Red-green color vision in three catarrhine primates

Francesca Fornalé,[1,2] Stefano Vaglio,[1,3,*] Caterina Spiezio[1] and Emanuela Prato Previde[2]

[1]Research and Conservation Department; Parco Natura Viva—Garda Zoological Park; Bussolengo, Italy; [2]Dipartimento di Scienze e Tecnologie Biomediche; Sezione di Psicologia; Università degli Studi di Milano; Segrate, Italy; [3]Laboratori di Antropologia; Dipartimento di Biologia Evoluzionistica; Università degli Studi di Firenze; Florence, Italy

The evolution of the red-green visual subsystem in trichromatic primates has been linked to foraging advantages, specifically the detection of either ripe fruits or young leaves amid mature foliage, and to the intraspecific socio-sexual communication, namely the signal of the male rank, the mate choice and the reproductive strategies in females. New data should be added to the debate regarding the evolution of trichromatic color vision. Three catarrhine primates were observed to achieve this goal. The research was performed on captive groups of vervet monkeys (*Chlorocebus aethiops*), pig-tailed macaques (*Macaca nemestrina*) and chimpanzees (*Pan troglodytes*) housed at Parco Natura Viva - Garda Zoological Park (Italy). Using pairs of red-green bags containing the same hidden reward in comparable outdoor enclosures, we recorded the choices by observed individuals (n = 25) to investigate the role of color cues in choosing an object. The results indicate that chimpanzees used red color as cue to choose an object that contains food by showing a preference toward red objects; in contrast, vervet monkeys and pig-tailed macaques do not demonstrate a clear choice based on the color of the object. Our findings highlight the importance of the foraging hypothesis but not rule out the potential role of the intraspecific socio-sexual communication and may serve to add useful information to the debate regarding the adaptive value of the evolution of color vision in order to fill a phylogenetic gap from Old World monkeys to humans. Future studies should address the role of socio-sexual communication, such as the selection of the reproductive partner of both high genetic quality and with compatible genes, to determine how this influenced the evolution of color vision in non-human primates.

Introduction

Due to four distinct cone receptor visual pigments in vertebrates, color vision is well developed in fishes, reptiles, and birds.[1,2] These pigments, which provide sensitivity to light in the UV to infrared range, are thought to have been present in ancestral vertebrates.[3] Later, when placental mammals became nocturnal, they lost two visual pigments and became dichromats. Finally, primates re-evolved to attain trichromacy.[4] In the nineteenth century, Grant Allen suggested that color vision in primates, birds, and insects evolved as an adaptation for foraging; this was related to colorful adverts displayed by plant fruits and flowers.[5] However, recent studies (for a review see ref. 6) have revealed that well developed color vision appeared long before the evolution of fruits and flowers. Accordingly, they emphasized that color vision is useful for several animals, in addition to species that eat colorful food.

Primates are the only placental mammals characterized by trichromacy; all other species examined to date are either dichromats or monochromats (for a review see ref. 7). This may indicate that trichromacy is particularly useful for primates and/or that, among placental mammals, primates have the unique ability to interpret signals provided by three spectrally distinct types of cones.[8]

In primate evolution, in two separate primate lineages, the deterioration of the olfactory repertoire occurred concomitant with the evolution of full trichromatic vision.[9] Thus, although it has not been demonstrated whether the decline in olfactory perception was a direct result of the development of color vision, it has been suggested that an exchange occurred in the significance of these two senses during evolutionary history. Trichromatic color vision is characterized by three retinal photopigments tuned to peak wavelengths of 430 nm, 535 nm, and 562 nm;[10] this characteristic evolved convergently in catarrhine primates and in one genus of New World monkey, the howlers (genus *Alouatta*).[11] The unique capacity to discriminate between red and green was proposed to benefit animals for long-range detection of either ripe fruit[12] or young leaves[13] against a background of mature foliage.[14,15] The reflectance spectra of several samples of fruit eaten by chimpanzees and other frugivorous monkey species has been measured.[16,17] When fruits were plotted in a color space appropriate for catarrhine primates, several distinct ripening patterns were evident. The degree of ripeness of many species would be discernible by dichromatic primates, but for most fruit a trichromatic consumer would be at an advantage. Primates are among the most frugivorous of mammals. Indeed, it was shown that, with the exception of tarsiers (Tarsius spp), all primate

