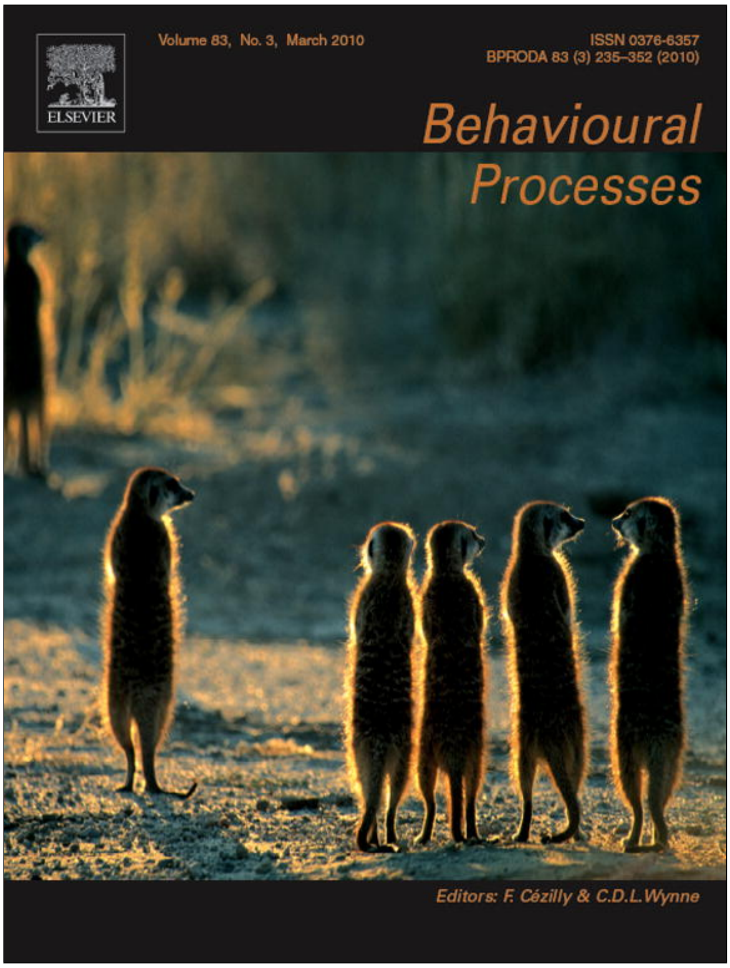
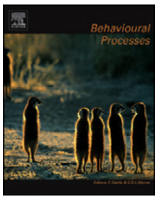

ELSEVIER
Volume 83, No. 3, March 2010
ISSN 0376-6357
BPRODA 83 (3) 235–352 (2010)
Behavioural Processes
Editors: F. Cézilly & C.D.L.Wynne

Behavioural Processes 83 (2010) 267–275

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



How to spend a token? Trade-offs between food variety and food preference in tufted capuchin monkeys (*Cebus apella*)

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A R T I C L E   I N F O

Article history:
Received 8 July 2009
Received in revised form 7 December 2009
Accepted 10 December 2009

Keywords:
Token exchange
Non-human primates
Variety-seeking

A B S T R A C T

Humans and non-human animals often choose among different alternatives by seeking variety. Here we assessed whether variety-seeking, i.e. the tendency to look for diversity in services and goods, occurs in capuchin monkeys – South-American primates which – as humans – are omnivorous and susceptible to food monotony. Capuchins chose between a Variety-token, that allowed to select one among 10 different foods (one more-preferred and nine less-preferred) and a Monotony-token, that – upon exchange with the experimenter – either allowed to select one among 10 units of the same more-preferred food or gave access to one unit of the more-preferred food. To examine how food preference affects variety-seeking, in the B-condition we presented nine moderately preferred foods, whereas in the C-condition we presented nine low-preferred foods. Overall, capuchins preferred the Variety-token over the Monotony-token and often selected one of the less-preferred foods. These results suggest that variety-seeking is rooted in our evolutionary history, and that it satisfies the need of experiencing stimulation from the environment; at the ultimate level, variety-seeking may allow the organism to exploit novel foods and obtain a correct nutritional intake. Finally, variety-seeking could have contributed to the transition from barter to money in many human cultures.

1. Introduction

Consumers are often attracted by large assortments of goods as they offer potential choice-related benefits. For one, it seems that the perceived complexity associated with the availability of numerous products and their novelty provides stimulation that is inherently satisfying (Berlyne, 1960; Bronyarczyk, 2008). Moreover, the possibility of choosing among a wide selection of items can increase intrinsic motivation (Deci, 1981), prediction of satisfaction (Botti and Iyengar, 2004), and the likelihood that an individual will find the optimal alternative (Chernev, 2003).

These benefits of large assortments enhance the appeal of making choices ("lure of choice", Bown et al., 2003) and extensive research on the influence of the features of a choice set on consumer decision making shows that humans prefer an option more when that option is offered as part of a choice than when it is offered alone (at least when all of the options are equal to, or of greater appeal than, the no-choice option; Suzuki, 1997, 2000). Moreover, variety-seeking, i.e. the tendency to look for diversity in services and goods, strongly affects individual behavior (Kahn, 1995; Inman, 2001; McAlister and Pessemier, 1982) and people consume more food when the perceived amount of variety in a choice set is larger than when it is smaller. For example, subjects presented with ten versus seven colors of M&M candies ate 43% more candy. Similarly, subjects presented with a mixed assortment of jelly beans ate 69% more than subjects presented with identical amount and variety of jelly beans, but sorted by color and flavor (Kahn and Wansink, 2004).

Similarly, animals prefer options that permit choices over options that do not (see Catania, 1980, for a review). Rats preferred a path leading to a choice between subpaths rather than a path leading directly to a food reward, though they all eventually led to the same reward (Voss and Homzie, 1970). Likewise, pigeons were more likely to peck a *choice* key (leading to *two* keys being lit, either of which could be pecked to obtain the same reward) than a *no-choice* key (leading to a single key being lit, to be pecked to obtain the reward), especially when pecking the terminal keys produced food only probabilistically rather than with certainty (Catania, 1975; Catania and Sagvolden, 1980; Ono, 2000). Long-tailed macaques (*Macaca fascicularis*) showed a similar attraction to choice, though it depended on the quality of the options. In fact, macaques preferred a *three-choice* option to a *no-choice* option only when two of the alternatives offered by the *three-choice* option were identical to the alternative offered in the *no-choice* option and

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doi:10.1016/j.beproc.2009.12.012

one was worse. When only one of the alternatives offered by the *three-choice* option was identical to the alternative offered in the *no-choice* option and two were worse they opted for the *no-choice* option (Suzuki, 1999; for similar results in humans see Suzuki, 1997, 2000).

