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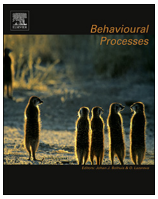

Spontaneous color preferences in rhesus monkeys: What is the advantage of primate trichromacy?

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ABSTRACT

Color perception and color signaling play an important role in various aspects of animal behavior. However, in mammals, trichromatic vision characterized by three retinal photopigments tuned to peak short, middle and long wavelengths is limited only to some primate species. In Old and New World primates a second photopigment has appeared repeatedly during phylogeny, allowing red colors to be distinguished from yellows and greens.

Several hypotheses aspire to explain the adaptive benefits of trichromatic vision for primates. The predominant one is foraging adaptation for facilitation visual detection of fruits or young leaves. Alternative explanations are based on the function of red color in aposematic signaling or its role in socio-sexual communication.

We tested spontaneous color preference in macaque monkeys (*Macaca mulatta*) for both food and non-food objects in a laboratory environment. We hypothesized that preference for or avoidance of red color together with the context of such behavior may help us to understand what the adaptive advantage leading to a rapid expansion of a gene for a second pigment in the long-wavelength region was.

We found neither preference nor avoidance toward red color in non-food objects, but we found a significant preference for red color in food; therefore, we suggest that the results support the foraging hypothesis in macaque monkeys.

1. Introduction

Colors and color-perception may play an important role in various aspects of animal behavior (foraging, intra- or inter-species communication, decision making). However, most mammals are dichromats and trichromatic color vision with an ability to perceive red color occurs only in some primate species. Trichromatic vision has developed as routine trichromacy in Old World monkeys and polymorphic trichromacy in New World monkeys, as well as in some prosimians (Jacobs, 1993).

Trichromacy evolved in primates via different molecular mechanisms in the Middle Cretaceous, around 65 million years ago, after the splitting of the New World and Old World landmasses (Carvalho et al., 2017). Trichromatic color vision, characterized by three retinal photopigments tuned to peak wavelengths of ~430 nm, ~535 nm and ~562 nm (Li et al., 2000, Jacobs and Deegan, 1999), has evolved convergently in catarrhine primates (Dulai et al., 1999; Nathans et al., 1986) and one genus of New World monkey, the howlers (genus *Alouatta*), as routine trichromacy. Routine trichromacy is characterized by the presence of both M and L (green and red sensitive, respectively) opsin genes on the X-chromosome both in males and females causing trichromatic vision in both sexes.

Routine trichromacy arose by gene duplication at the base of the Old World lineage ~40 mya (Goodman et al., 1998; Hunt et al., 1998). Sequence analysis of the two genes (M, L) indicates that the gene for red sensitive opsin in howlers, which is based on the same mechanisms as in Old World monkeys, has a more recent duplication than in Old World primates (Hunt et al., 1998). It occurred after the separation of the Old World and New World lineages approximately 7–16 million years ago (Jacobs, 1996; Cortes-Ortiz et al., 2003).

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In contrast, color vision among New World primates is generally more variable. Most species of New World primates have genes encoding multiple pigments that absorb in the middle to long wavelength regions of the spectrum; however, they only have one cone pigment gene per X-chromosome (Mollon et al., 1984; Jacobs and Nietz, 1987, Jacobs and Nietz1987; Jacobs et al. 1993). Males and homozygous females, therefore, rely on one M/L type pigment gene, whereas only heterozygous females have two genes - one from each X-chromosome to encode two different photopigments absorbing in the middle-to-long wavelengths. The single-origin hypothesis implies that this mechanism has persisted in these New World monkeys for more than 20 million years, because it has been estimated that the divergence of the howler monkey lineage and the squirrel monkey–marmoset lineage occurred ≈20 million years ago (Schneider et al., 1993, 1996, for more details see Boissinot et al., 1998). Sequence analysis of the two genes indicates that this is more recent than duplication in Old World primates (Hunt et al., 1998), which occurred after the separation of the Old World and New World lineages.

Considering Strepsirhini, the genetic analysis of 20 Strepsirhini species revealed allelic variation of M/L opsin genes in sifakas (*Propithecus verreauxi*) and ruffed lemurs (*Varecia variegata*) (Tan and Li, 1999). The presence of an M/L cone opsin polymorphism indicates the presence of trichromatic vision in heterozygous females.