species eat fruit; for folivorous species, fruit comprises 25–50% of the diet.[18] In addition, in contrast to species that are specialized seed predators, the majority of primates disperse the seeds of the tropical plant species they consume.[18] Consequently, given the importance of fruit to primates and of primates to the dispersal of plant species, co-evolution has produced a set of mutually beneficial characteristics: the dispersers have contemporary trichromatic vision to sense the color changes in fruit during maturation.[19] It has been hypothesized that the majority of primate species evolved trichromatic vision as a direct consequence of the chromatic signals produced by fruits[12] or leaves.[20] A primate feeding on fruit must first detect them against a background of leaves; vision and olfaction are probably the principal senses employed. Trichromacy has been predicted to be more efficient than dichromacy for detecting and identifying fruit against a leaf background.[12,14,21] In addition, to detecting fruiting trees, a primate has to select ripe from unripe fruits. The ripening process is often characterized by color changes; this gives a clear visual signal to potential dispersers regarding the tastiness of ripe fruit.[12] Theoretically, trichromats are thought to be capable of distinguishing ripe from unripe in a greater number of fruit species.[12,15]

Other authors[20] have shown that four trichromatic primate species, including the chimpanzee (*Pan troglodytes*), in the Kibale Forest (Uganda) eat leaves with discrimination based on red-greenness. This color axis is correlated with high/low protein levels and tenderness/toughness. Despite divergent digestive systems, these primates showed no significant interspecies differences in leaf color selection. On the other hand, the fruits eaten were generally discriminated from mature leaves based on red-green and yellow-blue visual channels and by luminance. These findings implied that maintaining trichromacy had unique value for survival in catarrhine primates, who rely on leaf consumption as a critical food source when fruit is scarce.[22] In addition, it has been reported[23] that some primates, including the chimpanzee (*Pan troglodytes*), consumed leaves with higher green-red values than the leaves they avoided-sensory mechanism that correlated with key nutritional variables, such as increased protein and reduced toughness. Moreover, they ingested leaves near dusk, when reddish targets may be more salient. Similar patterns were never observed with respect to edible fruits, the chromaticities of which did not differ from unconsumed fruits or correlate with nutritional properties.

Alternatively, other studies[24-28] supported a different theory from the foraging hypothesis. This hypothesis is based on the role of intra-species, socio-sexual communication. For example, brilliant displays of secondary sexual coloration occur throughout the animal kingdom; however, among mammals, these displays are limited to the primates. In particular, adult males of many Old World monkeys have particularly vivid coloration, usually involving the skin of the face and the anogenital regions, referred to as 'sexual skins'.[29] Various authors have proposed that these color displays function in male-male competition and dominance ranking.[24,25,30] Status has been associated with color intensity in three primate species: vervet monkeys (*Cercopithecus aethiops*);[31] gelada baboons (*Theropithecus gelada*);[30] and mandrills (*Mandrillus sphinx*).[24] In addition, several studies of insects,

fish, reptiles, and birds have reported that males used conspicuous coloration to attract mates (for a review see ref. 32); thus, another function of coloration might involve female mate choice. In addition, regarding this hypothesis on the role of intra-species socio-sexual communication, there are some studies (for a review see ref. 33) which represent another angle, based on the genetic evidence for the evolution of trichromatic color vision among catarrhines, stating that the gene duplication occurred relatively early in their radiation. Consequently, this alternative standpoint is based on the assertion that brightly colored secondary sexual characteristics evolved as a response to the visual adaptations. This viewpoint holds that trichromacy enabled some species of catarrhines to evolve red cues through both intra- and inter-sexual selection and that these cues could serve as honest signals because both males and females had the ability for discerning the hue and chroma of a red signal. However, other authors[34] showed that trichromacy evolved before red pelage and red skin, as well as before gregarious mating systems that would promote sexual selection for visual traits and other forms of intraspecific communication via red traits. They also defined that both red pelage and red skin were more likely to evolve in the presence of color vision and mating systems promoting sexual selection. These results provided statistical support for the hypothesis that trichromatic color vision in primates evolved in a context other than intraspecific communication with red traits, most likely foraging performance, but, once evolved, represented a pre-existing bias that promoted the evolution of red traits through sexual selection. It is considered that originally red-green visual system had evolved for foraging purpose and later it became to be used in socio-sexual context in some primate lineages. Despite its theoretical advantages, trichromacy is not a uniform trait across the primate order. Although all catarrhines studied to date are trichromatic, most platyrrhines have polymorphic color vision;[19,35] exceptions include the howler (Alouatta spp—uniformly trichromatic; see ref. 36), the night monkey (Aotus spp—uniformly monochromatic; see refs. 36–37), and some strepsirhines.[38,39] Most platyrrhine primates have both dichromatic and trichromatic individuals present in the same population. The selective forces acting to maintain the variation are hotly debated and are relevant to the evolution of the routine trichromatic color vision found in catarrhine primates. While trichromats have a foraging advantage for red food compared with dichromats, some studies[40,41] support dichromat advantage for certain tasks, related to the effects of light intensity on foraging success among marmosets (*Callithrix geoffroyi*), as contributes to maintenance of the color vision polymorphism. Furthermore, other authors report that particular trichromatic platyrrhine phenotypes may be better suited than others to foraging for particular fruits under particular conditions of illumination (for a review see ref. 42). However, all Old World monkeys have routine trichromatic vision achieved with separate loci for each of three opsins, leading to trichromacy in all individuals;[43] that is, their ability to distinguish colors does not depend on the genetic makeup, but appears in male and female individuals.[2,10] In this study, we tested the foraging hypothesis to determine whether this represented a key factor in selective pressure that induced primates to evolve trichromacy. We studied