Satiation, boredom, and curiosity are the hypothesized mechanisms underlying the search for variety (Gijsbrechts et al., 2000; van Trijp, 1995). In the food domain, comparative research has comprehensively investigated the phenomenon of within-meal sensory-specific satiety (i.e., the decline in pleasantness of a food following its consumption, e.g., Hetherington et al., 1989; Raynor and Epstein, 2001; Rolls et al., 1983)—demonstrating that sensory-specific satiety occurs both in humans and in non-human animals before any significant absorption takes place, and regardless of food initial pleasantness and macronutrient composition (Hetherington et al., 1989; Rolls, 1986).

Moreover, repeated exposure to a food for several days or weeks can result in the development of monotony (or "stimulus satiation", Glanzer, 1953), which is a decrease in food preference, acceptance, and/or consumption over time (Hetherington et al., 2002). For instance, refugees in an Ethiopian camp reported the taste of three foods they had been eating for about six months as less pleasant compared to three novel foods (Rolls and de Waal, 1985). Similarly, rats and hamsters presented over four days with either a four-course varied diet or with a four-course monotonous diet ate less of the latter (DiBattista and Sitzer, 1994; Treit et al., 1983); also, when fed one of two different diets for several consecutive days and subsequently offered to choose between these two diets, individuals of both species showed a reduced intake of the previously eaten diet (DiBattista, 2002; Galef and Whiskin, 2003, 2005). As a consequence, rats prefer a cafeteria diet (i.e. *ad libitum* access to an assortment of energy rich foods) to a standard maintenance diet (Rogers and Blundell, 1984).

In the present study, we used a novel paradigm based on token exchange to assess the robustness of variety-seeking in capuchin monkeys – South-American primates which shared a common ancestor with us about 35 million years ago. Capuchin monkeys are an ideal model species to investigate variety-seeking, since – as humans – they are omnivorous and susceptible to food monotony. Already Osman Hill (1960) reported that capuchins, when allowed to eat as much as they like of their preferred food, refused to accept again that food for about two days. Likewise, previous research demonstrated that, when offered a monotonous versus a varied food (with a similar caloric content and level of preference), capuchins significantly preferred the varied food since the first exposures (Addessi, 2008).

Here we investigated whether capuchins prefer a Variety-token, that allows them to choose one among 10 different foods (one more-preferred and nine less-preferred foods) or a Monotony-token, that either allows them to choose one among 10 units of the same more-preferred food or gives access to one unit of the more-preferred food. Three outcomes were possible: (i) if attracted by the more-preferred food, capuchins could opt for the Monotony-token, (ii) if "lured" by the opportunity of choosing among different alternatives, though attracted by the more-preferred food, capuchins could prefer the Variety-token and then select the more-preferred food, (iii) if guided by variety-seeking regardless of the level of preference of the foods offered, capuchins could prefer the Variety-token and then select one of the less-preferred foods.

In addition, to examine how food preference affects variety-seeking, we manipulated the appeal of the nine less-preferred foods that were presented in exchange for the Variety-token. In a first condition, we presented nine moderately preferred foods (B-foods), whereas in a second condition we presented nine low-preferred foods (C-foods).

2. Materials and methods

2.1. Subjects

Eight captive-born capuchin monkeys (four males, four females, mean age 19 years, range 6–29) were tested. All subjects were already proficient in token exchange. They lived in three groups at the Primate Center of the Istituto di Scienze e Tecnologie della Cognizione of CNR, in Rome; each group was housed in indoor–outdoor compartments (total area: 53.2–374.0 m^3, depending on group size) and tested in one of the two indoor compartments (12.2 m^3 each, for all groups). All the outdoor compartments were furnished with wooden perches, tree trunks and bark. Separation for individual testing was achieved by splitting the group into smaller units by means of sliding doors and then allowing one individual to enter the indoor compartment. This procedure was part of the daily routine. Monkeys were not food deprived for testing. The main meal took place in the afternoon when fresh fruits, vegetables, eggs, monkey chow, and cheese porridge were provided (for a total of about 875 kcal, 100 g of carbohydrates, 13 g of fats and 48 g of proteins per day for each subject). Water was available *ad libitum*. This study complied with protocols approved by the Italian Health Ministry. All procedures were performed in full accordance with the European law on humane care and use of laboratory animals and conformed to the "Guidelines for the use of animals in research".

2.2. Apparatus

Subjects were tested individually in the indoor compartment. In each trial two apparatuses were used consecutively (see below, Experimental phase). The "token choice apparatus" was a black PVC table (65 cm × 64 cm × 13.5 cm) with two sliding aluminum trays (6.5 × 40 cm; 2.5 cm high), positioned at 32 cm distance from one another. Each tray had two holes (1.4 cm in diameter), one at each end; one served to allow the subject's pulling, whereas the other hole allowed the experimenter to block the tray by inserting a pin into it (Fig. 1a). All subjects were already familiar with the apparatus (Addessi et al., 2007, 2008a,b).

The "food tray" was a Plexiglas box open on the back side. On the vertical side of the box facing the experimental subject, 10 holes (diameter 1.5 cm each) were drilled. According to condition, either one or 10 units of food were placed in small pits on the box's horizontal surface (see below, Experimental phase). The pits were in correspondence with the holes. The subject could indicate its choice by inserting its finger in one of the 10 holes (Fig. 1b). Two replicas of the food tray were available in each trial, the Monotony food tray and the Variety food tray (see below, Experimental phase).

2.3. Tokens

Tokens are intrinsically valueless objects that capuchins can learn to accurately value; recent research showed that they can represent, estimate and combine token quantities (Addessi et al., 2007, 2008a) and that they employ similar cognitive mechanisms to choose between tokens and between real foods (Addessi et al., 2008b). We used as tokens objects of similar dimensions, differing in shape, material, and color (e.g., poker chips, plastic cylinders, metal nuts). In particular, we pseudo-randomly assigned to each subject three objects as tokens, namely the Monotony-token (which could be exchanged with the experimenter for one unit of more-preferred food), the Variety-B-token (which could be exchanged for one unit of food to be chosen among one more-preferred food and nine moderately preferred foods), and the Variety-C-token (which could be exchanged for one unit of food to be chosen among one more-preferred food and nine low-preferred foods).

