

Preferences towards novel foods in *Cebus apella*: the role of nutrients and social influences

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Received 18 February 2003; received in revised form 14 August 2003; accepted 19 August 2003

Abstract

Information on the process of preference acquisition towards novel foods in nonhuman primates is lacking. This study aims to assess (1) whether nutrient and energy contents affect preferences towards novel foods encountered repeatedly by individuals when alone, (2) whether these preferences change after additional encounters with the novel foods, and (3) if the change is sensitive to social influences.

We presented seven novel foods to 26 socially housed tufted capuchins. In Phase 1, each subject was presented individually with the 21 possible binary combinations of the seven novel foods. Afterwards, during treatment, 13 subjects received the novel foods ad libitum with their group members (social condition) and 13 subjects received the foods individually (individual condition); subjects assigned to the individual and social conditions had shown similar food preferences in Phase 1. Finally, in Phase 2, each subject was presented again with 21 binary choices between each of the novel foods. In Phases 1 and 2, the number of times each food was chosen differed among foods. In Phase 1, food preference correlated positively with glucose and fructose and negatively with total fiber content. In Phase 2, irrespective of social or individual prior experience in the treatment condition, food preference changed and became correlated with total energy content. Our results broaden the findings already available for familiar foods by demonstrating that individual experience based on the feedback obtained from novel foods guides the establishment of preferences towards them. Moreover, individual experience is sufficient to determine food preferences similar to those individuals may acquire when together with group members eating the same foods.

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Keywords: *Cebus apella*; Novel foods; Food preferences; Energy content; Social influences

1. Introduction

To obtain a balanced diet, omnivorous animals have evolved physiological and behavioral adaptations that allow an advantageous food selection [1]. According to the optimal foraging theory, natural selection favors those animals that are able to optimize energy intake [2] and nutritional requirements (for a review, see Ref. [3]). Up to now, only a few studies have investigated the relation between food preferences and food nutrient content in nonhuman primates [4–6], although numerous field studies have shown that they do not feed on food sources randomly [7,8].

Another approach to primate feeding and food selection comes from a sensory perspective. According to Dominy et al. [9], primates are able to assess food quality through the

sensory information that comes from the food. Senses can help primates to make efficient decisions about foods; for example, taste provides an immediate and powerful feedback used to select foods. Primates are sensitive to bitter and/or astringent tastes that are associated with the presence in the foods of plant secondary compounds, such as alkaloids and glycosides. The latter substances can cause illness or even have lethal effects if they are ingested excessively, so their tastes can function as a cue to inhibit ingestion [10]. Soluble sugars, which are a very important energy source for primates, are also readily perceived and absorbed by the organism. All monkey species tested so far prefer sugar solutions to tap water [11]. Newborn primates already like sweet and dislike bitter substances [12], and although species differ in their taste thresholds for sugars, such as fructose and sucrose, and for quinine [13], interindividual variability within the same species is remarkably low (e.g., squirrel monkeys [14], spider monkeys [15]).

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Moreover, food preferences involve interactions between taste and the consequences of food ingestion [16]. However, we know little of how preferences for foods that have high energy content and the necessary nutrients develop and which physiological mechanisms are involved. A possible approach to study food preferences is the one used by Laska et al. In a first study [5], they repeatedly presented seven captive spider monkeys (*Ateles geoffroyi*) with all possible binary combinations of 10 familiar foods that were part of their diet and found that monkeys' preferences positively correlated with total energy, magnesium, copper, and manganese content and negatively correlated with water content. A subsequent study [6] showed that the food preferences of squirrel monkeys (*Saimiri sciureus*) correlated positively with total energy content, while those of pigtail macaques (*Macaca nemestrina*) correlated with total carbohydrate and fructose content. Laska argued that squirrel and spider monkeys are opportunistic feeders that try to maximize net gain of energy, whereas pigtail macaques prefer foods with high carbohydrate content to fulfill their requirements of metabolic energy.

