ORIGINAL ARTICLE

Color discrimination and color preferences in Chimpanzees (*Pan troglodytes*)

Camille H. M. Pene[1] · **Akiho Muramatsu[2]** · **Tetsuro Matsuzawa[2]**

Abstract

Chimpanzees (*Pan troglodytes*) have been known for a long time to have color vision identical to humans (Grether in J Comp Psychol 29(2):167–177, 1940b; Jacobs et al. in Vis Res 36(16):2587–2594, 1996). With this study, we wonder if chimpanzees, as humans, show preferences for some colors rather than others. During a first range of experiments, we test their ability to discriminate all the colors from our set, through easy matching-to-sample tasks. The seven chimpanzees that participate in this first test show the results we can expect from chimpanzees with normal color vision. Then, six of them are tested for preferences. This range of experiments results in the existence of consistent tendencies across all the trials and situations, as chimpanzees would mostly first choose some particular colors, and conversely choose last different colors. Although the results for color discrimination are identical for all the seven chimpanzees, preference tests demonstrate four different tendencies. This study is the first step toward broader experiments, including more chimpanzee subjects, but also different species, with the only requirement of being trained to the basic use of a touch panel interface.

Keywords Chimpanzees · *Pan troglodytes* · Color perception · Color preference · Touch panel

Abbreviations
MtS   Matching-to-sample
JPMA   Japanese Paint Manufacturers Association

Introduction

Chimpanzee (*Pan troglodytes*) color vision has long been determined as being close, if not highly similar, to human's color vision. Electro-retinograms (Jacobs et al. 1996) and behavioral experiments (Grether 1940b) have concluded to a sensibility slightly inferior to long wavelength emissions (reddish colors) than humans, which means they were less accurate in distinguishing color hues in the reddish tones. Matching-to-sample (MtS) experiments have been used to investigate color classification in chimpanzees (Matsuno

et al. 2004; Matsuzawa 1985). The results suggested similar characteristics in the classification of colors in chimpanzees and humans, regardless of the history of color name learning. The only noticeable difference was that the subject with a better training in color naming showed more stable performances. In the current study, we first adapt an identity color–color MtS test on touch panel to investigate the capacity to discriminate the ten colors from our sample panel. This first test, described here as Experiment 1, is to determine if any defect in color vision, leading to colors confusion, is present in the tested chimpanzees. We create this test as an easy-touch panel task. Thus, we ultimately aim at checking color vision of all new individuals introduced to touch panel experiments, eventually pointing out color blindness. In the second experiment, we wonder about color avoidance or, alternatively, color preference, expressed by chimpanzees.

Numerous studies investigate color preferences in humans and other animals, suggesting a preference for red and blue in different primate species (Adams 1987; Palmer and Schloss 2010; Wells et al. 2008). The way a preference is constructed is not straightforward, even for human studies. If life experience of each individual seems to be part of it, a more innate origin also tends to be highlighted. Preference or avoidance of some colors could be inherited from evolutionary history leading to the best choice for food, partner,

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environment … In captivity and experimental context, exploring avoidance or preference has a great interest for environment enrichment and to understand some behaviors or bias in experiments using colors as stimuli. Most of the studies relied on object manipulation, first glance analysis, or food preference. By using touch panels experiments, we want to test color preferences by determining the preferred choice order when presented with multiple choices. We hypothesized that chimpanzees would go first for the color that inspires the highest motivation. The use of touch panels allows us to test colors without placing them into any real-life context (food, toys, daily objects, etc.). As only six chimpanzees are tested here, the main objective of this experiment is to determinate the most efficient way to test color preference in individuals trained in the basic use of touch panels. Based on the results, we aim to extend the study to a greater number of subjects and different species.

Methods

Apparatus

This study took place at Kyoto University Primate Research Institute, in Inuyama, Japan. At the time of the study, the institute housed 13 chimpanzees, 12 chimpanzees divided into two groups housed in a multiple environment setting: indoor rooms, outdoor cages, outdoor enclosure, and one chimpanzee, who became disabled following an accident, housed in an adapted room. Environmental and cognitive enrichment are important parts of the housing conditions. Five days a week the chimpanzees are called from the outdoor enclosure or cage to the experimental booth, following the same schedule every day. Their participation is based on their free will to come.

The experimental room ("South Play Room") is composed of two experimental booths, approximately 1.8 m × 1.8 m × 2 m, with acrylic panels as walls, separated by a trapdoor. Both are equipped with touch panels (Mitsubishi Electric Engineering 15-inch LCD touch screen monitor, model *TSD-FT157-MN* for experiment 1, *TSD-AT1515-MN* for experiment 2) linked to two computers (Diginnos Biz EA, Windows 7). Experiments fully controlled by computers as well as participant observation or face-to-face experiments can be performed. Feeders (Biomedica, BUF-310 P50), composed of a 50-groove plate and a brush fixed on a rotor, are used to display small pieces of fruit (in this case, small cubes of apple and raisin) as rewards. Those feeders are connected to the computer and activated by the experiment program through a Contec USB module DIO-8/8 device. All the data are recorded by the computed program.

Experimenters stay behind the monitor, in front of the chimpanzees. They can observe the chimpanzee's behavior through the acrylic panels. The sessions are recorded by camera and displayed on TV screens so that the experimenters can monitor the answers.

Subjects

Seven chimpanzees, six females and one male, from the Primate Research Institute participated to the study. Six of them are mother–infant related pairs: Ai (born in 1976) and her son Ayumu (born in 2000), Chloe (born in 1980) and her daughter Cleo (born in 2000), Pan (born in 1983) and her daughter Pal (born in 2000). The seventh tested chimpanzee is Pendesa (born in 1977). All of them participated in Experiment 1. Ayumu could not participate enough in Experiment 2 to be included in the present study.