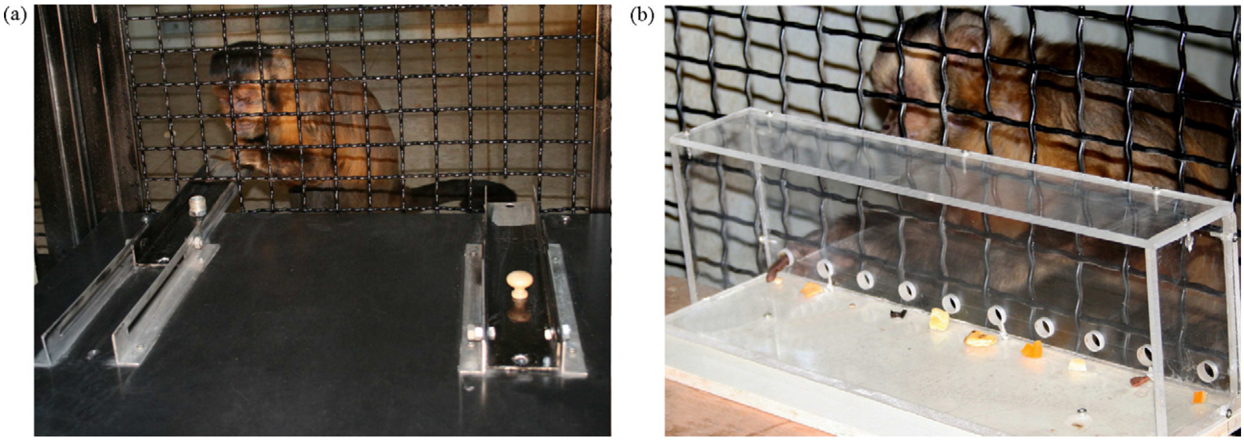

Fig. 1. Robot chooses the Variety-token from the token choice apparatus (left panel, a) and, after exchanging it with the experimenter (not shown), selects a pine nut from the food tray (right panel, b).

2.4. Procedure

For all subjects the entire procedure was repeated twice. First, capuchins received the B-condition (involving nine moderately preferred foods) and then the C-condition (involving nine low-preferred foods). Due to poor health conditions, one of our subjects (Carlotta) was not tested in the C-condition. The study took place between January and June 2008.

2.4.1. Preliminary phase

Before the onset of each condition, preliminary food preference tests were carried out in order to select the foods to be used with each subject in the experimental phase. Before the B-condition, in each trial capuchins faced a binary choice between one or two pieces of more-preferred food (A-food) and one to four pieces of potentially moderately preferred foods (B-foods). Therefore, the following comparisons were presented: 2A:1B, 1A:1B, 1A:2B, 1A:3B, and 1A:4B; each combination was presented four times for a total of 20 trials in a pseudo-random order. The left/right arrangement of the offers was counterbalanced within each session. Each subject received one session a day for each food pair and a potential B-food was selected when the indifference point for the A:B pair was between 1A:2B and 1A:3B in a single 20-trial session. These tests were repeated until nine B-foods satisfying these conditions were found for each subject.

Before the C-condition, the same procedure was employed with the following differences: (i) in each trial capuchins faced a binary choice between one piece of more-preferred food (A-food, the same used in the B-condition) and one to five pieces of potentially low-preferred foods (C-foods) and (ii) a potential C-food was selected when the indifference point for the A:C pair was between 1A:3C and 1A:4C in a single 20-trial session. Tables 1 and 2 report a list of the food used and the assignment of foods to subjects.

Thus, at the end of the Preliminary phase, for the B-condition we selected one more-preferred food (A-food) and nine moderately preferred foods (B-foods). For the C-condition we selected the same more-preferred food (A-food) as in the B-condition and nine low-preferred foods (C-foods).

2.4.2. Training phase

The training procedure consisted of placing 12 tokens of the same type on the floor of the indoor compartment, and repeatedly saying ‘give me’ to the subject while requesting a token, with left hand outstretched and palm up. The reward was given upon the placement of one token into the experimenter's left hand. There was a 10-s interval between one trial and the next one. Incorrect exchanges, in which tokens were thrown or incorrectly placed into the experimenter's hand, were not rewarded. Moreover, when the subject did not exchange a token within 30 s, the trial was considered incorrect and a new trial started after 10 s. Subjects received a training session per day. Each session consisted of two blocks of 12 trials each, for a total of 24 trials. Criterion was set at 90% correct exchanges within two consecutive sessions.

Before the onset of the B-condition, subjects learned to exchange first the Monotony-token and then the Variety-B-token. When criterion was reached for both types of token, each subject received six sessions of consolidation, in which the same procedure described above for the training phase was used and the two types of token (Monotony-token and Variety-B-token) alternated across days. Thus, three additional training sessions were carried out for each type of token. Before the onset of the C-condition, subjects learned to exchange the Variety-C-token and, after reaching criterion, they received six sessions of consolidation with the two types of token (Monotony-token and Variety-C-token) alternating across days. For exchanging the Variety-token, subject could choose as reward one among 10 different foods (one more-preferred and nine less-preferred foods). For exchanging the Monotony-token, subjects could choose as reward one among 10 units of the same more-preferred food or a single unit of the more-preferred food (according to condition, see below). Foods were presented on the same “food tray” used during the experimental phase (see below).

Capuchins completed training (including the six sessions of consolidation) in a mean of 9.4 ± 0.51 sessions. In particular, they reached criterion in a mean of 2.5 ± 0.27 sessions for the Monotony-token (range: 2–4), and 2.12 ± 0.12 sessions for the Variety-B-token (range: 2–3); all capuchins reached criterion for the Variety-C-token in 2 sessions. The rate of training of the present study is similar to that reported for capuchins learning to associate different type of tokens with different quantities of food (Addessi et al., 2007, 2008a).

2.4.3. Experimental phase

Each trial consisted of two choice stages. First, capuchins faced a binary choice between a Variety-token and a Monotony-token on the token choice apparatus (Token choice, Fig. 2; see also Fig. 1a). The left/right arrangement of the token offers was counterbalanced across trials. Soon after the subject performed its token choice, experimenter 1 asked the subject to exchange the token and experimenter 2 pushed one of the food trays (depending on the subject's choice) close to the wire mesh so that the subject could indicate its food choice to the experimenter (Food choice, Fig. 2; see also Fig. 1b).

Table 1
Caloric content and macronutrient composition for each food used.

