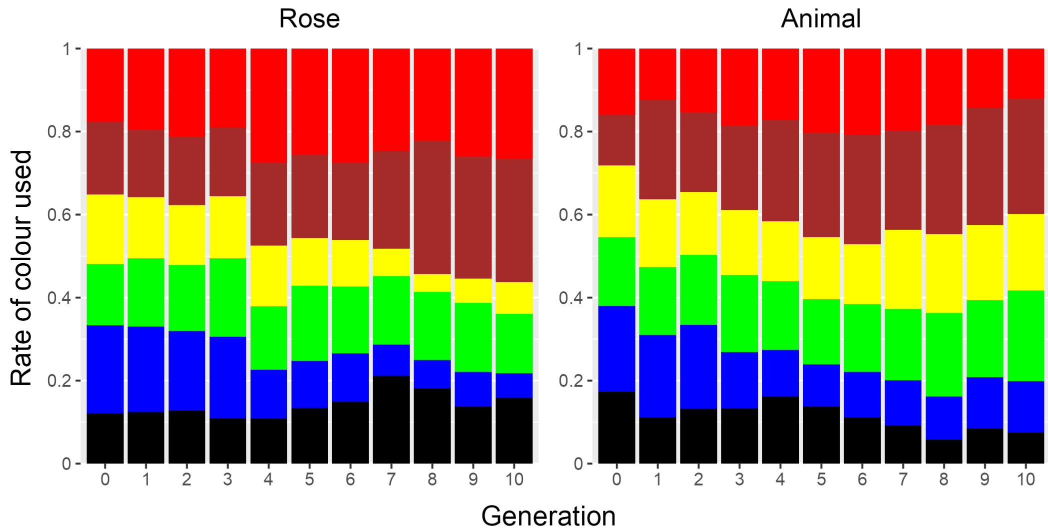


Figure 4. Proportions of the six colours used in each generation (Left: Rose type; Right: Animal type). As the transmission progressed, the relative frequency of the colours became uneven.