They all participated in other cognitive experiments on a daily basis and were well trained on touch panel use when the current study started. No additional preparatory training was performed.

Pendesa was diagnosed with an arachnoid cyst in 2012 (Miyabe-Nishiwaki et al. 2014) but cognitive tasks and records of previous experiments show that it does not affect her performances. Color classification experiments have shown a similar perception compared to Ai but less consistency in her answers, potentially resulting from the different training history between the two of them (Matsuno et al. 2004). Visual tests demonstrated that she is blind in her lower left visual field, without impact on her color perception (Kaneko et al. 2013).

Ayumu participated in a large-scale genetic investigation that concluded that he does not present any mutation affecting the genes coding for the red and green photoreceptors (Terao et al. 2005).

Ai was involved in a study where she was encouraged to choose some color above when presented by pairs (Kawai 2001, unpublished). The order was as follows: red > yellow, yellow > green, green > pink, pink > grey, yellow > pink. We will keep this training in mind while analyzing Ai's results.

The other chimpanzees participated in multiple cognitive experiments. The results did not suggest any color perception deficiency.

Kin relationship and age during the experiment period are as shown in Table 1.

Stimuli

Eleven color samples are used in the different tasks: red, orange, yellow, green, blue, pink, purple, brown, grey, black, and white. The stimuli were chosen as the standard color representative determined in Matsuno et al. (2004), color classification experiment. Although those stimuli were programmed the same, the perception of colors is slightly different during the first and second set of experiments, due to

Table 1 Subject name, age (years old) at the time of experiments 1 and 2 and kin relationship

Name	Age Exp. 1	Age Exp. 2	Relationship
Ai	35	38	Ayumu's mother
Ayumu	12	/	Ai's son/Pal's half brother
Chloe	31	34	Cleo's mother
Cleo	12	15	Chloe's daughter
Pan	28	31	Pal's mother
Pal	12	15	Pan's daughter/Ayumu's half sister
Pendesa	35	38	/

a change of touch panel. The chromaticity coordinate and luminance for both experiments are as shown in Table 2. These coordinates are double-checked by matching with the JPMA Standard Paint Colors by an experimenter and a second person not involved in the experiment. The touch panel replacement occurred during the time between the two different experiments, so that each set is fully performed with the same stimuli display. Thus, this replacement does not impact the results within each experiment.

The stimuli are presented as 95×95 mm color-filled squares. For color discrimination experiments, the symbol representing the start (Start key) of each trial is an empty 27-mm diameter white circle. For color preference tests, we use an empty 27-mm black or white circle (depending on the background condition, as explained later) presented on the bottom-center of the screen as Start key symbol.

Procedure

Experiment 1 For this experiment, we use the Identity Matching-to-Sample design. Two different tasks are performed: task 1 is ten stimuli (the ten colors described above) and ten alternatives (same ten colors), represented by 10s10a, task 2 is ten stimuli and two alternatives,

represented by 10s2a. In the first condition (task 1), each color is presented as a sample 100 times, so 1000 trials in total, divided in sessions of 50 or 90 trials. The order of the samples and the positions of the alternatives are randomized, using pseudo-randomized sequences. For the two alternatives conditions (task 2), each color pair (45 combination in total) is presented 20 times: a color appears ten times as a sample and ten times as an alternative. This resulted in 900 trials in total for task 2, divided into ten sessions of 90 trials each. The order of the sample and the alternatives, as well as the positions of the colors, are randomized using pseudo-randomized sequences.

A trial starts with a black screen and the Start key on the bottom-right of the screen. The subject has to touch the circle to make the sample appear. The sample first appears in a random position. When the subject touches it, the square appears in a different random position. When the subject touches the square again it appears on the bottom-center of the screen. The last touch lets the alternatives appear: ten colors on a 2×5 matrix, or two colors, one on the top-left and one on the top-right. The subject has to touch the sample again among the alternatives to get a reward (positive sound and piece of apple or raisin). If the wrong color is touched, a negative buzzer sound is displayed and the chimpanzee has to wait 3 s before the next trial. The procedure for both ten alternatives and two alternatives conditions is represented in Fig. 1.

Experiment 2 To test the expression of preference, we create tasks based on the target principle. The subject has to touch all the stimuli appearing on the screen to obtain a positive feedback and reward. There is no condition imposed, which means the subject is rewarded whatever the chosen color is. We focus on the influence of two parameters: number of choices and background color. We run four different tasks: the first block is with a black background and the second is with a white background. For each block, we run two-choice tasks and three-choice tasks. For the black background block, we follow an ABA design: 2–3 choices—two

Table 2 CIE 1931 *xy*-chromaticity coordinates and luminance (*Y*) of the stimuli