The gene for pigment perceiving the longest wavelengths (red) has therefore appeared in primates repeatedly and from all genes encoding opsins most recently and with a rapid expansion (Kainz et al., 1998). Although the genetic mechanisms of trichromacy are understood quite well, the question remains: what was the adaptive advantage responsible for the spreading of the above mentioned genes? (Carvalho et al., 2017)

There are several hypotheses that aspire to explain adaptive benefits of trichromatic vision in primate populations. The main hypothesis explains the evolution of trichromatic vision as a foraging adaptation of frugivors to facilitate visual detection of fruit (Mollon, 1989; Bowmaker et al., 1991). This capacity to distinguish red from green colors, which is not found in other mammals, has been proposed as an advantage for detection of ripe fruits (Regan et al., 1998). As fruit ripens, it changes from green to yellow, orange or red, what directly reflects the changing content of glucose in the fruit. Thus, the fruit advertises to the trichromat its actual nutritional value (Schaefer et al., 2004; Riba-Hernández et al., 2005). However, a literature survey of 43 primate species grouped into visual categories of dichromats, non-routine trichromats, and routine trichromats indicates that regardless of the visual capacity of the species, red and orange fruits combined (17–24 % of food species) are consumed less frequently than green fruits (30–65 % of food species) (Dominy et al., 2003a). This study and others (e.g. Wheelwright and Janson, 1985) suggest that the evolutionary value attributed to detecting orange and red fruit has been overstated. An alternative scenario interprets trichromatic vision as an adaptation for detection of young reddish leaves (Lucas et al., 1998; Coley and Kursar, 1996) against a background of mature foliage (Sumner and Mollon, 2000a,Sumner and Mollon, 2000bb). Reddish leaves are nutritionally preferred by folivores because they are more palatable and contain less toxins and fibers (Dominy and Lucas, 2001; Dominy et al., 2003b; Lucas et al., 2003; Milton, 1979). Africa is highly seasonal, with a phenology characterized by alternating periods of fruiting and leafing (Terborgh and van Schaik, 1987; van Schaik and Pfannes, 2005). Young leaves are an abundant source of nutrients and they probably represented stable resources for the earliest catarrhines, particularly as leafing generally occurs when insect abundance is the lowest (Wright and van Schaik, 1994). Indeed, young leaves still represent an important seasonal resource even for the predominantly frugivorous catarrhines (e.g. Doran, 1997).

One of the first experiments focusing on color preference in primates in food was performed by Barbiers (1985) who offered colored (red, orange, green, blue) and original dry food pellets (which are usually brown/grey) to orangutans. They showed a much higher interest in the colored food than the pellets of a normal color. Nevertheless, red color *per se* was preferred by just one out of five of the examined individuals.

Leonhardt et al. (2008) tested frugivory and folivory hypotheses in prosimian primates. They employed foraging tasks comparing species with dichromatic and trichromatic vision. The authors proved that heterozygous females of polymorphic trichromats would be more efficient than the dichromats in collecting red or green food presented on a background of green painted sawdust. They also demonstrated a preference for the red color. However, this preference was shown only when comparing red and green stimuli.

Only a few experiments have tested the color preference of primates in a non-food context and they were using different methodologies. In Humphrey's experiment (1971), monkeys (*Macaca mulatta*) had the possibility to select and project differently colored light on a wall in a testing chamber. This experiment revealed a preference for blue and an avoidance of red colors in a non-food context. In contrast, Wells et al. (2008) used a free exploration method with objects of different colors in chimpanzees and gorillas (Wells et al., 2008). The preferred colors were green and blue, without a significant difference between these two colors. Against the assumption, these colors were chosen significantly more often than the red color.

We tested spontaneous color preference for both food and non-food objects in macaque monkeys (*Macaca mulatta*) to better understand what an adaptive function of red-color perception was. Both the food and non-food objects were tested in the same individuals, under the same laboratory conditions and with precisely defined colors.

We hypothesized that preference for or avoidance of red color and the context of such behavior may help us to understand what the adaptive advantage leading to a rapid expansion of a gene for a second pigment in the long-wavelength region was. Although the fruits that signal to monkeys are mostly yellow or orange (the red fruits signal mainly to birds), a newly developed color channel would have offered an additional advantage for discrimination ripe fruits over the ancient color subsystem (Sumner and Mollon, 2000). Therefore, we assumed that the preference for red color in food objects may reflect the foraging hypothesis – either frugivory or folivory.