Experiments in nonhuman primates investigating the acquisition of preferences towards novel foods and their relation to nutrient and energy content are lacking. In the current study, we assessed preferences towards novel foods (i.e., foods that have never been encountered before by the individual) and the *tempo* of food preference acquisition in another opportunistic species, the tufted capuchin monkey (*Cebus apella*) [17]. For a generalist species like *C. apella*, it is important to taste new food items and to incorporate them into diet if they prove to be adequate. Therefore, it is of interest to assess how quickly preferences develop and on which characteristic of the foods preferences are built. Based on Dominy et al.'s work [9], we expected capuchins to initially prefer foods with high sugar content, which is readily perceived through taste. Furthermore, we expected capuchins to change their preferences after repeated encounters with the foods, responding to the feedback coming from the foods' energy content, to maximize net gain of energy, as squirrel and spider monkeys did with familiar food in Laska's experiments.

Primates usually eat while others are nearby and the behavior of group members has been considered important for acquiring food preferences [18,19]. Tufted capuchins are very tolerant and eat in proximity of group members and they see and smell the food (or the mouth) of others [20,21]. Therefore, it is possible that an individual's food preferences are affected by what others eat. No experiment has investigated whether food preferences developed by individuals encountering novel foods when alone differ from those developed by individuals encountering the same foods with group members. In this respect, the only indirect evidence comes from Milton's [22] observations on a group of captive young spider monkeys released in the wild. Although they had no contact with more experienced adults of the same species, they developed the species' typical

diet. Therefore, a further aim of our study was to investigate whether initial preferences towards novel foods change in different ways according to whether the individuals repeatedly encounter these foods alone or with group members.

2. Materials and methods

2.1. Animals

We tested 26 capuchins: 10 males, 16 females. Five were juveniles (<4 years old) and 21 were adults (>4 years old); the range was 2–35 and the average age was 13. All the animals were born in captivity (in our laboratory or in the Bioparco of Rome), except five adult individuals (three males and two females that were of unknown origin, but probably wild-born). The subjects lived in four groups, called after the dominant male's names: Zapotec, Cammello, Patè, and Rosso; group size ranged from 3 to 12 subjects. In each group, there were a dominant male and a dominant female and the other group members were subordinate to them. Groups were housed in indoor–outdoor cages and tested in indoor cages. During the cold months in the indoor cages the temperature was kept at about 21 °C and the light to a 12:12-h light/dark cycle. During the rest of the year, the indoor cages' temperature and light corresponded to those of the outside environment.

Zapotec's group area consisted of three indoor–outdoor cages (total 105 m³), Cammello's group area consisted of two indoor–outdoor cages (total 70 m³), Patè's group area consisted of three indoor–outdoor cages (total 135 m³), and Rosso's group area consisted of two indoor–outdoor cages (total 90 m³). The space available to each monkey is far higher than EU guidelines require. Cages were furnished with perches and slides; a variety of plastic toys and wooden blocks were given on a daily basis. Animals can move from a cage to the adjacent one(s) by passing through a sliding door operated by the experimenter. By passing through one or more sliding doors, an individual animal can be separated from the rest of the group and reach the testing cage.

In the morning, capuchins receive grains of wheat, pumpkin seeds, peanuts, and three times a week, a spoonful of a mixture of curd cheese, vitamins, egg, bran, oats, and sugar. Every afternoon, they receive the main meal consisting of monkey chow (Altromin-A pellets, Rieper standard diet for primates), fresh fruits, and vegetables.

2.2. Apparatus

The apparatus was a rectangular Plexiglas tray (27 × 40 cm). The tray was divided in half by a Plexiglas divider, perpendicular to the tray (27 × 1 × 9 cm high). The apparatus had a plastic handle on each side, permitting it to move easily. The tray had a 0.5-cm deep hollow (1.5 cm

diameter) on both sides of the divider. The two hollows were 15 cm distant from one another, and during the experiment, foods were positioned one in each hollow.

2.3. Foods

We used seven foods never previously tasted by the subjects: tomato, savoy cabbage, pineapple, grapefruit (all of which were fresh), canned meat (in jelly), boiled string bean, and boiled pasta. Data on the nutritional characteristics of the foods derive from INRAN's on-line data bank [23] and from Matthews et al. [24]. The foods were cut into pieces of similar sizes and each piece was weighed with a digital scale (AND compact scale; 0.1 g accuracy, 200 g capacity).