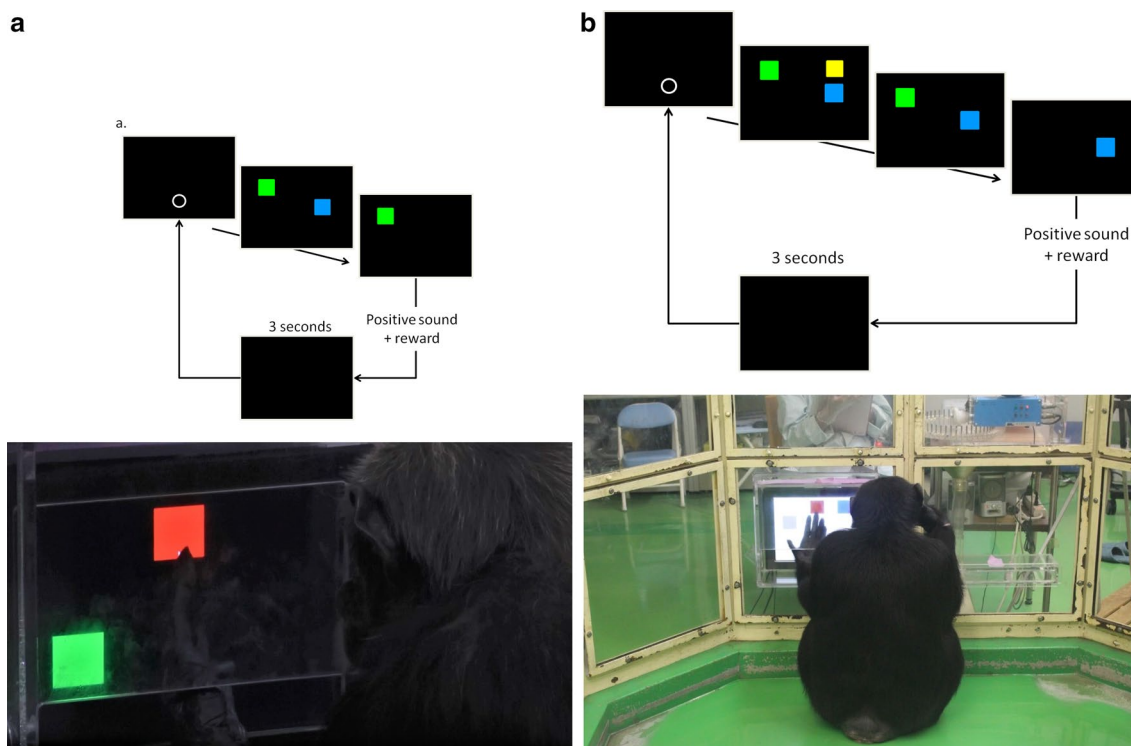| Color name	Experiment 1			Experiment 2		
	x	*y*	*Y* (cd/m²)	*x*	*y*	*Y* (cd/m²)
Red	0.598	0.330	29.3	0.640	0.329	21.3
Orange	0.499	0.414	43.0	0.499	0.414	43.0
Yellow	0.451	0.480	59.5	0.450	0.480	55.9
Green	0.299	0.548	30.3	0.379	0.498	59.4
Blue	0.197	0.230	20.4	0.197	0.230	20.4
Pink	0.419	0.308	29.9	0.287	0.209	29.9
Purple	0.287	0.210	21.7	0.351	0.306	42.9
Brown	0.488	0.343	11.9	0.488	0.343	11.9
Grey	0.314	0.384	31.2	0.314	0.38	31.2
White	0.307	0.373	78.2	0.307	0.373	78.2
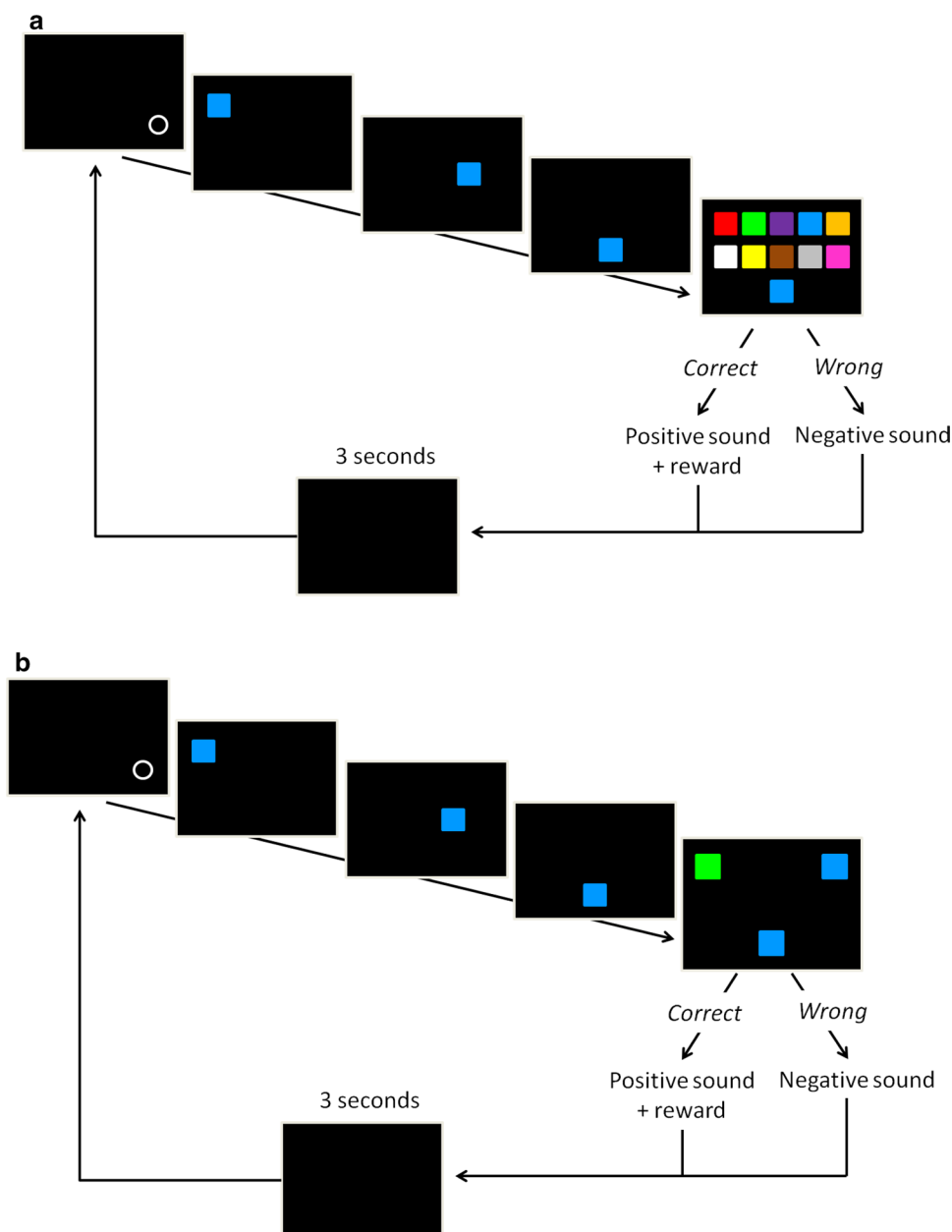
choices, to test the consistency of the results, and for the white background only two choices, then three choices.