Table 1. The frequency of occurrences for red-green first and overall choices shown by individuals belonging to the three study groups

| Species	Name	First choice			Overall choices		
		Green	Red	z-score	Green	Red	z-score
Vervet monkeys	Alf	4	4	-	4	4	-
	Chicca	9	1	-2.21	36	9	-3,88
	Fauna	3	3	-	20	18	-0,16
	Fiamma	3	3	-	12	13	0
	Florio	8	2	-1.58	45	31	-1,49
	Freccia	3	7	0.95	39	44	0,44
	Nicola	3	7	0.95	21	34	1,62
	Pansa	3	7	0.95	28	50	2,38
	Amelia	4	6	0.32	28	28	0
	Reda	4	5	-	13	12	0
	Ricky	4	5	-	26	23	-0,29
Pig-tailed macaques	Paula	6	4	-0.32	37	40	0,23
	Olaf	8	2	-1.58	37	42	0,45
	Ugla	2	8	1.58	25	31	0,67
	Betty	2	1	-	2	2	-
	Nemmy	7	3	-0.95	26	39	1,49
	Judy	2	8	1.58	20	35	1,89
	Samy	2	8	1.58	44	47	0,21
	Mary	5	5	0	15	18	0,35
	Camilla	4	6	0.32	22	23	0
Chimpanzees	Valentina	5	5	0	19	22	0,31
	Giorgina	4	5	-	14	17	0,36
	Luisa	5	4	-	9	8	0
	Davidino	4	3	-	10	11	0
	Tommy	1	1	-	6	6	0

Vervet monkeys (Chicca - first choices - Binomial test: Z = - 2.21; p < 0.05; Chicca - overall choices - Binomial test: Z = - 3.88; p < 0.05; Pansa - overall choices - Binomial test: Z = 2.88; p < 0.05); pig-tailed macaques (each individual - first and overall choices - Binomial test: N.S.); chimpanzees (each individual - first and overall choices - Binomial test: N.S.).

three catarrhines: vervet monkeys (*Chlorocebus aethiops*), pig-tailed macaques (*Macaca nemestrina*), and chimpanzees (*Pan troglodytes*); all these are routinely trichromatic species, but they have different phylogenetic placements. The study design was to present food rewards in red and green packages to determine whether these species showed a preference for a specific color.

Results

All colored (red/green) parcels were detected and consumed by groups belonging to the three study species (vervet monkeys, pig-tailed macaques and chimpanzees). None ignored any food items provided by the experimenter. At the individual level, regarding both first and overall choices, only two individuals, belonging to the same species (vervet monkeys), demonstrated a significant preference for a specific color—which was green (Chicca - first choices - Binomial test: Z = -2.21; p < 0.05; Chicca - overall choices - Binomial test: Z = -3.88; p < 0.05) or red (Pansa - overall choices - Binomial test: Z = 2.88; p < 0.05) (**Table 1**). At the group level, regarding both first (**Fig. 1**) and overall