2.4. Procedure

The experiment consisted of Phase 1, treatment phase, and Phase 2. In Phases 1 and 2, subjects were tested individually, while during the treatment phase, half ($n = 13$) of the subjects was tested in an individual condition (e.g., alone in the experimental cage) and the other half ($n = 13$) was tested in a social condition (e.g., with three to five other group members present in the experimental cage).

In Phase 1, the subjects were presented with all possible 21 binary combinations of the seven foods using a two-alternative choice test. Almost all subjects completed the 21 trials in 1 day. To counterbalance position preferences, positions (right or left) of the two foods on the tray were randomized. Within each session, the same food was not presented for more than four times on the same side of the tray and for more than three trials in a row.

During each trial, the tray was presented to the subject by an experimenter (G.S. or M.S.) and, as soon as the subject chose one of the foods, was immediately retrieved. Before choosing, the subject could look at and smell the foods through the wire-mesh. Once it made a choice by touching one of the two foods, the subject could not take the other one. If the subject left the foods on the tray, without choosing either of the two pieces, the experimenter waited for 3 min and then moved to the next trial. If the subject discarded the chosen food without eating all or part of it, the experimenter noted it, waited for 50 s, and then moved to the next trial.

Treatment was aimed to familiarize the subjects with the foods presented in Phase 1. The subjects received a 10-min session per day for five consecutive days. In each session, the seven foods, cut in pieces of sizes similar to those in Phase 1, were scattered on the entire floor of the cage. Treatment was carried out in two conditions. In the individual condition, subjects were alone in the cage and had eight pieces of each food. In the social condition, the same quantity of food was available for each of the subjects. Subjects assigned to the individual and to the social condition of treatment were balanced, as much as possible, for

sex, age, rank, and food preferences (as expressed in Phase 1). In the social condition, there were 6 males and 7 females and 5 dominant and 8 subordinate individuals, the average age was 14 years (range 3–35); in the individual condition, there were 4 males and 9 females and 3 dominant and 10 subordinate individuals, the average age was 10 years (range 2–20). All foods were presented in very abundant quantities to avoid competition among individuals (as evidenced by leftovers on the floor at the end of the session). Each trial started when the sliding door separating the subject (individual condition) or subjects (social condition) from the foods was opened, so it/they could have access to them. During treatment, since the aim was to familiarize the subjects with the food presented in Phase 1, we did not collect quantitative data.

In Phase 2, each subject was again presented individually with the 21 binary choices between the foods. The experimental procedure was the same as in Phase 1. Almost all subjects completed the 21 trials in 1 day.

Tests were performed during late morning, early afternoon hours (always before the daily meal, that occurred at 4 p.m.). Subjects were not food deprived although testing occurred before their main meal.

2.5. Behaviors scored

In Phases 1 and 2, in each trial, we scored which of the two foods was chosen by the subject. At the end of the trial, we scored whether the chosen food was completely eaten, or partially eaten, or not eaten at all. A food was defined as completely eaten when the only discarded parts were not edible (e.g., the skin for grapefruit, tomato, or pineapple). During treatment, we noted whether all individuals had access to the foods and whether at the end of the trial the preferred foods were still available.

2.6. Data analysis

Since the assumptions of parametric statistics were not met, we chose to use nonparametric tests. During Phases 1 and 2, to assess differences in food preferences (total number of choices for each food), we carried out the nonparametric Friedman ANOVA. To assess differences in food preferences between males and females and between dominants and subordinates, we carried out a Mann–Whitney *U* test.

In Phases 1 and 2, to assess if the subjects' preferences were similar, we compared them using Kendall's coefficient of concordance.

To assess if subjects assigned to the individual and social condition of the treatment did not differ in their initial preferences towards any of the seven novel foods, we carried out a Mann–Whitney *U* test.