Food	Energy (kcal/100 g)	Carbohydrates (g/100 g)	Fats (g/100 g)	Proteins (g/100 g)
All-bran	260	74.2	4.9	13.1
Bacon	276	0	23.6	15
Banana chips	529.4	61.8	29.4	2.9
Boiled carrots	35	8.2	0.2	0.8
Boiled lupines	116	9.3	2.9	15.6
Boiled potatoes	86	20	0.1	1.7
Canned black olives	235	0.8	25.1	1.6
Canned Borlotti beans	91	15.9	0.5	6.7
Canned chickpeas	100	13.9	2.3	6.7
Canned corn	98	19.5	1.3	3.4
Canned crab	77	2	0.5	18
Canned mushrooms	25	5.1	0.3	1.9
Canned peas	50	9.2	0.3	3.1
Canned shrimps	99	0	1.4	20.4
Cheerios	367	74.7	5.9	11.3
Cocoa krispies	381	86	2.9	5.2
Corn pops	378	90	0.7	3.7
Dark raisins	300	79.1	0	2.3
Diced coconut	490	64	24	4
Dried apples	300	75	0	2.5
Dried apricots	300	72.5	0	2.5
Dried cantaloupe	350	87.5	0	0
Dried cranberries	350	82.5	0	0
Dried kiwi	340	16	0	0
Dried mango	400	100	0	0
Dried papaya	350	87.5	0	0
Dried pear	350	90	2	2
Dried plums	240	64	0	4
Dried potato chips	559	52	38.4	4.4
Glazed pineapple	330	82	0	0.8
Glazed citron	310	78	0	0.2
Glazed orange peel	374	72	0	1.5
Gruyere cheese	413	0.4	32.3	29.8
Parmesan cheese	392	3.2	25.8	35.7
Pine nuts	671.4	14.3	67.9	14.3
Pretzels	378	79.2	2.6	10.3
Pumpkin seeds (no shell)	642.9	14.3	50	32.1
Raw Brazil nuts (no shell)	678.6	14.3	67.9	14.3
Raw sunflower seeds (no shell)	571.4	17.9	50	21.4
Rice krispies	387	85.2	1	6.8
Roasted cashews	571.4	28.6	50	17.9
Roasted pistachios (no shell)	614.3	28.6	53.6	20
Romano cheese	387	3.6	26.9	31.8
Rosetta bread	269	57.6	1.9	9
Sun dried tomatoes	200	40	0	13.3
Unleavened bread	377	87.1	0,8	10.7

Data are from the following sources: http://www.inran.it/servizi_cittadino/per_saperne_di_piu/tabelle_composizione_alimenti; http://www.acaloriecounter.com/; http://www.dieta-dimagrante.com/nutrienti/index.htm and http://www.nutsonline.com/.

If subjects preferred the Monotony-token, they could exchange it for one unit of more-preferred food offered on the Monotony food tray. To control for the effect of perceived numerousness on capuchins' choices, our sample was split in two experimental groups in which the number of units of more-preferred food presented on the Monotony food tray differed: half of the subjects ($group_1$) received only a single unit of more-preferred food, whereas half of the subjects ($group_{10}$) received a choice among ten units of the same more-preferred food. If subjects preferred the Variety-token, they could exchange it for one unit of food to be chosen among one more-preferred food and nine less-preferred foods offered on the Variety food tray. The food trays were baited out of view of the experimental subject during the intertrial interval; the relative position of the 10 foods on the Variety food tray was modified across trials in a pseudorandom way.

In both conditions, the caloric content of the less-preferred foods did not significantly differ from that of the more-preferred food, whereas the macronutrient composition did. In particular, the carbohydrate amount was higher for the more-preferred food than for the less-preferred foods, whereas an opposite trend was observed for the protein and fat amount. Moreover, the mean caloric content of the less-preferred foods significantly differed between conditions, whereas the macronutrient composition did not (Table 3).

Though capuchins had different more-preferred foods and different arrays of less-preferred foods (depending on the preferences expressed by each subject during the Preliminary phase, see above), in both conditions the caloric content and the macronutrient composition of the more-preferred foods and of the less-preferred food arrays did not significantly differ among subjects (caloric content, B-condition: More-preferred food: $\chi^2_7 = 7.94$; $p = 0.34$, Less-preferred foods: $\chi^2_7 = 0.75$; $p = 0.99$, C-condition: More-preferred food: $\chi^2_6 = 7.52$; $p = 0.27$, Less-preferred foods: $\chi^2_6 = 1.02$; $p = 0.98$; carbohydrate amount, B-condition: More-preferred food: $\chi^2_7 = 2.65$; $p = 0.91$, Less-preferred foods: $\chi^2_7 = 0.09$; $p = 0.99$, C-condition: More-preferred food: $\chi^2_6 = 1.11$; $p = 0.98$, Less-preferred foods: $\chi^2_6 = 0.18$; $p = 0.99$; fat amount, B-condition: More-preferred food: $\chi^2_7 = 3.75$; $p = 0.81$, Less-preferred foods: $\chi^2_7 = 0.43$; $p = 0.99$, C-condition: More-preferred food: $\chi^2_6 = 0$; $p = 1.0$, Less-preferred foods: $\chi^2_6 = 2.76$; $p = 0.84$; protein amount, B-condition: More-preferred food: $\chi^2_7 = 0.49$; $p = 0.99$, Less-

Table 2
High-preferred food and less-preferred food assigned to each subject in the two conditions.

Subjects	High-preferred food	Less-preferred foods (B-condition)	Less-preferred foods (C-condition)
Cammello	Glazed citron	Banana chips, Brazil nuts, Cheerios, Diced coconut, Dried kiwi, Pine nuts, Raw sunflower seeds, Roasted cashews, Rosetta bread	All bran, Canned corn, Canned crab, Canned mushrooms, Canned peas, Cocoa krispies, Corn pops, Dried cantaloupe, Dried cranberries
Carlotta	Roasted pistachios	Banana chips, Brazil nuts, Cheerios, Dark raisins, Diced coconut, Dried papaya, Glazed citron, Roasted cashews, Sun dried tomatoes	-
Gal	Glazed pineapple	Banana chips, Canned black olives, Cheerios, Dark raisins, Dried apples, Dried cranberries, Dried kiwi, Glazed citron, Parmesan cheese	Bacon, Boiled carrots, Canned corn, Corn pops, Dried pear, Dried plums, Gruyère cheese, Romano cheese, Unleavened bread
Paprica	Glazed pineapple	Banana chips, Brazil nuts, Canned black olives, Diced coconut, Dried mango, Parmesan cheese, Pine nuts, Roasted cashews, Rosetta bread	All bran, Boiled lupines, Canned corn, Canned shrimps, Dried apples, Dried cantaloupe, Dried kiwi, Gruyère cheese, Rice krispies
Pippi	Glazed citron	Banana chips, Brazil nuts, Cheerios, Dark raisins, Diced coconut, Dried kiwi Dried plums, Parmesan cheese, Rosetta bread,	All bran, Canned crab, Canned peas, Cocoa krispies, Dried cranberries, Gruyère cheese, Pretzels, Rice krispies, Unleavened bread
Robinia	Dried apricots	Banana chips, Brazil nuts, Dark raisins, Dried apples, Dried cranberries, Parmesan cheese, Pine nuts, Raw sunflower seeds, Roasted cashews	Boiled carrots, Canned Borlotti beans, Canned chickpeas, Canned crab, Canned peas, Canned shrimps, Cocoa krispies, Dried pear, Rosetta bread
Robot	Dried apricots	Banana chips, Brazil nuts, Canned black olives, Dried plums, Glazed orange peel, Parmesan cheese, Pine nuts, Roasted cashews, Rosetta bread	Boiled potatoes, Cocoa krispies, Dried apples, Dried pear, Gruyère cheese, Pretzels, Pumpkin seeds, Rice krispies, Unleavened bread
Sandokan	Dried apricots	Banana chips, Canned black olives, Cheerios, Dried apples, Glazed orange peel, Parmesan cheese, Pine nuts, Roasted cashews, Sunflower seeds	Boiled carrots, Boiled lupines, Canned chickpeas, Canned corn, Canned shrimps, Corn krispies, Dried potato chips, Gruyère cheese, Romano cheese