For each block of the two-choice tasks, all color pairs (45 pairs) are presented 20 times, which means 900 trials, divided into ten sessions of 90 trials. The order of pairs is pseudo-randomized, using a sequence order generated by associating a rank to all the 90 arrangements with Excel's random formula. The sequence starting point is changed every session. The position sequence is randomized the same way. Thus, the association between color pairs is different every session. For the three-choice tasks, all color pairs (360 pairs) are presented twice, which means 720 trials, divided into eight sessions of 90 trials. The color pairs sequence

and the position sequence are randomized the same way as described above and the starting points are also changed for every session.

A trial starts with a black screen and a white empty circle on the bottom-center of the screen, or a white screen and a black empty circle on the bottom-center of the screen, depending on the session's parameters. When touched, two or three color squares appear, depending on the session's parameters, in a random position. The subject has to touch all the color squares, without any required order. When the last color is touched, a positive sound and a reward (piece of apple or raisin) are received. Then the next trial starts (see Fig. 2 for schematic representation).

Fig. 2 Trial description for color preference experiment. **a** Two-choice task; the background can be black or white, illustration by Chloe performing two choices on black background. **b** Three-choice task; the background can be black or white, illustration by Pal performing three choices on white background

Data analysis

Experiment 1 For the first task (ten alternatives), we fill a confusion matrix, with sample and answer as entry. A similarity index was calculated, using a modify Shepard Index formula, as determined by (Matsuzawa 1990), in form perception and visual acuity experiments, as follow:

$$S_{ij} = \frac{P_{i/j} + P_{j/i}}{P_{i/i} + P_{j/j}}$$

with $P_{i/j}$ as the conditional probability of choosing the color i while color j is presented.

Based on those similarity indices, we calculate the Euclidean distances between the colors (R {proxy} package, "dist" function) and run a Multi-Dimensional Scaling (R{MASS} package, "isoMDS" function) plotting and a cluster analysis (R {stats} package, "hclust" function, method = average).

With the two-alternative task, we calculate a personal mean answer latency for each individual, as a reflection of the individual reaction time. Answer latencies for each color pair are compared to this reaction time ("delta to mean latency") and the difference is expressed in percent.

Experiment 2 For each trial, the color, position, and the stimuli choice order are recorded. For each subject, color preference indices are calculated.

For the two-choice condition, this index is based on the frequency of first choice when the color is presented, balanced by a factor representing the position preference of the stimuli as:

$$kf_i = 2\left(1 - \%Pos_i\right) \text{ and } ks_i = 2 \times Pos_i$$

with kf_i being the factor balancing the choice weight if the first choice is in position i. ks_i is the factor balancing the choice weight if the second choice is in position i. $\%Pos_i$ is the frequency a position i was chosen first during the session.

This way, choosing a color first even when appearing in one less preferred position will increase the weight of the trial in the index calculus. On the contrary, the trials respecting the position preference of the subject will have less weight in the calculus.

The preference index for a color x is calculated as below:

$$PI_x = \frac{\sum_{i=1}^{9} nFCP_i \times kf_i}{\sum_{i=1}^{9} nFCP_i \times kf_i + \sum_{i=1}^{9} nSCP_i \times ks_i}$$

with nFCP$_i$ being the number of times the color was chosen first when appearing in the position i, nSCP$_i$ is the number of times the color was chosen second when appearing in position i. kf$_i$ is the factor balancing the first choices weight. ks$_i$ is the factor balancing the second choices weight.

This index is calculated so that PI = 1 if the color is always chosen first if presented, and PI = 0 if the color is always chosen last if presented.

For the three-choice condition, the preference index for a color x was calculated based on the frequency of first, second, or third choice only, so that:

$$PI_x = \%FC + 0.5 \times \%SC$$

with %FC is the frequency of first choice for the color in question and %SC is the frequency of second choice for the color in question.

This index is calculated so that PI = 1 if the color is always chosen first, PI = 0.5 if the color is chosen first, second, or third the same amount of time, and PI = 0 if the color is always chosen last.

Then, for each subject, we calculated a Color Factor Index (CFI) and a Position Factor Index (PFI), indicating the importance of the color and of the position of the stimuli in the order choice. The CFI is based on the slope formed by the Preference Index of all the tested colors when ordered from the largest to the smallest, multiplied by 10. The PFI is based on the standard deviation of the frequency of first choice of all the positions, compared to the standard deviation of an hypothetic choice order only based on the stimuli position (the subject always choose the closest to the starting key first), designated as a "perfect position-based choice":

$$PFI = \frac{SD_{Subject}}{SD_{Perfect}}.$$

with SD$_{Subject}$ being the standard deviation of the first choice frequency for all the nine positions and SD$_{Perfect}$ being the standard deviation of first choice frequency for a perfect position-based choice, SD$_{Perfect}$ = 0.33 for two choices and SD$_{Perfect}$ = 0.37 for three choices.