To assess whether food preferences differed between Phases 1 and 2, we carried out a Wilcoxon matched pairs test. We confronted the total number of choices of each food in Phase 1 with the total number of choices of each food in

Table 1

Phase 1: Total number of choices per individual and average number of choices per subject and male, female, dominant, and subordinate individuals

	Pineapple	Meat	Pasta	Grapefruit	Tomato	Savoy cabbage	String bean
Brahms	1	3	6	0	5	3	2
Cammello	5	4	3	0	5	1	3
Carlotta	3	4	4	6	3	1	0
Cognac	6	1	2	5	3	1	1
Gal	4	4	6	1	3	2	1
Narciso	2	3	5	3	6	1	1
Pacajà	4	2	0	6	1	3	0
Pacchia	3	3	2	6	1	2	1
Panna	2	4	3	2	5	1	2
Paprica	5	5	2	3	3	3	0
Paquita	4	6	3	5	1	2	0
Patè	3	2	3	6	2	4	1
Penelope	5	1	4	5	2	2	0
Pepe	4	5	1	3	5	3	0
Pippi	6	5	3	2	4	1	0
Punk	6	4	4	2	4	1	0
Rame	5	2	2	3	6	1	2
Roberta	4	6	0	3	4	3	1
Robin hood	4	3	1	5	6	1	1
Robinia	4	2	5	0	3	1	6
Robiola	4	4	2	6	3	1	1
Robot	6	2	1	4	3	3	2
Rosso	6	5	4	0	3	1	2
Viola	4	2	0	4	4	1	0
Virginia	3	6	3	5	2	0	1
Zapotec	3	6	0	1	4	1	1
Average (<i>n</i> = 26)	4.08	3.61	2.65	3.31	3.50	1.69	1.11
Males (<i>n</i> = 10)	4.30	3.50	2.60	2.80	4.00	1.80	1.30
Females (<i>n</i> = 16)	3.94	3.69	2.69	3.63	3.19	1.63	1.00
Mann– Whitney <i>U</i>	70	75	76	62.5	58	75.7	54
<i>P</i>	.59	.79	.83	.35	.24	.79	.15
Dominants (<i>n</i> = 8)	4.38	3.88	3.13	1.75	4.13	1.63	1.38
Subordinates (<i>n</i> = 18)	3.94	3.50	2.44	4.00	3.22	1.72	1.00
Mann– Whitney <i>U</i>	56	62	54.5	29	45.5	63.5	50
<i>P</i>	.36	.57	.32	.02*	.13	.60	.20

* *P* < .05.

Phase 2. We used a Mann–Whitney *U* test to assess whether the condition of familiarization (social or individual) of the treatment affected preferences in Phase 2.

A Spearman test was carried out to assess the relation between food preferences and food nutrient content, between food preferences and energy content, and between food preferences and whether the food was eaten or not.

To assess whether the choice of a food type corresponded to total ingestion of the food, we compared the total number of choices of each food with the number of times subjects ate the food entirely (discarding only the skin of tomato, grapefruit, and pineapple).

3. Results

3.1. Phase 1

Capuchins performed a choice in 95% of the trials. The chosen food was completely eaten in 68% of the cases, partially eaten in 19%, and not eaten at all in 13% of the cases. Therefore, what a subject chooses is a good estimate of what it is willing to eat. During Phase 1, some subjects never chose some types of food: 9 of 26 never chose string bean, 4 of 26 never chose pasta, 4 of 26 never chose grapefruit, and 1 of 26 never chose savoy cabbage. Only 2 of the 26 subjects never chose two of the foods presented; for both subjects, the two foods were pasta and string bean.

The seven novel foods were chosen by capuchins a significantly different number of times [$\chi^2(6) = 51.45$, $P < .0001$, $n = 26$] (see Table 1). Preference rank was (from most preferred to least preferred) pineapple, meat, tomato, grapefruit, pasta, savoy cabbage, string bean. The food

Table 2
Spearman's rank-order correlation statistics (Food Preferences × Nutrient Content) in Phase 1