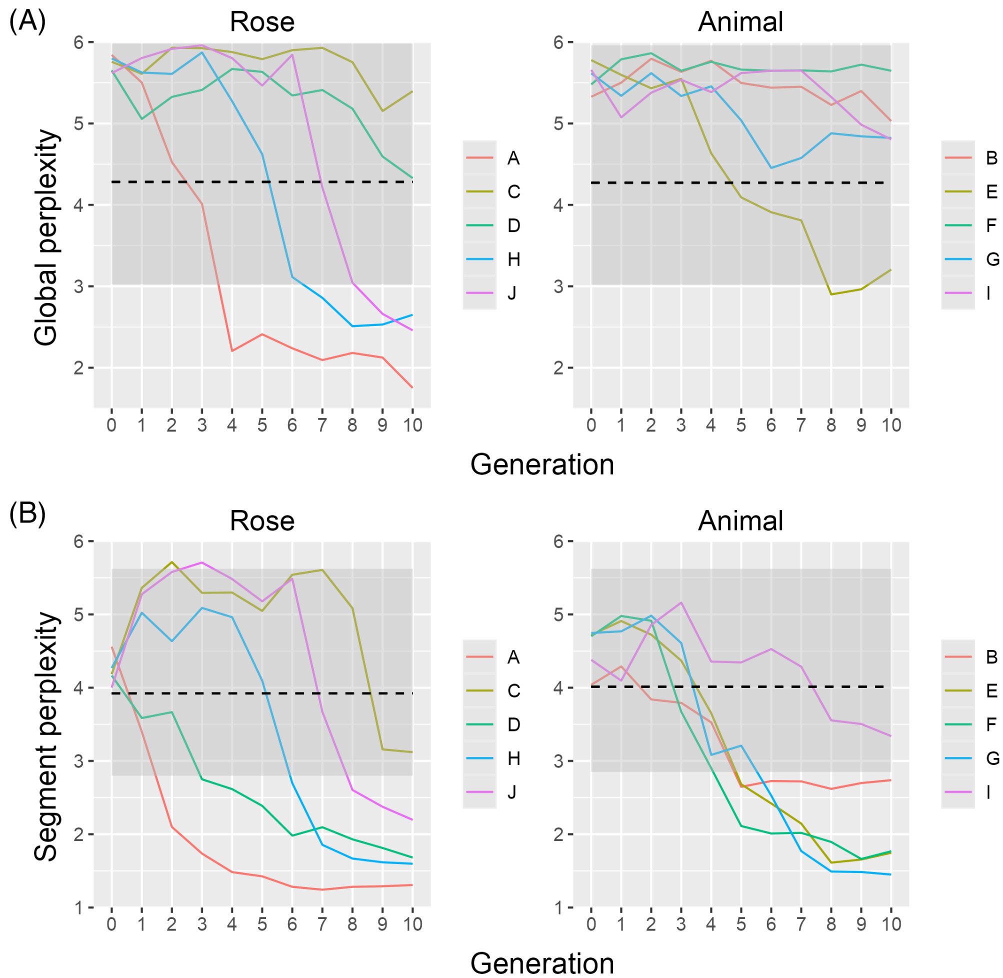


Figure 5. (A) Line plots of the global colour perplexities for each generation (Left: Rose type; Right: Animal type). Shaded regions represent the 95-percentile range of the random perplexities estimated by the Monte Carlo method. (B) Line plots of the geometric-average perplexity within each painting (Left: Rose type; Right: Animal type). Shaded regions represent the 95-percentile range of the random perplexities estimated by the Monte Carlo method

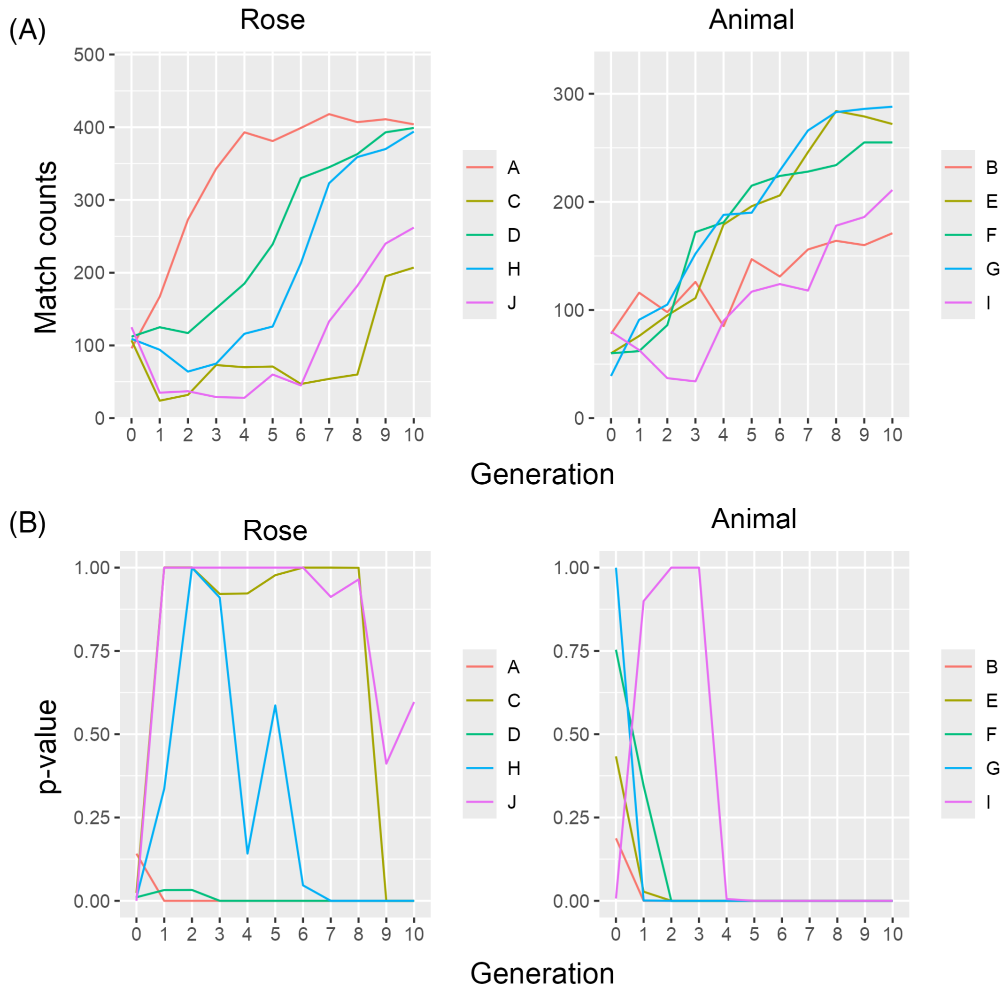
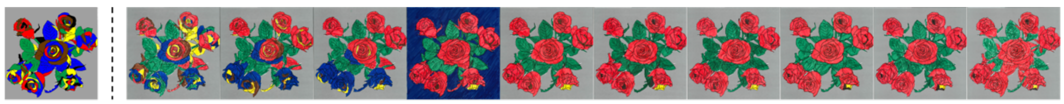


Figure 6. (A) Line plots of the counts of colour match between neighbouring areas for each generation (Left: Rose type; Right: Animal type). (B) Line plots of p-value (the proportion of the random colour re-assignments that resulted in greater match counts than the observed values) of each generation.