Nevertheless, if there was a perceptual preference of red color across all contexts with a similar valence, the interpretation would not be clear. In contrast, avoidance of both food and non-food objects may reflect the function of red color in aposematic signaling (advertisement of unprofitability of a potential prey to a predator).

2. Methods

2.1. Ethical statement

All of the procedures complied with the Animal Protection Code 192 of the Czech Republic and with the European Council directives (2010/63/EC; 86/609/EEC). The study protocol was approved by the Animal Care Committee of the Third Faculty of Medicine at Charles University, Prague, Czech Republic. Primates were kept in a specialized facility owned by the Third Faculty of Medicine at Charles University in Prague, at the Department of Physiology. The facility is authorized by the Central Commission for Animal Welfare of the Ministry of Agriculture of the Czech Republic (accreditation No. 36505/2015-MZE-17214).

2.2. Subjects

Four macaque rhesus (*Macaca mulatta*) males examined under laboratory conditions.

The monkeys were tested individually but they were housed in suitable indoor cages in pairs. The two older (Attila, Puck, aged 14 at the beginning of the experiment) and two younger (Dante, Vergilius, aged 6) macaques were housed together, respectively. In 2016, two the younger males had to be separated because of a changing hierarchy and aggressive interactions. All of the monkeys had visual, auditory and olfactory contacts with the other monkeys. Their diet consisted of standardized granulated feed for omnivore primates with a daily addition of fresh fruits and vegetables and free access to water.

The experiments took place between 2014 and 2016. The macaques previously participated in various tests and cognitive training including spatial tasks using a touchscreen (Nekovarova at al., 2006; Nedvidek et al., 2008; Nekovarova et al., 2009, 2013), object permanence (unpublished data) and neophobia vs. neophilia experiments (Englerova et al., 2019). In these experiments we did not use any particular color as reward stimuli. Most of the stimuli were white patterns on a black background. The presented color preference experiment was performed simultaneously with numerical competency testing.

2.3. Color selection

Neural processing of information in the visual pathways and spectral sensitivity in humans and macaques are very similar (Harwerth and Smith, 1985), what also allows us to assess colors by humans.

In order to choose the most representative hues of the particular colors, we used a RAL color standard chart (RAL-K7, classic) containing examples of more than 200 colors. To narrow down the number of suitable hues, we asked 10 respondents to subjectively choose the most different hues for each color according to their personal preferences. Based on this, we made a set of 51 hues.

Each hue of the colors selected for the experiment (blue, green, red, yellow, including transitive colors as orange and purple) was measured with an OceanOptics USB4000 spectrophotometer, using a PX-2 Pulsed Xenon lamp source. Each hue was measured three times from a 5 mm distance and 45° angle to avoid interfering reflections from the paper's glossy surface in a shaded room. We re-calibrated the spectrometer before every third measurement using the WS-1 Diffuse Reflectance Standard. An average reflectance for each hue was calculated from the three consecutive measurements.

Black (5% reflection) and white (95 % reflection) were chosen as backgrounds on which the colored stimuli were presented. The final color samples were chosen by selecting hues with the highest distances (contrasts) from each other and the background colors. We used the CIE model for human vision (Wright, 1928, Guild, 1932) and ran the calculations with Avicol_v6 software (Gomez, 2006). The final colors were black, white, three shades of yellow, two shades of green, blue, red and gray (Table 1). This choice of colors guaranteed standard conditions and repeatability of the experiment.

The color stimuli were printed on a calibrated printer.

To standardize the test conditions throughout the testing, we used a lamp (reflector, LED 30 W, 4500 K).

Table 1
The colors used in the experiment.