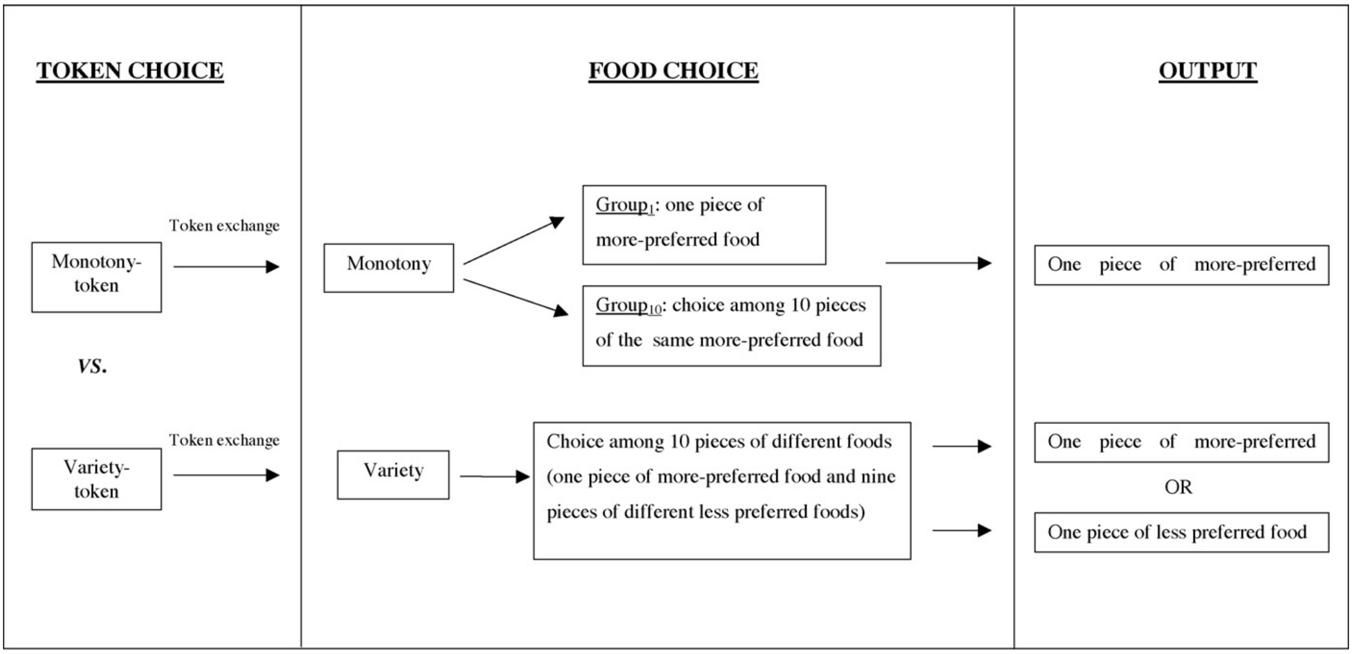

Fig. 2. Schematic representation of the experimental phase.

Table 3
For each condition, median and interquartile range of the caloric content and macronutrient composition of the high-preferred food and of the less-preferred foods and results of the statistical comparison of (i) caloric content and macronutrient composition between high-preferred food and less-preferred foods for each condition and (ii) caloric content and macronutrient composition of the less-preferred foods between conditions.

	B-condition ($N=8$)			C-condition ($N=7$)			B-condition *vs.* C-condition
	High-preferred food	Less-preferred foods	High-preferred *vs.* less-preferred foods	High-preferred food	Less-preferred foods	High-preferred *vs.* less-preferred foods	Less-preferred foods
kcal	0.90 (0.48)	0.92 (0.11)	$T=7$, p exact = 0.15	0.90 (0.68)	0.47 (0.14)	$T=3$, p exact = 0.08	$T=0$, p exact = 0.02
Carbohydrates	0.22 (0.11)	0.09 (0.02)	$T=4$, p exact = 0.05	0.22 (0.09)	0.08 (0.03)	$T=1$, p exact = 0.03	$T=6$, p exact = 0.22
Fats	0	0.06 (0.03)	$T=1$, p exact = 0.02	0	0.01 (0.01)	$T=0$, p exact = 0.02	$T=3$, p exact = 0.08
Proteins	0.004 (0.01)	0.02 (0.01)	$T=1$, p exact = 0.02	0.02 (0.01)	0.02 (0.01)	$T=0$, p exact = 0.02	$T=5$, p exact = 0.16

preferred foods: $\chi^2_7 = 0.06$; $p = 1.0$, C-condition: More-preferred food: $\chi^2_6 = 0.17$; $p = 0.99$, Less-preferred foods: $\chi^2_6 = 0.10$; $p = 0.99$).

Testing was carried out by two experimenters: experimenter 1 sat in front of the subject's indoor compartment and operated the token choice apparatus, which was placed on the floor between the experimenter and the wire mesh of the indoor compartment. Experimenter 2 sat next to experimenter 1 and, during the baiting of the token choice apparatus, covered the apparatus with an opaque screen to prevent the subject from seeing the baiting process. Then, she lifted the screen and experimenter 1 pushed the apparatus towards the wire mesh, so that the subject could pull one of the two trays, each containing a token. Both experimenters refrained from looking at the apparatus so as not to provide cues to the subject. Each subject received one 20-trial session a day for a total of 20 sessions (400 trials); the inter-trial interval was about 10 s.

2.4.4. Post-test phase

In both conditions, to assess whether the order of preference for the foods has changed in the course of the experimental phase, upon its conclusion the food preferences of each individual were assessed by presenting all the possible binary combinations between the 10 foods (the more-preferred food and the less-preferred foods) on the token choice apparatus.

2.5. Data analysis

2.5.1. Experimental phase: B-condition

Both at the individual and at the group level, we assessed whether capuchins preferred the Monotony- or the Variety-token with a Chi-square test performed on the number of choices. Moreover, to evaluate whether their choices were affected by perceived numerousness (i.e., by the number of units of the more-preferred food presented on the food tray when the Monotony-token was exchanged), we compared the Variety-token choices between the two experimental groups (group$_1$ and group$_{10}$, see above) by the Mann–Whitney *U* test.