Results

Color discrimination

Task 1 Accuracy across the sessions was stable for each chimpanzee. Mean accuracy for each sample color was a first indicator to which colors are more easily confused with other (mean accuracy for red is 61%, brown 70%, pink 76%, purple 83%, grey 86%, and orange 86%) and which are less confusing for the subject (white 95%, blue 95%, green 96%, yellow 99%).

Figure 3 represents the similarities between colors for a normal color perception in chimpanzees. Different main clusters appeared. First were reddish colors, with the highest similarities between red and brown, then pink and purple. Orange also entered this cluster. Then, confusions between grey and white were often encountered in different chimpanzees. Yellow, green, and blue were the less ambiguous colors and were rarely confused with others. On the Multi-Dimensional Scaling shown in Fig. 4, we can recognize the different clusters: red–brown–purple–pink–orange, white–grey and the three last colors more dispersed as prone to less confusions. Those similarities were commonly expressed by all the seven subject tested. On an individual level, different pairs were also perceived as similar: green–blue for Ayumu, orange–yellow for Pan and Pendesa, and grey-blue for Pal. Pal's case is surprising, as she did not answer correctly to the blue sample for half of the sessions, without a clear pattern except that she chose more often grey instead (hence the grey-blue similarity on her final results), then turned to match blue sample correctly for the rest of the sessions.

Task 2 As expressed in Fig. 5, for the color pairs that were never or rarely confused in task 1, the answer latency did not differ from the reaction time. On the contrary, we observed significant increasing (one-sample t test against the value of 0, degree of freedom = 131) of the latency when the colors were confused more often: red–brown ($-a$ and $-h$, + 23.60% [+ 17.65 to 29.56], p value < 0.001), red–orange ($-a$ and $-b$, + 11.08% [4.52–17.65], p value = 0.0011), red–pink ($-a$ and $-f$, + 6.27% [1.08–11.46], p value = 0.018), pink–purple ($-f$ and $-g$, + 13.97% [6.61–21.33], p value < 0.001) and white–grey ($-i$ and $-j$, + 11.23% [6.21–16.26], p value < 0.001). Pal's confusions with blue did not appear on this task's results.
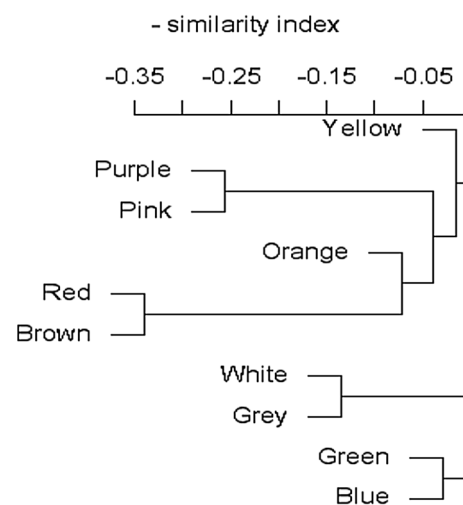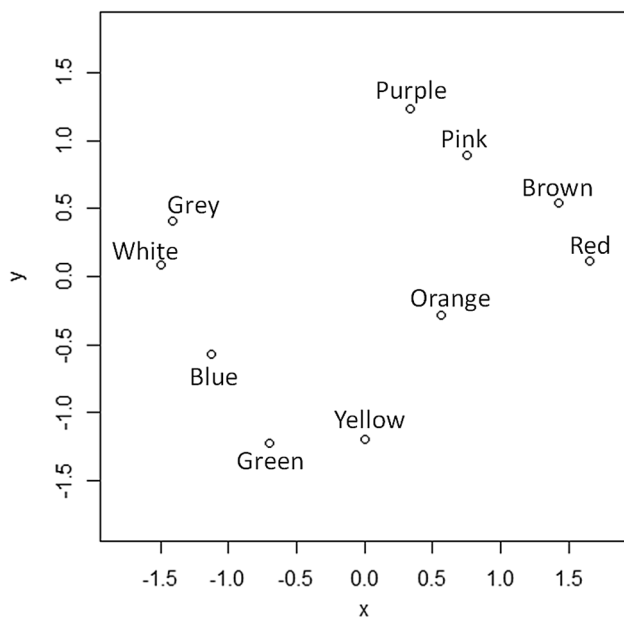

Fig. 3 Cluster analysis on the similarity indices for each color pair

Fig. 4 Multi-dimensional scaling based on colors similarity indices

Color preference

Significantly different preference indices across the colors All subjects showed individual tendencies of choosing first some colors rather than others, and on the opposite choosing last some colors rather than others. Those patterns resulted in indices superior to chance level for the preferred colors and inferior to chance level for the less preferred colors, allowing us to establish an order in the nine tested colors. When expressed, those patterns were constant across the four different conditions for most of the subjects. A Friedman test (see Table 3) confirmed that significant differences in the color preference indices were significant in all tests, except for Ai in the three-choice conditions and Chloe in the white background and three-choice condition.

Consistent results across the tasks parameters To investigate the consistency of the results of the two choices on black background (A1 BBG), we ran a correlation analysis. Spearman and Pearson correlation factors are summarized in Table 4. Indices obtained with black background and three choices (B BBG) were highly consistent with the results of A1 BBG, and indices from the second two choices on black background task (ABA design) were also comparable. Lower correlations observed for Pan and Pal were due to variations in the indices and rank of intermediary colors but the most preferred and less preferred colors were stable across the sessions. Color choices on white background were also consistent when two choices were displayed, except for Pan and Pendesa. For those two subjects however, some colors always appeared on most preferred or less preferred

positions, corroborating the results from the black background tasks.