Color	RAL number
BLACK	9005
WHITE	9003
RED	3020
YELLOW 1	1016
YELLOW 2	1021
YELLOW 3	1006
GREEN 1	6018
GREEN 2	6026
GREY	9022
BLUE	5002

2.4. Procedure 1 and Analysis (non-food objects)

Color preference of the macaques with non-food objects was tested in a laboratory environment as a two choice test. Two cups of different colors were presented in a pseudo-random order on a black or white background to control the effect of contrast. The right and left positions were also pseudorandomized. An edible reward of the same type and size (pieces of fruits, nuts etc.) was placed under each cup in sight of the monkey. The macaque subsequently chose one of the cups (lifted it or knocked it over) and took the reward placed underneath. The stimuli were presented on a platform outside the cage, so the monkeys can manipulate them. The color of the selected cup was considered to be a preferred one. This procedure was repeated 360 times (each color pair was repeated eight times, two times for each combination (side, background), for each of the four macaques. One session consisted of a maximum of thirty choices and lasted about 30 min. All of the experiments were video-recorded for later analysis. Pre-training with two cups of the same color took place before the actual experiment to eliminate the effects of neophobia or neophilia.

The data were analyzed using the R program (R Development Core Team, 2010). We employed a generalized linear model (glm, quasibinomial model, logit link function, X^2 test) for the statistical analysis of this data set. The choice of a stimulus in the trial (coded as presence/absence) was given as a dependent variable. We introduced color combination, black/white background, left/right side position and selected interactions of these factors as explanatory variables. Since there was no effect of the individual, we decided not to use a mixed model that would lead to the unnecessary addition of another variable.

2.5. Procedure 2 and analysis (food context)

Color preference of the macaques for food objects was examined under the similar laboratory conditions as in Procedure 1. This time, all of the colors were presented simultaneously on a black or white background. Edible stimuli were small pieces of sweet bread dyed by hand with food coloring. The appropriate color was achieved by subjectively comparing the shade with a printed color sample during preparation. All ten differently colored pieces were of the same size and taste.

The color of the selected piece of food was considered to be a preferred one. This procedure was repeated 40 times for each of the four macaques. The arrangement of colors was pseudorandom (10 different arrangements, same on the black and white background, with a balanced distribution of colors at the center or at the sides). One session consisted of a maximum of five presentations (trials) and lasted about 30 min. In the case that the monkeys chose more than one piece, we considered only the first choice. Before testing, we pre-trained the animals for the procedure using uncolored food.

Relationships between the selected COLOR, BACKGROUND on which the food objects were presented, the experimental SUBJECT, and all interactions of these factors were analyzed by a generalized linear model (GLM). Selection frequency was treated as a dependent variable with Poisson distribution and the log link function (procedure analogous to the log-linear analysis). The full model was further reduced by removing non-significant interactions and factors (SUBJECT and its interactions). The reduced model including COLOR, BACKGROUND and their interactions. Predictions, 95 % confidence intervals and post-hoc comparisons were computed from the model. The calculations were performed in an R environment (R Development Core Team, 2010).

3. Results

3.1. Experiment 1 (non-food objects)

The monkeys selected the colors in similar frequencies. The cumulative results for the entire group of macaques are shown in Fig. 1. The analysis of deviance revealed that none of the studied factors (color

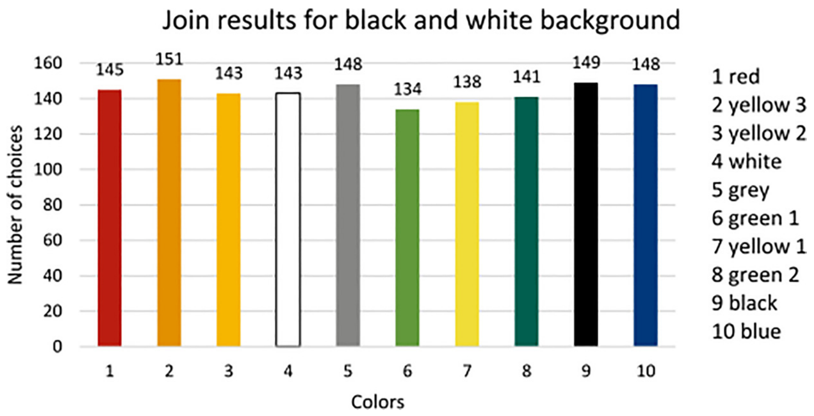

Fig. 1. Non-food objects: The cumulative results for the entire group of macaques, black and white backgrounds were analyzed together.

Table 2
The analysis of deviance examining the effects of predictors (factors) on choice of color in experiment with non-food objects.