(**Fig. 2**) choices, vervet monkeys and pig-tailed macaques did not demonstrate a significant preference (vervet monkeys: first choices - Wilcoxon test: tied Z = - 0.412; tied p = 0.680; overall choices - Wilcoxon test: tied Z = 0.000; tied p = 0.999; pig-tailed macaques: first choices - Wilcoxon test: tied Z = - 0.170; tied p = 0.865; overall choices - Wilcoxon test: tied Z = - 1.472; tied p = 0.141) for a specific color. In contrast to these two species of Cercopithecinae, regarding overall (Fig. 2) but not first (Fig. 1) choices, chimpanzees showed a significant preference (chimpanzees: first choices - Wilcoxon test: tied Z = - 1.382; p = 0.167; overall choices - Wilcoxon test: Z = - 2.459; p = 0.014) for red over green objects. Moreover, regarding the dependence between first and overall choices, vervet monkeys and chimpanzees showed a significant positive correlation between first choices toward red and overall choices toward red (vervet monkeys: tied ρ = 0.842; tied p = 0.039; chimpanzees: tied ρ = 0.945; tied p = 0.012) while pig-tailed macaques did not demonstrate a significant correlation. These results indicate that chimpanzees used red color as cue to choose an object that contains food by showing a preference toward red objects; in contrast, vervet monkeys
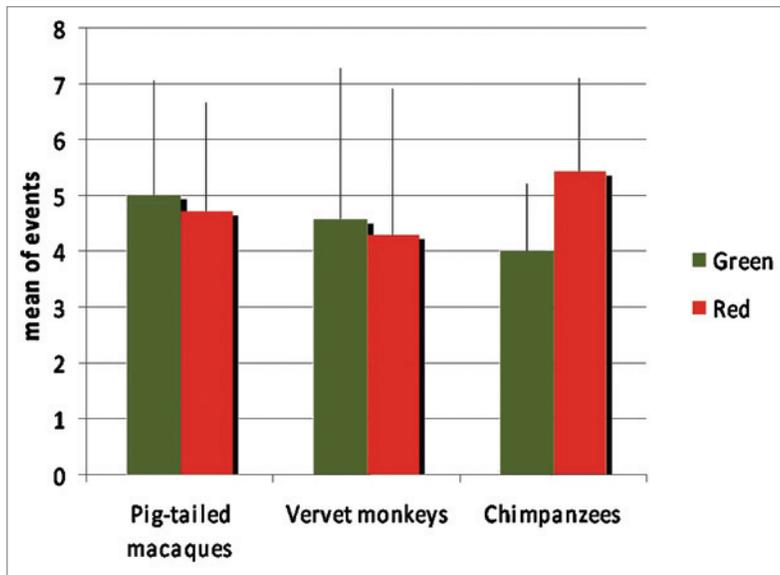
Figure 1. The average frequency of occurrences for red-green first choices shown by groups belonging to the three study species; error bars stand for the standard deviation; * p = 0.05. Vervet monkeys (Wilcoxon test: N.S.); pig-tailed macaques (Wilcoxon test: N.S.); chimpanzees (Wilcoxon test: Z = N.S.).
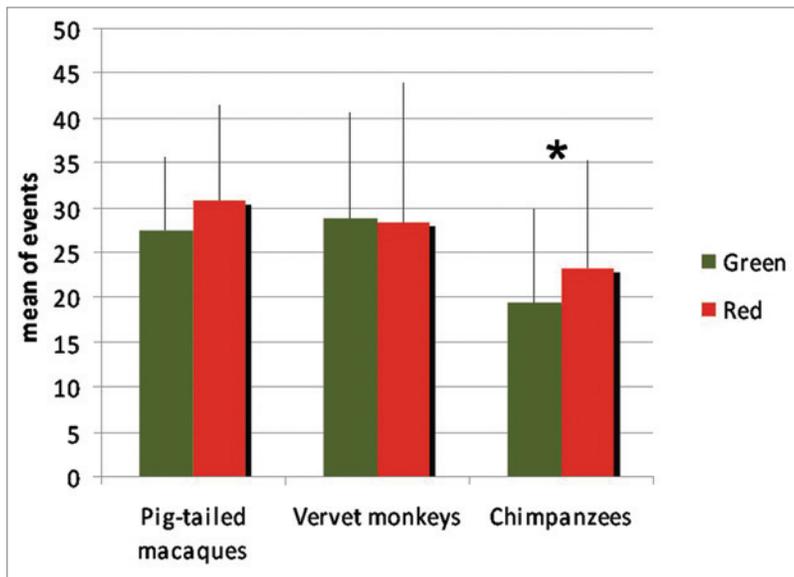
Figure 2. The average frequency of occurrences for red-green overall choices shown by groups belonging to the three study species; error bars stand for the standard deviation; * p = 0.05. Vervet monkeys (Wilcoxon test: N.S.); pig-tailed macaques (Wilcoxon test: N.S.); chimpanzees (Wilcoxon test: tied Z = - 2.459; tied p = 0.0139).

and pig-tailed macaques do not demonstrate a clear choice based on the color of the object.