Supplementary informations

Supplementary Figure S1. Overall results of transmissions of "rose" colouring books

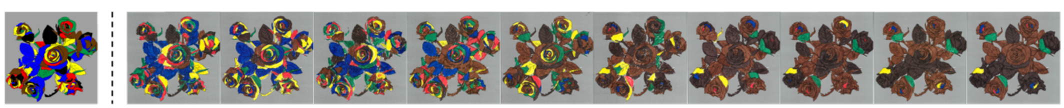
Chain A



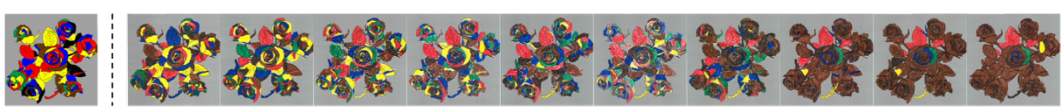
Chain C

Chain D

Chain H



Chain J



The left-hand end of each row is the initial stimulus used for the first-generation participants (called the "generation 0"), which was constructed by assigning a random colour to each line-distinct area of the colouring book. Transmission results are shown from next to the dashed line to the right (the right-hand end is "the generation 10").

Supplementary Figure S2. Overall results of transmissions of "animal" colouring books

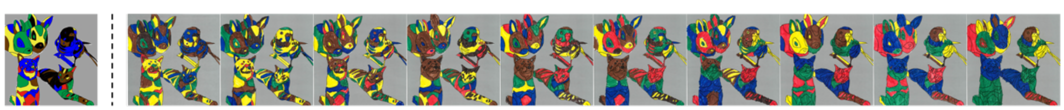
Chain B

Chain E

Chain F

Chain G

Chain I



The left-hand end of each row is the initial stimulus used for the first-generation participants (called the "generation 0"), which was constructed by assigning a random colour to each line-distinct area of the colouring book. Transmission results are shown from next to the dashed line to the right (the right-hand end is "the generation 10").

Supplementary Table S1. Results of GLMM of "rose" in transmission accuracy analysis

	Estimate	SE	z value	Pr (>|z|)	95% CI
Intercept	-0.347	0.395	-0.878	0.380	[-1.121, 0.427]
generation02	0.073	0.055	1.321	0.187	[-0.035, 0.181]
generation03	0.168	0.030	5.577	< 0.001	[0109, 0.227]
generation04	0.039	0.021	1.847	0.065	[-0.002, 0.081]
generation05	0.159	0.016	10.238	< 0.001	[0.129, 0.190]
generation06	0.101	0.013	7.993	< 0.001	[0.076, 0.125]
generation07	0.110	0.010	10.437	< 0.001	[0.089, 0.130]
generation08	0.164	0.009	17.869	< 0.001	[0.146, 0.182]
generation09	0.168	0.008	20.149	< 0.001	[0.152, 0.185]
generation10	0.117	0.007	16.064	< 0.001	[0.103, 0.132]

Results of GLMM of "rose" that predicts the binary accuracy values from the generation. This was implemented in R, using the "glmer" function in the "lme4" package. The generation effect was categorically represented in the reverse Helmert coding and treated as fixed effect terms. The transmission chains were used as a random effect, and the error distribution was binomial (formulated as glmer(correct ~ generation + (1|chain)). The 95 % confidence intervals were calculated using the "Wald" method by the "confint.merMod".

Supplementary Table S2. Results of GLMM of "animal" in transmission accuracy analysis

	Estimate	**SE**	**z value**	**Pr (>|z|)**	**95% CI**
Intercept	0.323	0.227	1.419	0.156	[-0.123, 0.768]
generation02	0.457	0.052	8.757	< 0.001	[0.355, 0.560]
generation03	0.093	0.029	3.199	0.001	[0.036, 0.149]
generation04	0.083	0.020	4.141	< 0.001	[0.044, 0.122]
generation05	0.118	0.015	7.715	< 0.001	[0.088, 0.148]
generation06	0.204	0.013	15.624	< 0.001	[0.179, 0.230]
generation07	0.156	0.011	14.005	< 0.001	[0.134, 0.178]
generation08	0.131	0.010	13.284	< 0.001	[0.111, 0.150]
generation09	0.174	0.010	17.376	< 0.001	[0.154, 0.193]
generation10	0.164	0.010	17.008	< 0.001	[0.145, 0.182]

Results of GLMM of "animal" that predicts the binary accuracy values from the generation. This was implemented in R, using the "glmer" function in the "lme4" package. The generation effect was categorically represented in the reverse Helmert coding and treated as fixed effect terms. The transmission chains were used as a random effect, and the error distribution was binomial (formulated as glmer(correct ~ generation + (1|chain)). The 95 % confidence intervals were calculated using the "Wald" method by the "confint.merMod".