Factor	Df	Deviance	Resid.Df	Resid.Dev	Pr (> X^2)
color combination	44	37.59	1395	1958.7	0.92
background	1	0.73	1394	1957.9	0.43
subject	3	3.89	1391	1954.0	0.35
side position	1	0.06	1390	1954.0	0.82
color combination: background	44	45.85	1346	1908.1	0.72
color combination: subject	132	126.12	1214	1782.0	0.96
background: subject	3	2.61	1211	1779.4	0.53
color combination: background subject	132	149.60	1079	1629.8	0.68

combination, black/white background, left/right side position) or their interactions affected the choice of color made by the macaques in this experiment (Table 2).

The results did not show any preference or avoidance to any of the colors of the presented non-food objects. Therefore, our data suggest that in non-food objects, colors do not play an important role for macaques.

3.2. *Experiment 2 (food objects)*

The choices on the black background were clearly biased in favor of Red and Yellow 3 colors, which were significantly ($\alpha = 0.05$) preferred over the other colors (Fig. 3). In contrast, the color preferences assessed on the white background were less apparent. Black color, exhibiting the highest contrast of lightness was selected most frequently, followed by Red, Blue, Grey, Green 2 and Yellow 3 (Fig. 2).

The effect of the experimental SUBJECT and its interactions appeared negligible (SUBJECT*COLOR: df = 27, p = 0.1340). Hence, this factor was removed from the final GLM including COLOR, BACKGROUND and their interactions. This revealed significant effects of COLOR (Dev. = 58.591, df = 9, $p < 0.0001$) and interaction (Resid. Dev. = 63.495, Resid. Df = 60, Dev. = 40.503, df = 9, $p < 0.0001$) (see Table 3).

4. Discussion

Our study clearly demonstrated preference for red color in food, but no preference in the case of non-food objects. The results of our experiments, supports one of the foraging hypotheses (frugivory or folivory).

Our experiment expanded on the existing research into color preference of primates by defining a comparison between food and non-food objects. Both experiments were performed under the same laboratory conditions, on the same subjects, with stimuli of the same precisely defined colors. We are aware that a certain preference for a color may also be a result of experience; however, as we know, the monkeys studied in this experiment were never previously trained to prefer (or avoid) any particular color. Nevertheless, some preference may have developed unintendedly (e.g. as they prefer black stimuli on a white background, which they experienced, but not the opposite contrast).

While our results for the color preference in food support the predominant results from existing research by showing preference for reddish colors, our results did not prove preference for any color in the case of non-food objects. The results of the non-food color preference task in our experiment suggest that unless the object is food or is presumed to be food, its color per se is irrelevant for the macaques, what

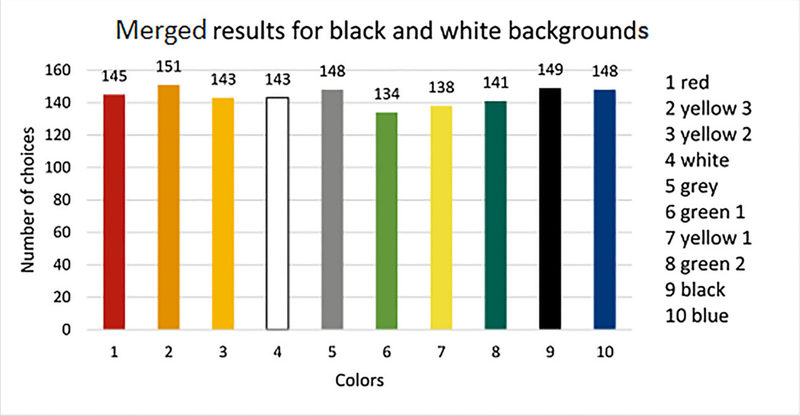

Fig. 2. Food objects: The cumulative results for the entire group of macaques, stimuli were displayed on a white background.