Main patterns By calculating the cosine distance between the vectors formed by all color preferences for each chimpanzee, we recognized four main different patterns in the preferences among the subject. Those clusters are represented in Fig. 6: Pal and Chloe preferred yellow–green colors, Pan and Cleo expressed higher indices in blue-purple colors, Ai showed a tendency to choose red-brown colors first, and Pendesa had a preference in achromatic (grey, white, black) and brown colors. Less preferred colors were more variable among the subjects. We noted however that Pal constantly chose blue stimuli last in all test conditions.

Best task setting for future experiments The final goal of this study is to determine the best task to be used in further experiments to test color preferences. During the first task, all the subjects expressed an order choice based on the color rather than the position of the stimuli: ratio CFI/PFI > 1 (mean = 3.11, one-sample t test against a value of 1: $t = 2.4024$; $p = 0.03072$). As shown in Fig. 7, when three choices were presented, the ratio CFI/PFI decreased significantly compared to the two-choice conditions. This means the chimpanzees expressed color preferences more explicitly when confronted with two choices than with three choices. Also, we observed a decrease of the ratio across time, as the subjects got used to the task and tended to pay less attention to the stimuli and answered more and more according to the position. As some of the subjects expressed interesting variations in the preferences when performing the task on white background, we tested the representativeness of the results obtained with the five first sessions of two choices on black background and the five first sessions of two choices on white background. This setting means 20 presentations of each pair of color, ten for each background color. By using Spearman (ρ) and Pearson (r) correlation test, we found that the results obtained from those ten sessions were highly correlated with the general results from all the sessions (mean $\rho = 0.95$ [0.88; 0.98], mean $r = 0.96$ [0.94; 0.98], p value < 0.001, $df = 8$), which mean that this task configuration will give us sufficient data to determine an individual color preference.

Discussion

This experiment aims to investigate chimpanzee's color perception through easy touch panel tasks. By researching the similarities between the different colors, we obtain evidence of chimpanzee's trichromatism being slightly less sensitive to long wavelength (red), as described by Grether (1940a, b) and Jacobs et al. (1996). The two tasks evaluate the similarities thanks to two different approaches. First, the direct consequence of a similarity is confusion of the colors and
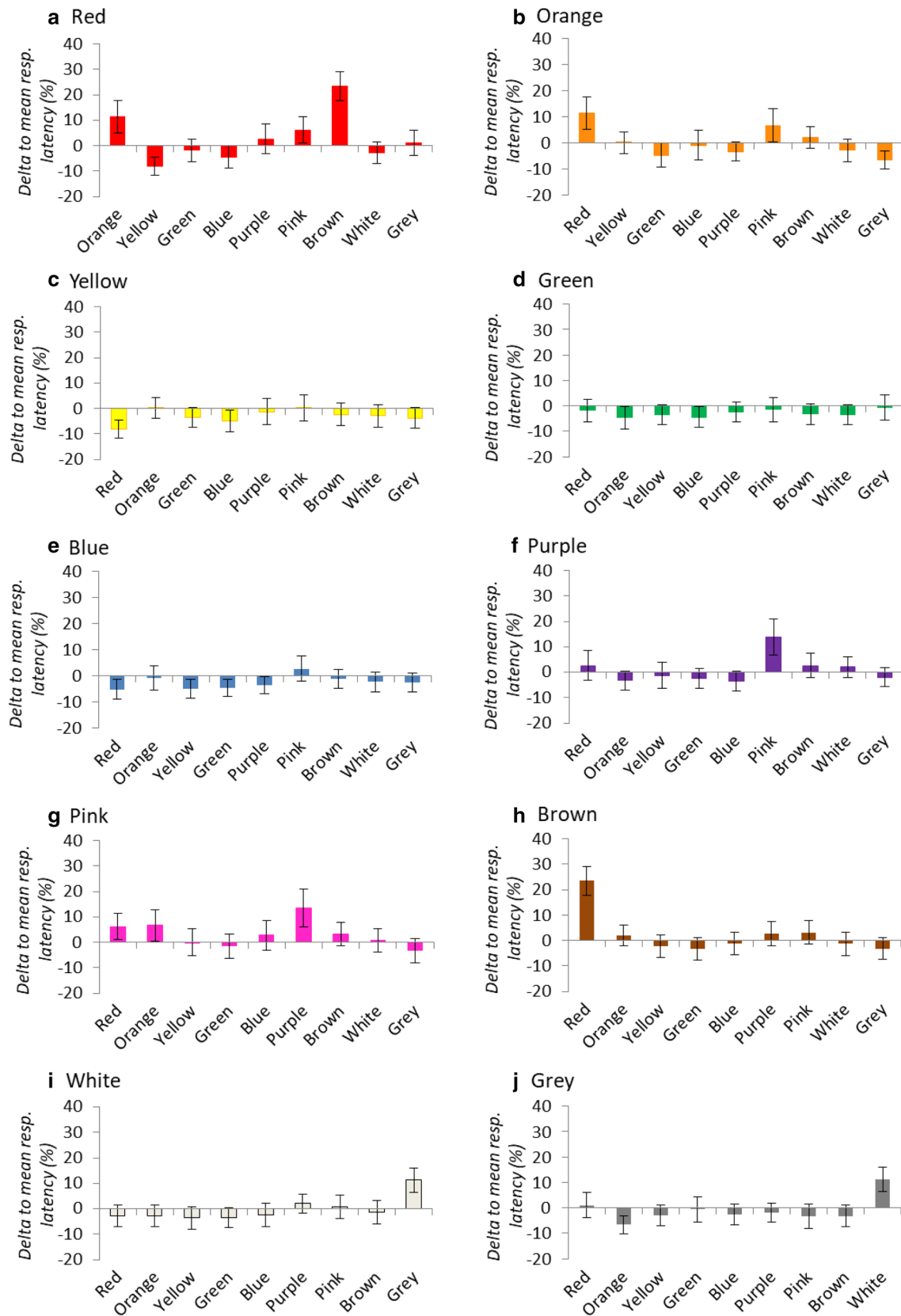
Fig. 5 Delta to mean answer latency for each color when confronted to the other alternatives. Delta is expressed in percentage of the individual reaction time (confidence intervals: $\alpha = 0.05$)