Discussion

We tested the foraging hypothesis to determine its putative role in selective pressure that induced primates to evolve trichromacy. In particular, we investigated whether three catarrhines (vervet monkeys, pig-tailed macaques, and chimpanzees) showed a real capacity to select objects based on color features and possible preferences of red over green if they were given the opportunity to retrieve colored stimuli according to their species-specific ecology. On the basis of the foraging hypothesis the advantage of trichromacy is the ability to see ripe fruits (orange or red)[12] or edible leaves (dappled with red)[13] against a background of mature foliage.[14,15] Trichromatic vision is believed to be an important advantage in finding those palatable fruits or leaves. These would appear dark to dichromatic primates and be deceptive by making both fruits and leaves look different (lower in quality) than they actually are, resulting in decrease of the perceived window of feeding opportunity for such primates. Consequently, it is possible that trichromacy in catarrhine primates may have originally evolved for the detection of red coloration in both fruits or leaves of tropical plants, enabling the better exploitation of food resources. In the case of vervet monkeys and pig-tailed macaques, our results do not seem to support the foraging hypothesis. Indeed, neither group expressed a clear preference for red colored parcels in this plain, food-oriented research context. However, this behavior may have changed in a different context. For example, some researchers[30,44] hypothesize that the ability to distinguish between red and green is associated with the need to discern visual cues in the framework of social-sexual communication. These studies have suggested that the capacity for distinguishing red color would provide an advantage in selecting reproductive partners with both high genetic quality and compatible genes. Indeed, mate choice seems to be based on the recognition of red-colored, phenotypic features. These typically include secondary sexual ornamentations, like swelling in pig-tailed macaques (*Macaca nemestrina*),[29] facial coloration in mandrills (*Mandrillus sphinx*),[24-28] scrotal color in vervet monkeys (*Chlorocebus aethiops sabaeus*)[30] and geladas (*Theropithecus gelada*),[30] and hormonally-regulated increased reddening of facial and anogenital skin during the mating season in rhesus macaques (*Macaca mulatta*).[45] On the contrary, other authors,[33,34] based on genetic evidences, suggested that brightly colored secondary sexual characteristics evolved as a response to the visual adaptations. Therefore, they supported the hypothesis that trichromacy permitted some catarrhines to evolve red cues through sexual selection and that these cues could serve as honest signals. Consequently, we could not rule out the possibility that intra-species socio-sexual communication may have influenced the choice of color. On the other hand, at the group level the chimpanzees showed a clear preference for red-colored parcels. A positive correlation between first and overall choices toward these red objects was found, suggesting

the predictable pattern was followed by experimental evidence. Thus, in the case of chimpanzees our findings seem to support the foraging hypothesis. This outcome is inconsistent with findings of other authors reporting that captive chimpanzees paid significantly less attention to the red-, than to the blue- or green-colored stimuli[46] and, moreover, that red may function as a subtle stop signal working outside of focused awareness in humans[47] which can negatively affect human performance in a variety of contexts.[48] Nevertheless, these studies examined preference for color under different experimental designs and frameworks. In addition, currently the functional meaning of red color in primate communication, including the case of humans, is still a controversial issue.[24-26,49,50] However, our results might provide a framework for speculating about the adaptive value of the evolution of color vision in order to fill a phylogenetic gap from Old World monkeys to humans. Indeed, when all the evidence from this and the literature (i.e., primates are unique among the mammals in possessing trichromatic color vision, but not all primates are trichromatic and, in particular, among the haplorhine primates, the catarrhines possess uniformly trichromatic color vision while most of the platyrrhines exhibit polymorphic color vision)[10,12,13] was taken together, it suggested that the preference for red over green would appear to increase from primates that are more distantly related to humans (i.e., Old World monkeys) to primates that are less distantly related (i.e., Apes). In conclusion, our findings seem to provide support for the hypothesis that linked the evolution of trichromatic color vision to the foraging context. Nevertheless, we did not investigate a potential synergy between selective pressures from the foraging environment and intra-species socio-sexual communications in the achievement of color vision in the primate order. On top of that, this study provided additional pieces of information for the current debate on the evolution of trichromacy in primates. However, future studies should address the role of socio-sexual communication. In addition, a candidate should be identified for a key species that represents the branch-point in the evolution of color vision within the primate order.