	<i>r_s</i>	<i>n</i>	<i>P</i>
<i>Macronutrients</i>			
Energy	.45	7	.3104
Water	-.18	7	.7016
Protein	-.29	7	.5345
Lipids	0	7	1
Carbohydrates	0	7	1
Fiber	-.82	7	.0234*
<i>Fiber</i>			
Insoluble fiber	-.79	7	.0362*
Soluble fiber	-.71	7	.0713
<i>Carbohydrates</i>			
Sucrose	.20	6	.6997
Fructose	.90	5	.0373*
Glucose	.89	6	.0188*
Soluble sugars	.68	7	.0937
Starch	-.58	7	.1731
<i>Vitamins</i>			
Vitamin A	-.12	6	.8268
Vitamin C	-.16	7	.7283
Thiamin	.07	7	.8733
Niacin	.07	7	.8768
Riboflavin	-.41	6	.4246
<i>Minerals</i>			
Sodium (Na)	-.05	7	.9083
Potassium (K)	.32	7	.4820
Calcium (Ca)	-.51	7	.2431
Phosphorus (P)	-.89	6	.0188*
Iron (Fe)	-.16	7	.7283

n indicates the number of foods for which the nutrient values were available.

* *P* < .05.

preferences of the subjects showed a high level of concordance ($W=0.33$, $n=26$, $P<.001$). As shown in Table 1, sex and rank did not significantly affect food preferences, except for grapefruit, which was chosen significantly more by subordinate individuals.

Preferences were significantly positively correlated to the foods' glucose content ($r_s=.88$, $n=6$, $P<.05$) and fructose content ($r_s=.90$, $n=5$, $P<.05$) and negatively to the foods' total fiber content ($r_s=-.82$, $n=7$, $P<.05$), insoluble fiber content ($r_s=-.79$, $n=7$, $P<.05$), and phosphorus content ($r_s=-.89$, $n=6$, $P<.05$) (see Table 2). Since foods high in sugars are usually low in fiber, to exclude the possibility that avoidance of fiber was merely the result of preference for sugars, we assessed the relation between these variables. Glucose content was negatively correlated with total and insoluble fiber content ($r_s=-.83$, $n=6$, $P<.05$ in both cases), whereas fructose content was not ($r_s=-.3$, $n=5$, NS). To determine if the correlation between food choices and phosphorus content was a byproduct of the others, we

assessed whether glucose, fructose, total, and insoluble fiber contents were correlated with phosphorus content. Phosphorus content was negatively correlated with glucose content ($r_s=-.1$, $n=5$, $P<.001$), but not with fructose and fiber contents ($r_s=-.80$, $n=5$, NS; $r_s=-.66$, $n=6$, NS; $r_s=-.54$, $n=6$, NS, respectively).

Finally, the subjects assigned to the individual or to the social conditions had similar food preferences (pineapple: $U=63$; $n_1=13$; $n_2=13$; NS; meat: $U=55.5$; $n_1=13$; $n_2=13$; NS; pasta: $U=74$; $n_1=13$; $n_2=13$; NS; grapefruit: $U=59.5$; $n_1=13$; $n_2=13$; NS; tomato: $U=53$; $n_1=13$; $n_2=13$; NS; string bean: $U=59.5$; $n_1=13$; $n_2=13$; NS; savoy cabbage: $U=70.5$; $n_1=13$; $n_2=13$; NS).

3.2. Phase 2

Capuchins performed a choice in 98.9% of the trials. The chosen food was completely eaten in 76.3% of the cases, partially eaten in 15.6% of the cases, and not eaten at

Table 3

Phase 2: Total number of choices per individual and average number of choices per subject and male, female, dominant, and subordinate individuals