Table 3 Friedman test results on color preference indices from two-choices—black background task (A1 BBG, $N=100$), three-choices—black background task (B BBG, $N=80$), two-choices—black background (A2 BBG, $N=100$), two-choices—white background (A WBG, $N=100$) and three-choices—white background (B WBG, $N=80$)

Subjects	Sessions code				
	A1 BBG	B BBG	A2 BBG	A WBG	B WBG
Ai					
χ^2	52.58	11.37	31.2655	31.1698	16.2903
p	**< 0.001**	*0.2507*	**< 0.001**	**< 0.001**	*0.0611*
Chloe					
χ^2	74.5191	19.0994	66.3273	41.5636	6.5027
p	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	*0.6887*
Cleo					
χ^2	53.2364	57.5277	62.3564	61.3954	57.5004
p	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Pan					
χ^2	67.2873	51.1091	30.4145	38.2213	30.6874
p	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Pal					
χ^2	79.5055	65.5812	69.5127	78.1711	59.8589
p	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Pendesa					
χ^2	43.4039	59.3194	24.5985	41.1031	19.4943
p	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.05**

Significant p values are written in bold, non-significant p values are represented in italics

Table 4 Spearman (ρ) and Pearson (r) correlation factors of the preference indices (degrees of freedom $= 8$) on three choices—black background (B BBG), two choices—black background (A2 BBG), two choices—white background (A WBG) and three choices—white background (B WBG) when compared to the results of the first two choices—black background task (A1 BBG)

Subjects	Session code			
	B BBG	A2 BBG	A WBG	B WBG
Ai				
ρ	0.8**	/	0.8**	/
r	0.72*	/	0.74*	/
Chloe				
ρ	0.87**	0.97***	0.83**	/
r	0.85**	0.99***	0.85**	/
Cleo				
ρ	0.95***	0.88**	0.88**	0.92***
r	0.96***	0.94***	0.89**	0.96***
Pan				
ρ	0.93***	0.42	0.2	0.53
r	0.94***	0.59°	0.32	0.6°
Pal				
ρ	0.87**	0.5	0.78**	0.5
r	0.91***	0.7*	0.86**	0.66°
Pendesa				
ρ	0.97***	0.75*	0.47	0.4
r	0.91***	0.79*	0.49	0.34

Significance code: $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $p < 0.1$ °
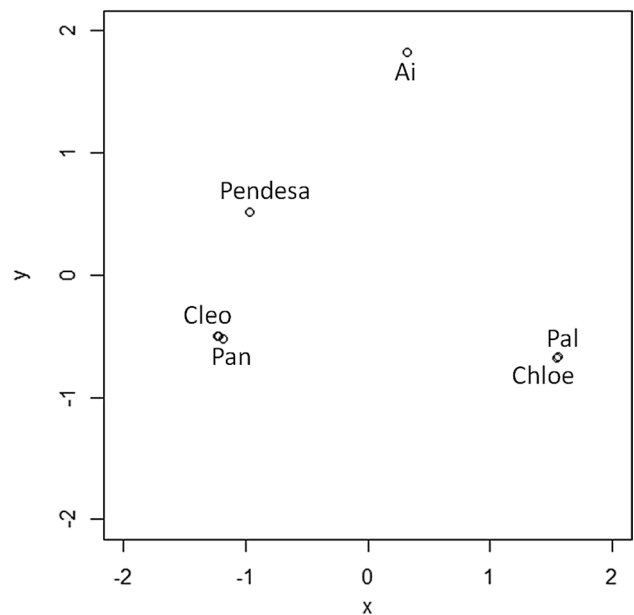
mistakes in the matching-to-sample trial. Then we hypothesize that if two colors appear close to one another, then the subject will hesitate and take a little longer to answer. By evaluating the answer latency, we obtain a picture of the most confused colors. Those two methods lead to consistent results. Red and brown are the most confused colors in the panel we tested, then pink and purple. Colors as green, yellow, or blue are on the contrary the colors prone to less confusion. Individual differences lead to greater confusion between different colors pairs but most of those are from the same chromatic category (red–orange, orange–yellow). Ayumu presented a blue–green confusion on the task 1 but no significant increase of the latency in task 2.

The only particular case is Pal, who showed surprising answers when the color blue was presented as sample. For the first half of the session, she picked a wrong color. She choose almost all the alternatives at least once (red is the only color she did not pick when the sample was blue), and more often grey than the other colors. Then, for the second half of experiment 1, she turned to answering the blue sample correctly for most of the occurrences. The hypothesis of a color vision deficiency has been outlined, but no other confusions than blue–grey could support this possibility.
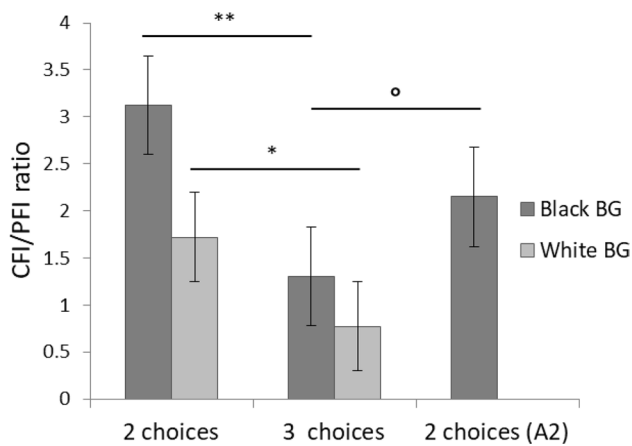