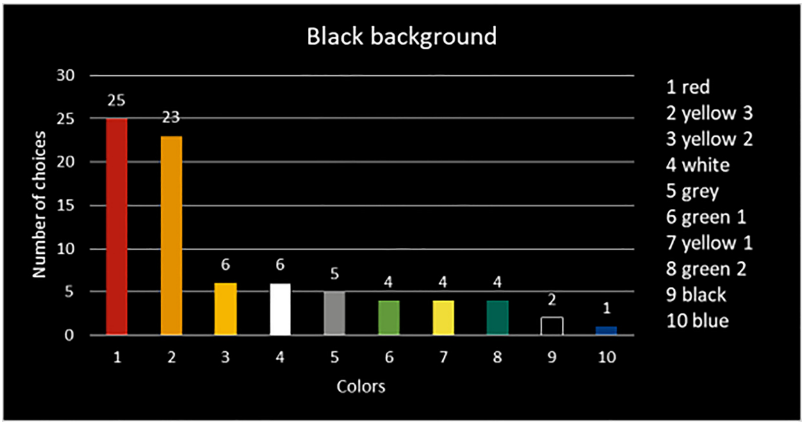

Fig. 3. Food objects: The cumulative results for all the macaques, stimuli were displayed on a black background.

illustrates the importance of the context in which the color is presented.

Our results for color preference in the case of non-food objects were, therefore, not in accordance with other studies: e.g. Wells (2008) found preferred colors (blue and green) in a free-exploration study. Such findings may be explained by the use of different experimental methods. In free-exploration tasks animals may explore objects directly and for that reason the objects can be associated with food or a threat. In our experiment the animals chose objects placed outside their cage. Moreover, they were trained in the previous experiment for similar two-choice tests and were familiar with such testing (Englerová et al., 2019). They obtain a reward after each choice, what may have also decreased the motivation for any selection. In that case, color did not necessarily play a role in the macaque's choice as it did not represent a threat, nor did it affect the food reward.

However, there may be another possible explanation connected with the different ecology of species involved in the experiments. In their natural environment, both species of apes (western lowland gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes*)) consume a substantial proportion of leaves, shrubs, herbs (all green in color) and fruits, either wild-growing or crop-raided (e.g., bananas-yellow, figs-blue/purple, pawpaws-green). The tendency of the animals in Wells' study (2008) to incline more towards the blue and green-colored stimuli may, therefore, arise from the association between these colors and more ecologically relevant types of food (Wells et al., 2008).

In contrast to the results of our experiments, which did not confirm either preference or aversion for non-food objects, Humphrey (1971) demonstrated avoidance to red color in a task where choices of the colors were not associated directly with food or sexual signalization. He led the macaque monkeys to control the color of lighting in their housing. He argued that monkeys may feel an aesthetic pleasure or non-pleasure based on aversion to red color, which could evoke blood or fire. Alternatively, according to Humphrey, red may be associated with a sunset or sunrise, the times during which their predators are most active. These findings suggest that color preferences may differ in the context in which the colors are presented. Whereas sunset or sunrise may bring aversive connotations, red colors may be attractive even in a non-food context. For example, Waitt et al. (2003, 2006) showed that a modified color of body parts (redder) is more attractive to other monkeys on such body parts, where it is naturally present.

In our study we demonstrated a significant preference for the red colors of food stimuli presented on both monochromatic backgrounds, what supports the dietary (frugivory and folivory) hypothesis. However, dark colors (e.g. black, blue and dark green) were also preferred, but only on the white background (Fig. 2).

This may also suggest the significance of achromatic contrast, as the importance of achromatic vision may be superior to color vision in recent mammals, including primates (Lišková et al., 2015). The ancestor of all mammals was characterized as a small nocturnal animal

Table 3
Coefficients and predictions of GLM.

Color x Background	Estimated coeficient	p	Predictions	Interval of confidence 2.5 %	Interval of Confidence 97.5 %
Red White	1.25	< 0.001***	3.50	1.97	5.67
Red Black	1.83	< 0.001***	6.25	4.11	9.03
White White	−0.29	0.62	0.75	0.19	1.94
White Black	0.41	0.32	1.50	0.60	3.04
Black White	1.32	< 0.001***	3.75	2.16	5.98
Black Black	−0.69	0.33	0.50	0.08	1.54
Blue White	1.10	< 0.001***	3.00	1.61	5.03
Blue Black	−1.39	0.17	0.25	0.01	1.10
Grey White	0.92	0.003**	2.50	1.25	4.38
Grey Black	0.22	0.62	1.25	0.45	2.69
Green 1 White	−0.29	0.62	0.75	0.15	1.94
Green 1 Black	0.00	1.00	1.00	0.31	2.32
Green 2 White	0.81	0.015*	2.25	1.08	4.06
Green 2 Black	0.00	1.00	1.00	0.31	2.32
Yellow 1 White	0.00	1.00	1.00	0.31	2.32
Yellow 1 Black	0.00	1.00	1.00	0.31	2.32
Yellow 2 White	−1.39	0.17	0.25	0.01	1.10
Yellow 2 Black	0.41	0.32	1.50	0.60	3.04
Yellow 3 White	0.81	0.015*	2.25	1.08	4.06
Yellow 3 Black	1.75	< 0.001***	5.75	3.71	8.43