	Pineapple	Meat	Pasta	Grapefruit	Tomato	Savoy cabbage	String bean
Brahms	6	4	5	2	3	1	0
Cammello	5	5	3	1	5	0	2
Carlotta	2	6	3	3	5	2	0
Cognac	6	5	4	2	1	2	1
Gal	5	5	5	1	2	1	2
Narciso	1	3	6	2	3	2	3
Pacajà	5	6	3	4	1	0	2
Pacchia	6	3	3	5	3	1	0
Panna	6	3	3	3	3	0	3
Paprica	4	6	5	2	2	2	0
Paquita	5	6	4	3	1	1	0
Patè	3	3	5	6	2	1	1
Penelope	5	4	3	5	2	1	1
Pepe	5	6	1	4	3	0	2
Pippi	5	6	4	2	3	1	0
Punk	5	5	5	3	2	1	0
Rame	6	3	4	2	4	0	1
Roberta	4	6	3	3	4	0	1
Robin hood	5	3	1	6	3	2	1
Robinia	5	3	4	3	3	0	3
Robiola	4	2	4	6	3	1	1
Robot	4	1	2	6	1	3	4
Rosso	5	6	3	0	4	0	2
Viola	4	3	5	6	1	2	0
Virginia	4	6	4	3	3	1	0
Zapotec	6	2	1	3	3	1	3
Average ($n=26$)	4.65	4.27	3.58	3.31	2.69	1	1.27
Males ($n=10$)	4.50	3.90	3.10	3.10	2.70	1.20	2.10
Females ($n=16$)	4.75	4.50	3.88	3.44	2.69	0.88	0.75
Mann–Whitney U	72.5	63.5	59	68	76	75	23.5
P	.67	.37	.25	.52	.83	.77	.00*
Dominants ($n=8$)	5.13	4.25	3.75	2.38	3.25	0.63	1.13
Subordinates ($n=18$)	4.44	4.28	3.50	3.72	2.44	1.17	1.33
Mann–Whitney U	50.5	70.5	62	38	44	46	68.5
P	.19	.93	.56	.05	.10	.12	.84

* $P<.005$.

Table 4
Spearman's rank-order correlation statistics (Food Preferences × Nutrient Content) in Phase 2

	r_s	n	P
<i>Macronutrients</i>			
Energy	.83	7	.0212 *
Water	-.68	7	.0937
Protein	-.11	7	.8191
Lipids	.07	7	.8768
Carbohydrates	.36	7	.4316
Fiber	-.93	7	.0025 *
<i>Fiber</i>			
Insoluble fiber	-.96	7	.0004 *
Soluble fiber	-.50	7	.2532
<i>Carbohydrates</i>			
Sucrose	.32	6	.5379
Fructose	.30	5	.6238
Glucose	.77	6	.0724
Soluble sugars	.46	7	.2939
Starch	-.09	7	.8494
<i>Vitamins</i>			
Vitamin A	-.58	6	.2278
Vitamin C	-.56	7	.1924
Thiamin	.00	7	1
Niacin	-.09	7	.8463
Riboflavin	-.23	6	.6584
<i>Minerals</i>			
Sodium (Na)	-.27	7	.5577
Potassium (K)	-.25	7	.5887
Calcium (Ca)	-.65	7	.1106
Phosphorus (P)	-.54	6	.2657
Iron (Fe)	.02	7	.9694

n indicates the number of foods for which the nutrient values were available.
* $P < .05$.

all in 8.1% of the cases. Therefore, what a subject chooses in Phase 2 is a better estimate of what it is willing to eat than in Phase 1. During Phase 2, some subjects never chose

some types of food: 9 of 26 never chose string bean, 8 of 26 never chose savoy cabbage, and 1 of 26 never chose grapefruit. Only 1 of the 26 subjects never chose two of the foods presented; the two foods were savoy cabbage and grapefruit.

The seven foods were chosen by capuchins a significantly different number of times [$\chi^2(6) = 76.07, P < .0001, n = 26$]. The food preferences of the subjects showed a high level of concordance ($W = 0.49, n = 26, P < .001$). Preference rank was (from most preferred to least preferred) pineapple, meat, pasta, grapefruit, tomato, string bean, savoy cabbage. As shown in Table 3, sex and rank did not influence subjects' food preferences, except for the string bean that was chosen significantly more by males.

Preferences were significantly positively correlated to total energy content ($r_s = .83, n = 7, P < .05$) and negatively to total fiber content ($r_s = -.93, n = 7, P < .01$) and insoluble fiber content ($r_s = -.96, n = 7, P < .001$) (see Table 4). Since foods high in total energy are usually low in fiber, to exclude that avoidance of fiber was merely the result of preference for energy, we assessed the relation between these variables. Total energy content was negatively correlated with total and insoluble fiber content ($r_s = -.85, n = 7, P < .05; r_s = -.79, n = 7, P < .05$, respectively).