At the individual level only, for each choice of the Variety-token we assessed whether subjects chose one of the less-preferred food or the more-preferred food with a Chi-square test. Moreover, we evaluated whether choices for one of the less-preferred foods after exchanging the Variety-token varied across sessions by performing a Spearman rank-order correlation. Furthermore, in each session we appraised whether sensory-specific satiety occurred by performing, for each food chosen (more-preferred or less-preferred), a Spearman rank-order correlation between the subject response in each trial (1 corresponding to choosing the food, 0 corresponding to not choosing the food) and the number of trials. We also calculated the mean percentage of energy and macronutrients consumed during each session relatively to the energy and macronutrient composition of the basal diet. Finally, we appraised whether individual food preferences were stable across sessions by the Kendall Coefficient of Concordance.

2.5.2. Experimental phase: C-condition

All the analyses performed in the B-condition were carried out also in the C-condition.

2.5.3. Experimental phase: B-condition versus C-condition

We assessed whether capuchins behaved differently when faced with moderately preferred foods (B-condition) or low-preferred foods (C-condition) by the Wilcoxon matched-pairs signed-ranks test. In particular, we compared (1) the percentage of choices for the Variety-token, (2) the percentage of choices for one of the less-preferred foods (regardless of the food chosen), (3) the mean number of different less-preferred foods chosen in each session in which subjects chose the Variety-token and then one of the less-preferred foods, (4) the total energy and macronutrient intake. All the comparisons between the B- and the C-condition were performed on the seven subjects that took part to both conditions.

2.5.4. Post-test phase

In each condition, we assessed each individual's preference for all the 10 foods (the more-preferred and the less-preferred ones).

3. Results

3.1. Experimental phase: B-condition

At the group level, capuchins preferred the Variety-token significantly above chance (mean% ± SE: 73.94 ± 5.23, $\chi^2_7 = 24.46$; $p < 0.001$). At individual level, six out of eight capuchins preferred the Variety-token significantly above chance (all $p_s < 0.01$), whereas two capuchins (Cammello and Robinia) were indifferent between the Variety- and the Monotony-token. Whether the more-preferred food was presented as a single unit or as 10 units of the same food to choose from, capuchins chose the Variety-token to a similar extent (group$_1$: median and IQR: 13.87 (6.11); group$_{10}$: median and IQR: 16.07 (1.29); $U = 7$, $n_{1,10} = 4$; p exact = 0.89).

When choosing the Variety-token, all capuchins significantly preferred one of the less-preferred food over the more-preferred food since the first session (all $p_s < 0.03$); moreover, they selected one of the less-preferred foods in the first trial in which they chose a Variety-token in 17.5 ± 0.96 sessions (out of 20) on average. For four capuchins (Gal, Robot, Robinia, and Pippi), the number of choices for one of the less-preferred foods after exchanging the Variety-token increased across sessions (Gal: $r_s = 0.48$, $N = 20$; $p = 0.03$; Robot: $r_s = 0.82$, $N = 20$; $p < 0.001$; Robinia: $r_s = 0.66$, $N = 20$; $p < 0.01$; Pippi: $r_s = 0.63$, $N = 20$; $p < 0.01$), for one capuchin (Cammello) it decreased across sessions ($r_s = -0.49$, $N = 20$; $p = 0.03$), and for three capuchins (Sandokan, Paprica, and Carlotta) there was no significant variation (Sandokan: $r_s = 0.38$, $N = 20$; $p = 0.10$; Paprica: $r_s = 0.26$, $N = 20$; $p = 0.28$; Carlotta: $r_s = 0.01$, $N = 20$; $p = 0.95$).

Sensory-specific satiety accounted for capuchins' behavior only to a limited extent. On average, there was a significant decrease of the choice of a specific food over the course of each session in 17.5% of the sessions ($0.44 < r_s < 0.67$, $0.05 < p < 0.001$ – min 5% of the sessions for the subjects Cammello and Robinia – max 40% of the sessions for the subject Carlotta). The foods consumed by capuchins during the B-condition accounted for 4% of energy, 5% of carbohydrates, 14% of fats and 1% of proteins, on average, of the energy and macronutrient composition of their basal diet. Four subjects out of eight showed stable food preferences across sessions (Cammello: $W = 0.20$, $N = 20$; $p < 0.01$; Gal: $W = 0.24$, $N = 20$; $p < 0.001$; Robinia: $W = 0.26$, $N = 20$; $p < 0.001$; Sandokan: $W = 0.16$, $N = 20$; $p = 0.03$), whereas this was not the case for the remaining four subjects (Carlotta: $W = 0.09$, $N = 20$; $p = 0.52$; Paprica: $W = 0.90$, $N = 20$; $p = 0.60$; Robot: $W = 0.06$, $N = 20$; $p = 0.91$; Pippi: $W = 0.10$, $N = 20$; $p = 0.51$).

3.2. Experimental phase: C-condition

At the group level, capuchins preferred the Variety-token significantly above chance (mean% ± SE: 65.39 ± 8.27, $\chi^2_6 = 18.84$; $p < 0.01$). At individual level, three out of seven capuchins (Gal, Robinia, and Robot) preferred the Variety-token significantly above chance (all $p_s < 0.001$), whereas four capuchins (Cammello, Pippi, Paprica, and Sandokan) were indifferent between the Variety- and the Monotony-token. Whether the more-preferred food was presented as a single unit or as 10 units of the same food to choose from, capuchins chose the Variety-token to a similar extent (group$_1$:

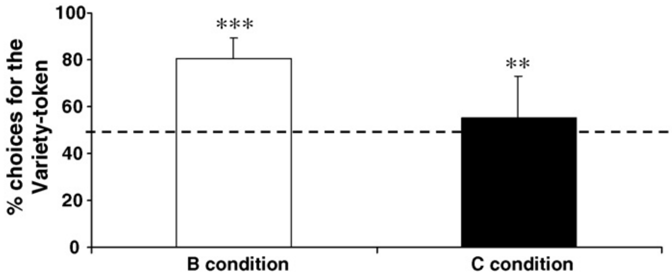

Fig. 3. Percentage of choices for the Variety-token (median and semi-IQR) in the B-condition (white bar) and in the C-condition (black bar). In both conditions, capuchins' chose the Variety-token significantly above the chance level (50%, indicated by the dotted line), $^{*}p < 0.01$, $^{**}p < 0.001$.

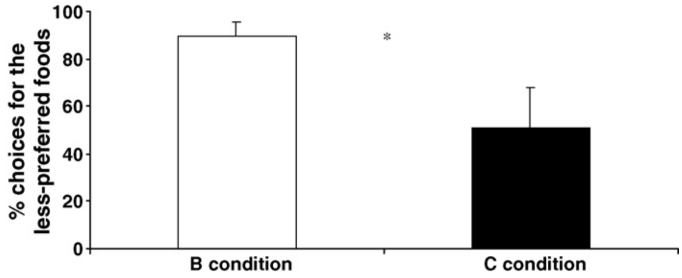

Fig. 4. Percentage of choices for a less-preferred food (median and semi-IQR) in the B-condition (white bar) and in the C-condition (black bar). Capuchins chose one of the less-preferred foods significantly more in the B-condition than in the C-condition, $^{*}p = 0.05$.