Fig. 6 Multi-dimensional scaling on total preferences indices

Fig. 7 Ratio CFI/PFI across the different tasks parameters. Paired student test, significance code: $p < 0.001***$, $p < 0.01**$, $p < 0.05*$, $p < 0.1°$; black background: 2 ch.–3 ch.: $t = 4.7578$, p-value = 0.0025; 2 ch.(A2)–3 ch.: $t = 1.608$, p-value = 0.084; white background: 2 ch.–3 ch.: $t = 2.7979$, p-value = 0.019

If Pal was blue–yellow color blind, colors such as yellow and purple or a strong blue–green similarity would appear. Then, would it be possible that those incorrect answers are the result of an avoidance of blue rather than a vision deficiency? Pal's case led to the second experiment: do chimpanzees show preferences or a dislike for particular colors?

All the subjects in this study demonstrate patterns of preference or avoidance of particular colors presented as filled squares stimuli on a touch screen. One of the hypotheses was that they based their choice order on the saliency with the background, especially for the yellow–green preferences. Indeed, each stimulus has particular luminance (see Table 2) that leads to different contrasts with the background. One can hypothesize that the color that contrasts the most (here yellow and green on black background) is more susceptible to attract attention and draw the subject to touch them first. To investigate this possibility, we changed the background to white, so that the saliency of each stimulus is reversed. They consistently chose first the same colors rather than the others across the different settings, supporting the hypothesis that the choice order is based on the color itself. Among the subjects, individual differences in the preference tendencies are observed, as we can isolate four main patterns: preference for yellow–green, preference for pink–purple, preference for red–brown, and preference for achromatic. The only subject who had performed a training involving a required color choice order, Ai, demonstrated a preference for red and brown color. In this previous training, she was asked to touch red first only when confronted with yellow. In our study, she showed a preference for red stimuli even when presented with other colors. The other color pairs tested by Kawai et al. do not stand out in the results. Thus, we do not consider the impact of this training as significant enough to

be a bias, even more considering Ai's wide experience with diverse experiments using color as stimuli. As confirmed by the correlation analysis, a task consisting of ten sessions presenting two color choices, five on black background and five on white background, is sufficient to obtain significant data and determine the color preferences. By testing more chimpanzees from different groups, training or history, it would be important to confirm those main patterns and explore color preferences on the species level.

It is important to notice that this experiment tested color preferences based on stimuli displayed on a screen. Hence, those stimuli are removed from any natural context and are not associated with any objects or situations bearing positive or negative valence. As hypothesized by studies on humans and animals, color preferences may be shaped with emotional value of objects one associates to the color (Palmer and Schloss 2010) or psychological context (Franklin et al. 2012; Maier et al. 2009). Comparing those results to other tests relying on real objects (food, toys, etc.) would be interesting.

This experiment was initiated by unexpected results of one subject on experiment 1, Pal, who presented abnormal answers when presented with blue. The results of color preference demonstrate a strong avoidance for blue and purple stimuli. We have no explanation for this, as she shares the same history as Cleo who was raised with her and who, on the contrary, shows a preference for bluish colors. But this result corroborates the hypothesis that her avoidance for blue can be the origin of her response pattern in experiment 1.

We also observed that the ratio CFP/PFI decreases with the number of sessions performed. This may be linked to the fact that we only used one pseudo-randomized position sequence, containing 72 lines. It is possible that the chimpanzees got used to the sequence after several iterations, especially because they are daily trained on memory-based tasks, making them rely more and more on the position of the stimuli rather than the color when confronted with neutral colors (not most preferred nor less preferred). For future projects, we recommend using several sequences to reduce this bias.

Conclusions

With this study, color perception in Chimpanzees is discussed from two approaches: color discrimination (investigated through color confusions) and color preference. The first experiment results in comparable similarities between the subjects and tends to confirm a sensibility slightly inferior to reddish colors, as most of the similarities concern red, brown, orange, and pink. With the second experiment, we illustrated that chimpanzees show consistent color preferences when confronted with multiple color choices, but

those preferences are variable among the individuals. The case of Pal's avoidance of blue is also striking: this tendency was observed in both the discrimination task and the preference task. Her case confirms the possibility of having results from an experiment based on color stimuli impacted by the preference or, as seen here, avoidance of some colors.

From those results, we validate the method of a task based on ten sessions displaying two colors, five sessions on black background, and five sessions on a white background, so that each color pair appears ten times in each background condition. If similar results are obtained from both background conditions, we can conclude on the preferences of the individual. From this easy target task, without requiring a specific choice order to obtain the reward, a broader sample of subjects can be tested, as long as they have basic training on touch panel experiments. We can also consider testing other species trained to touch panels, humans, primates, and non-primates animals, to conduct inter-species comparisons.

The conclusions from this study are limited by the fact that the stimuli are presented as filled squares on a screen, without any context. Color preferences are more and more associated to context or emotional valence of the support of the color. Most of the studies on color preferences in primates conclude on the particular valence of red color (Hurlbert and Ling 2007; Nunn 1999), yet red preference is only observed in one out of six subjects in the current study, Ai. The absence of connection to real context may influence the expression of color preferences. Testing more subjects may be critical to determine the main tendencies in the species.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval The research proposal for the project "Studies on sequential learning, memory, and language comprehension in chimpanzees" was approved by the Animal Welfare and Animal Care Committee of Primate Research Institute, Kyoto University (Nos. 2015- 063). All procedures adhered to the Japanese Act on the Welfare and Management of Animals.

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