Materials and Methods

Subjects and housing. We studied a total of 25 captive primates (**Table 2**), including eight vervet monkeys (*Chlorocebus aethiops*), seven pig-tailed macaques (*Macaca nemestrina*), and 10 chimpanzees (*Pan troglodytes*). The animals were housed at Parco Natura Viva - Garda Zoological Park (Italy).

Vervet monkeys. This group included eight animals at the beginning of data collection (five adults, and three juveniles). The animals lived in a 29-m² indoor and 454-m² outdoor enclosure. They were observed from September 2008 to March 2009.

Pig-tailed macaques. This group included seven animals at the beginning of data collection (all adults). The animals lived in a 45-m² indoor and 119-m² outdoor enclosure. They were observed from September 2008 to March 2009.

Chimpanzees. This group included 10 animals at the beginning of data collection (five adults, four subadults, and one juvenile). The animals lived in a 133-m² indoor and 1,357-m²

Table 2. Composition of the study groups during data collection

	Juveniles & Subadults		Adults		Total
	Male	**Female**	**Male**	**Female**	
Chlorocebus aethiops	2	1	2	3	8
Macaca nemestrina	.	.	2	5	7
Pan troglodytes	2	3	1	4	10
Total	4	4	5	12	25

outdoor enclosure. They were observed from March to September 2010.

Experimental procedure. We investigated the ability to select objects on the basis of color, and we determined possible preferences of red over green. Uniform food rewards, consisting of food that captive primates especially liked (i.e., gelatine, peanuts, sunflower seeds, and walnuts), were wrapped in red or green paper towels (33 x 33 cm). The paper towels were folded into small parcels that did not allow subjects to see the food rewards. Thanks to the standard method HSB system the color and lightness of both red (Hue = 0°; Saturation = 100°; Brightness = 86°) and green (Hue = 169°; Saturation = 100°; Brightness = 70°) paper towels were properly measured.

Experimental sessions were conducted in the usual social contexts. The colored stimuli (pairs of red and green parcels containing the same hidden reward) were dispensed to the study groups in the outdoor enclosure that animals were accustomed to using during the day. In each experimental session, two pairs of red and green parcels per animal were hung in the trees with strings (in the case of vervet monkeys) or scattered on the ground covered by a green grassland (in the case of pig-tailed macaques and chimpanzees) according to the ecology of each species, easily accessible to the primates. All the pairs were widespread to avoid competition and provide the opportunity to each individual to make their choice between only two parcels. If the choice of an individual appeared to be affected by those one of other group members, then data were not recorded.

Overall, 10 sessions were performed, 15 min each. Sessions were conducted at three-day intervals to avoid habituation by the study animals to the experimental procedure. This prevented the animals from learning a behavior, rather than making a spontaneous choice. Similarly, we varied the order of the parcels within each pair to avoid associations between color and position and, moreover, the type of food contained in the parcels over the test sessions to avoid possible associations between color and food reward. On top of that, we must stress that the experiment was designed under the same socio-ecological context that affect these species in the wild and, in addition, was conducted on the basis of procedures properly planned to avoid the possible influence by social learning.

Data collection. All experimental sessions were videotaped to allow accurate data collection. We assessed displays of preference for a specific color and, in particular, the preference for red over green, both at the individual level and at the group level. Thus, we evaluated (1) the first choice of red over green parcels in each test session (so-called "first choices"); and (2) the overall number

of times red was chosen over green in the same test session (so-called "overall choices"). The first choices permit to achieve the "validity" of choice, because not related to possible conditioning, habituation or learning processes; on the other hand, the overall choices follow a predictable pattern in reflecting decision-making.

All the behaviors shown by group members during the tests were recorded with the all occurrences sampling method.[51]

Data analysis. The statistical analysis was aimed at investigating the effect of color cues associated with objects. Data analysis was based on frequencies. To avoid problems associated with very low absolute amounts, we retained frequencies that comprised at least 6 and 17 events in the case of first and overall choices respectively. We used non-parametric statistical tests.[57] At the individual level, the binomial test was used for assessment of color choice preferences. At the group level, the Wilcoxon test was applied for comparison between red and green choice frequencies and the Spearman correlation was performed for measure of dependence between first and overall choices. All tests were two-sided, with the significance level set to 0.05. Analyses were performed with PASW Statistics version 18.0 (IBM Corp.).

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