3.3. Phase 1 versus Phase 2

Although preferences differed significantly between Phases 1 and 2 for pasta ($Z = 2.88, n = 26, P < .01$), for savoy cabbage ($Z = 2.43, n = 26, P < .05$), for canned meat ($Z = 2.19, n = 26, P < .05$), and for tomato ($Z = 2.54, n = 26, P < .01$) (see Fig. 1), preferences in Phase 2 were not affected by the condition (individual or social) in which subjects were tested during treatment (pineapple: $U = 68; n_1 = 13; n_2 = 13; NS$; meat: $U = 74.5; n_1 = 13; n_2 = 13; NS$; pasta: $U = 60; n_1 = 13; n_2 = 13; NS$; grapefruit: $U = 67.5; n_1 = 13; n_2 = 13; NS$; tomato: $U = 49.5; n_1 = 13; n_2 = 13;$

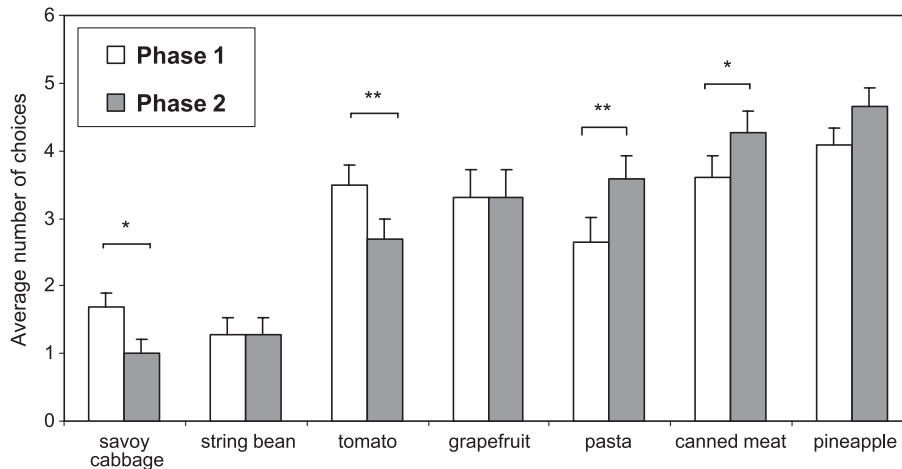


Fig. 1. Average number (± S.E.M.) of times in which each food was chosen by capuchins ($n = 26$) in Phases 1 (white bar) and 2 (gray bar). Asterisks above a given food indicate a significant difference between phases (* $P < .05$, ** $P < .01$; Wilcoxon matched pairs test).

NS; string bean: $U=59.5$; $n_1=13$; $n_2=13$; NS; savoy cabbage: $U=79$; $n_1=13$; $n_2=13$; NS).

3.4. Other results

Both in Phases 1 and 2, there was a significant positive correlation between total number of choices of each food and total number of times subjects entirely ate the food ($r_s=.96$, $n=7$, $P<.001$; $r_s=1$, $n=7$, $P<.001$, respectively). Therefore, food choice is a very reliable measure of liking and eating the food.

4. Discussion

Many experiments (especially on rats, ruminants, human primates, birds) have investigated the role of food preferences for the optimization of internal physiology (for example, see Refs. [5,6,25–27]). In the current study, capuchins markedly preferred certain novel foods to others. Very early on (during Phase 1), preferences were positively correlated with the glucose and fructose content of the foods, and negatively with their total and insoluble fiber content and phosphorus content, whereas later (during Phase 2) preferences were positively correlated with total energy content, and still negatively correlated with total and insoluble fiber content. Capuchins' ability to select foods according to their energy content enables them to fulfill the high-energy requirements due to their metabolic rate.