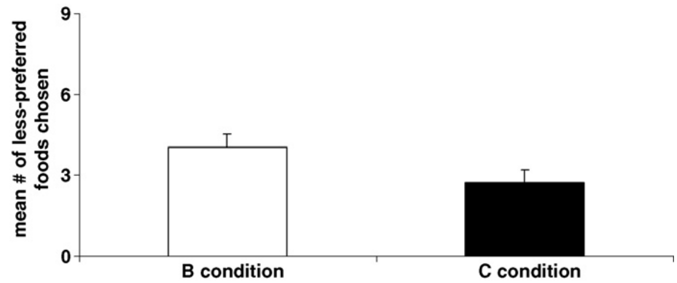

Fig. 5. Mean number (and standard error) of different types of less-preferred foods chosen by capuchins in the B-condition (white bar) and in the C-condition (black bar). There was no significant difference between conditions.

median and IQR: 17.27 (3.86); group_{10}: median and IQR: 10.15 (3.49); $U = 3$, $n_1 = 3$, $n_{10} = 4$; p exact $= 0.40$).

When choosing the Variety-token, three capuchins out of seven significantly preferred one of the less-preferred food over the more-preferred food since the first session (Sandokan and Gal) or the second session (Robot); one capuchin (Robinia) significantly preferred the more-preferred food. These subjects selected one of the less-preferred foods in the first trial in which they chose a Variety-token in 15.3 ± 2.03 sessions (out of 20) on average. The remaining three capuchins (Cammello, Paprica, and Pippi) were indifferent between the less-preferred foods and the more-preferred food. For the three capuchins who significantly preferred to select one of the less preferred foods after exchanging the Variety-token (Sandokan, Gal, and Robot), the number of choices for one of the less-preferred foods did not vary across sessions (Sandokan: $r_s = -0.31$; $p = 0.18$; Gal: $r_s = 0.40$; $p = 0.08$; Robot: $r_s = 0.21$; $p = 0.38$).

Again, sensory-specific satiety accounted for capuchins' behavior only to a limited extent. On average, there was a significant decrease of the choice of a specific food over the course of each session in 16.4% of the sessions ($0.45 < r_s < 0.72$, $0.04 < p < 0.001$ – min 0% of the sessions for the subject Pippi – max 30% of the sessions for the subject Robot). The foods consumed by capuchins during the C-condition accounted for 3% of energy, 5% of carbohydrates, 3% of fats and 1% of proteins, on average, of the energy and macronutrient composition of their basal diet. All subjects showed stable food preferences across sessions (Cammello: $W = 0.31$, $N = 20$; $p < 0.001$; Gal: $W = 0.26$, $N = 20$; $p < 0.001$; Paprica: $W = 0.42$, $N = 20$; $p < 0.001$; Pippi: $W = 0.51$, $N = 20$; $p = 0.001$; Robinia: $W = 0.16$, $N = 20$; $p = 0.03$; Robot: $W = 0.19$, $N = 20$; $p = 0.01$; Sandokan: $W = 0.41$, $N = 20$; $p < 0.001$).

3.3. Experimental phase: B-condition versus C-condition

The percentage of choices for the Variety-token did not significantly differ between the B-condition (in which moderately preferred foods were involved) and the C-condition (in which low-preferred foods were involved) ($T = 10.0$, $N = 7$; p exact $= 0.58$; Fig. 3). However, after selecting and exchanging the Variety-token, capuchins preferred to select one of the less-preferred foods significantly more in the B-condition than in the C-condition ($T = 2.0$, $N = 7$; p exact $= 0.05$; Fig. 4), though the mean number of different less-preferred foods chosen in each session did not significantly differ between conditions ($T = 1.0$, $N = 7$; p exact $= 0.06$; Fig. 5). Finally, capuchins' average energy intake was significantly higher in the B-condition than in the C-condition ($T = 0$, $N = 7$; p exact $= 0.02$), whereas the macronutrient intake did not differ between conditions (carbohydrate amount: $T = 11$, $N = 7$; p exact $= 0.69$; fat amount: $T = 3$, $N = 7$; p exact $= 0.08$; protein amount: $T = 4$, $N = 7$; p exact $= 0.11$).

3.4. Post-test phase

When we assessed individual preferences for all the 10 foods (the more-preferred and the less-preferred ones) at the end of the experimental phase, in the B-condition three out of eight capuchins (Paprica, Gal, and Cammello) maintained their preference for the original more-preferred food, for two subjects (Carlotta and Robot) the original more-preferred food now ranked second, for one subject (Sandokan) it ranked third, and for two subjects (Robinia and Pippi) it ranked sixth. In the C-condition, four out of seven capuchins (Paprica, Cammello, Robinia, and Pippi) maintained their preference for the original more-preferred food, for two subjects (Sandokan and Robot) the original more-preferred food now ranked second, and for one subject (Gal) it ranked fourth.

4. Discussion

Overall, capuchins preferred the Variety-token, which allowed them to choose among several different alternatives, over the Monotony-token, which either allowed them to choose one among 10 units of the same more-preferred food or gave access to one unit of the more-preferred food, with no significant differences between the B-condition (in which the Variety-token was exchangeable for either a more-preferred food or a variety of moderately preferred foods) and the C-condition (in which the Variety-token was exchangeable for either a more-preferred food or a variety of low-preferred foods). Similarly, in one of the few studies which so far investigated active choice for variety in non-human animals, lambs preferred to forage at a "variety location", where a diet with a variety of added flavors was available, rather than at a "monotony location", where the same diet with only the most preferred flavor was provided (Scott and Provenza, 1998).

However, more capuchins significantly preferred the Variety-token in the B-condition (six out of eight subjects) than in the C-condition (three out seven subjects), probably due to the higher hedonic value of the less-preferred foods used in the B-condition.

It is unlikely that the above individual differences are due to the caloric content and the macronutrient composition of the less-preferred foods, as calories and macronutrients did not significantly differ among subjects and corresponded to a very small percentage of those provided by capuchins' basal diet. In contrast, ruminants can forage at a variety of locations to complement their basal diet and meet their individual nutritional needs. For example, lambs fed a basal diet low in protein and high in energy prefer to forage where a high-protein food is available (Scott and Provenza, 2000) and by doing so they improve intake, rate of gain and feed efficiency (Atwood et al., 2006). Nonetheless, since in capuchins the less-preferred foods were higher in carbohydrates and lower in fats and proteins than the more-preferred food, it cannot be excluded that overall macronutrient composition could have affected capuchins' choices for the Variety-token, though the caloric content did not significantly differ between more-preferred and less-preferred foods.