(Kemp, 2005) for which the ability to distinguish achromatic contrast and patterns is essential. However, opposite contrast, i.e. a white stimulus on a black background, had no effect at all. Therefore, we suggest that the preference for dark colors on a white background may be more likely caused by the long-term experience of monkeys with naturally dark colored food (e.g. grapes, raisins, nuts etc.) presented on a light-colored plate (background).

Our results showing preference for reddish food also support the results of previous research. Barbiers (1985) demonstrated higher interest in colored food than in food without additional colors (standard food pellets). One of the five tested subjects (juvenile females) even chose and preferred red food. The author of the study (Barbiers, 1985) believes that color preference might also be shown in other individuals in cases they were isolated from each other because dominant individuals monopolized food and prevented others from picking it up.

Leonhardt et al. (2008) found that heterozygous females of polymorphic trichromats of prosimian primates are more efficient than dichromats in collecting food that was presented on a background of green painted sawdust. They also demonstrated preference for the red color, but only when red and green stimuli were presented. Van Lawick-Goodall (1968) also observed color preference in chimpanzees as they chose red, yellow or purple fruit from a pile that included less ripe fruit.

The frugivory hypothesis explains the evolution of trichromatic vision as a facilitation of the visual detection of fruit by frugivors (; Mollon, 1989; Bowmaker et al., 1991). The second scenario interprets trichromatic vision as adaptation for the detection of young reddish colored leaves (Lucas et al., 1998; Coley and Kursar, 1996) against a background of mature foliage (Sumner and Mollon, 2000a,Sumner and Mollon, 2000bb). Although there may be a different development in other primate lines, the dentition of the earliest known *Catarrhines* (e.g., *Catopithecus* and *Propliopithecus* spp.) by 33-34 Ma clearly indicates substantial leaf consumption (Kirk and Simons, 2001). The gene duplication in *Catarrhines* leading to routine trichromacy is estimated at ca. 35 Ma (Yokoyama and Yokoyama, 1989), what is further evidence supporting the folivory hypothesis in Catarrhines.

An alternative hypothesis assigns the evolution of trichromacy to socio-sexual communication. Past studies manipulated the skin and fur color of macaques (*Macaca mulatta*) in digital images presented to the primates of the same species (Waitt et al., 2003, 2006). The results showed that redder versions of specific anatomical features (e.g. female buttocks) attracted more attention to the opposite sex than the paler versions of those areas. A preference for the red color in sexual selection is connected to socio-sexual signaling (Waitt et al., 2003, 2006). However, recent data comparing color vision, sexual habits and the presence of colors on the skin or fur in 203 different primate species have challenged this hypothesis (Fernandez and Morris, 2007). According to the authors, signaling red skin and fur in intraspecies communication is a secondary adaptation to food selection.

5. Conclusion

The results of our experiments, i.e. preference for red color of food and no preference for any color in non-food objects, from the point of ecology and phylogeny indicate that the main advantage of trichromatic vision is not to detect nature's warning signals, but rather to be more efficient in food selection. We cannot contribute to the hypothesis of socio-sexual communication and the role of red color because we did not directly test it.

Author statement

T.N. designed and directed the project, interpreted the results and worked on manuscript; P.S. performed the experiments; processed the experimental data, worked on manuscript and designed the figures; R.R. was involved in planning and supervised the work, A.A. was involved in developing methods and in preparing color stimuli for the experiment. D.F. processed the experimental data, performed the analysis and interpreted the results. All authors discussed the results and commented on the manuscript.

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Declaration of Competing of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2020.104084.

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