The behavior of the capuchins who preferred the Variety-token may be accounted for by either lure of choice (i.e., the appeal of making choices, Bown et al., 2003) or variety-seeking (i.e., the tendency to look for diversity in services and goods, McAlister and Pessemier, 1982; Kahn, 1995; Inman, 2001). If a capuchin was "lured" by the opportunity of choosing among different alternatives, it should have preferred the Variety-token and then the more-preferred food, whereas if variety-seeking guided its choices, it should have preferred the Variety-token and then one of the less-preferred foods. Capuchins' behavior favors the latter explanation, since in both conditions all capuchins but one (Robinia) chose one of the less-preferred foods rather than selecting the more-preferred food. The lure of choice hypothesis is further ruled out by the fact that those subjects which, in exchange for the Monotony-token, received the opportunity to choose one among 10 units of the same more-preferred food, did not select this type of token significantly more than those subjects which, for the same token, received a single unit of food without the possibility of choosing. Instead, the lure of choice hypothesis could account for the behavior of Robinia in the C-condition, as she opted for the Variety-token but then consistently selected the more-preferred food. Therefore, capuchins behaved differently from long-tailed macaques, for which a *no-choice* option was preferred to a *three-choice* option when the latter gave access to foods less preferred than the food offered for selecting the *no-choice* option (Suzuki, 1999).

Food quality also affected capuchins' response towards the less-preferred foods chosen after exchanging the Variety-token. When presented with moderately preferred foods (B-condition) all subjects selected one of the less-preferred foods rather than the more-preferred food, whereas when offered low-preferred foods (C-condition) only three out of seven subjects did so. Either the flavor of the food or the energy intake deriving from its consumption could have affected capuchins' choices, since in the C-condition the average energy intake was significantly lower than in the B-condition. However, even when offered low-preferred foods capuchins' indeed sought variety rather than attempting to get a specific food emerging from a newly acquired food preference, as indicated by the fact that in both conditions capuchins exploited the available variety of foods to a similar extent.

Variety-seeking might be the byproduct of monotony effects, short-term sensory specific satiety (Hetherington et al., 1989, 2002; Raynor and Epstein, 2001; Rolls et al., 1983) or motivation deriving by the utility inherent in variation per se (van Trijp, 1995). In the B-condition (moderately preferred foods), food monotony partially affected capuchins' variety-seeking, since for half of the subjects the food rank order was stable over the entire course of the experiment and the number of choices for one of the less-preferred foods increased across sessions. However, food monotony did not seem to affect individual choices in the C-condition (low-preferred foods), since the food rank order was stable for all subjects and there was no variation across sessions in the number of choices for one of the less-preferred foods. Moreover, in both conditions, for all but one subjects who preferred the Variety-token and then the less-preferred foods, at the end of the experiment the preference for the more-preferred food was unchanged or slightly decreased. Only for one subject in each condition the original more-preferred food ranked medium, and for no subject it ranked at the lower end of the scale. Likewise, only occasionally choices for a particular food decreased within a session, as expected on the basis of sensory-specific satiety.

Thus, the most important proximate mechanism underlying variety-seeking in capuchins seems the need of experiencing stimulation from the environment (Gijsbrechts et al., 2000; van Trijp, 1995). As for other animal species tested with different paradigms, also for capuchins the sensory change provided by a variety of stimuli to choose from or by novel stimuli appears to be intrinsically motivating and might serve the goal of maintaining optimal levels of the central nervous system arousal (for a review see Hughes, 1997). Previous findings support the view that capuchins are strongly attracted by item novelty. When presented with choices between novel foods and monkey chow, capuchins chose the former more than chow, although in half of the occasions they did not actually eat the novel foods (Addessi et al., 2005), possibly because of food neophobia (Visalberghi and Fragaszy, 1995).

From an evolutionary perspective, the most adaptive choices are those that keep our options open, especially in an unpredictable environment (Hutchinson, 2005). For omnivorous animals as capuchins, seeking variety in their food choices might be advantageous for at least three reasons. First, a behavioral mechanism that allows not to become dependent on a single food precludes starvation should the food become unavailable; second, since a single food cannot provide all the nutrients that omnivores require, avoiding the intake of large amounts of the same food prevents nutritional deficiency (Addessi, 2008; Galef and Whiskin, 2003); third, seeking variety in food choice permits not to avoid a food because containing toxins, thus meeting nutrient requirements without consuming too high levels of potentially dangerous toxic compounds (Provenza, 1996; Provenza et al., 2003).

In conclusion, capuchins preferred a Variety-token, which allowed them to choose from a variety of foods, and then often preferred to choose one of the less-preferred foods rather than the more-preferred food. Since food quality, monotony and sensory-specific satiety can account for capuchins' behavior only partially, the key proximate mechanism determining their variety-seeking seems to be the need of experiencing stimulation from the environment. At the ultimate level, for omnivorous animals as capuchins, seeking variety might be adaptive since it allows them to exploit novel foods and to avoid the risk of starving when staple foods should become unavailable, thus ensuring a correct nutritional intake.

Though it cannot be excluded that variety-seeking in humans and non-human animals is the result of convergences rather than homologies, this behavior seems deeply rooted in our evolutionary history. Variety-seeking might have evolved in the food domain to subsequently become a general trait that encompasses different kinds of stimuli in our own species (Inman, 2001). However, since in humans the optimal number of alternatives to choose from seems to be between 10 and 15 (Reutskaja and Hogarth, 2009), whereas too larger assortments of goods to choose from can reduce the accuracy of choice and lead to choice aversion (Iyengar and Lepper, 2000; Shah and Wolford, 2007), further studies are needed to explore how the number of alternatives presented in a choice set impact variety-seeking in non-human animals.

As Jevons (1875) pointed out, in our species seeking for variety in order to satisfy as many different desires as possible is one of the main factors that promoted the transition from barter to money, at least in some cultures. In the search for variety, the kind of token that allows us to experience the most flexibility and variety is of course something that can be spent on virtually unlimited variety of goods and services—which is the most basic attribute of money (Smith, 1776/1937).

Acknowledgements

We thank Sabrina Rossi, Luigi Baciadonna and Valentina Focaroli for helping with data collection, Valentina Truppa and Francesco Natale for statistical advice, and two anonymous reviewers whose thoughtful suggestions greatly improved a previous version of the manuscript. We also thank the Fondazione Bioparco for hosting our Primate Centre and our keepers Massimiliano Bianchi and Simone Catarinacci. Funded by VI Framework, NEST Pathfinder Initiative "What it means to be human", Contract no. 29088, "Humans-The Analogy-Making Species" – ANALOGY and by VII Framework, Grant agreement no. 231722, "Intrinsically Motivated Cumulative Learning Versatile Robots – IM-CleVeR". This study complied with protocols approved by the Italian Health Ministry and all procedures were performed in full accordance with the European law on humane care and use of laboratory animals.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.beproc.2009.12.012.

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