Feedback coming from taste is important for establishing initial food preferences [9] and, because of their sweet taste, primates prefer energy-carrying molecules, like sugars. Soluble sugars are readily perceived and absorbed by the organism and are a very important energy source, especially for active species like capuchins, whose diet is, in fact, primarily composed of fruit generally rich in soluble sugars, such as glucose and fructose. Capuchins' choices in Phase 1 were influenced by the perception of sugar concentrations: after having tasted the novel foods only a few times they preferred foods with higher sugar content. This finding extends Laska's [6] results concerning familiar foods, for which he demonstrated that food preferences could be related to the species' feeding ecology. In fact, the food preferences of squirrel and spider monkeys, which are opportunistic feeders, correlated positively with total energy content, whereas the food preferences of pigtail macaques, which prefer foods with high carbohydrate, correlated with total carbohydrate and fructose content. In our study, sugar perception operates efficiently also when evaluating an array of foods never encountered before. Since sweet taste is usually not associated with toxicity [28], it seems adaptive for an omnivorous species, such as *C. apella*, to rely on sugar content for choosing foods during the very first encounters. In this way, it is possible to enlarge the diet without risking too much.

In addition, capuchins' initial choices between foods never encountered before could also be indirectly influenced by foods previously eaten during their life. Studies with human and nonhuman primates [29] showed that color is a salient property of food, and cebids prefer yellow fruits to green ones [9]; also, red colored chow is more attractive to orangutans than noncolored one [30]. These color preferences may account for our finding that, from the very beginning, the two most preferred foods were yellow (pineapple) and red (meat) and the least preferred ones were green (savoy cabbage and string bean). In another study, capuchins presented with familiar foods disliked lettuce, similar in color to savoy cabbage [31]. Although primates rely on vision as a major source of information about the environment, olfaction is also important [32]. Although capuchins could have used olfactory cues to make their initial choice, we observed only a few instances in which an individual smelled the food before performing its choice.

It is difficult to explain why capuchins' food preferences correlated negatively with foods' phosphorus content. Although we cannot exclude other possibilities, this finding could be a byproduct of capuchins' preference for foods rich in glucose. In fact, phosphorus content was negatively correlated with glucose content.

During treatment, capuchins had further experience with the novel foods and after this familiarization period their preferences changed. They selected foods according to total energy content rather than to sugar content. In particular, the change in rank between Phases 1 and 2 of pasta and tomato can be ascribed to the higher energy content of pasta compared to tomato. Pasta, that has very little soluble sugar, became more appreciated with experience because it has a high energy content deriving from carbohydrates (polysaccharide starch). Tomato lost positions, possibly because although it has a higher sugar content than pasta (tomato's glucose and fructose contents are 5 and 14 times higher than those of pasta, respectively) it provides 7 times less energy. In both phases, canned meat ranked second in capuchins' preferences; this might be related to the fact that its high glucose and fructose contents were already perceived in Phase 1, although most of canned meat's energy comes from fats as sources of fatty acids and the non-nitrogenous portion of the proteins' amino acids. Therefore, meat's high energy content determined the increased preference for this food in Phase 2. On the contrary, the decreased preference for savoy cabbage in Phase 2 might be due to its low energy content. Our findings that capuchins' food choice does not rely only on one source of metabolic energy may contribute to explain the high degree of flexibility of their diets in natural habitats, as well as their great adaptability.

Overall, we showed that sensory feedback precedes feedback from nutrients and their interaction affects food preferences. Similarly, rats learn to prefer flavors associated with solutions in which carbohydrates are present and to prefer higher carbohydrate concentrations to lower ones

[33]. Lambs discriminate between the postingestive effects of energy (starch) and protein (casein), associate these effects with specific cues, such as added flavors, and consequently modify food choices to regulate the ingestion of these different macronutrients [34]. Lambs also prefer foods higher in readily available carbohydrates but, when a high-energy food has tannin added to it, their preference switches to the lower energy one [35]. In addition, in rats, postingestive nutritive feedback can reinforce the acquisition of preferences based on taste [36]. In humans, 3- to 4-year-old children learn to prefer a food with high caloric content over one with low caloric content and use different flavors as immediate cues to distinguish foods [37]. Therefore, it is possible that, after treatment, capuchins learned to associate the sensory properties of the foods to their postingestive consequences and afterwards directed their selection towards foods with higher energy content. However, it is not clear how selective associations between each novel food and its feedback are made when many foods are consumed at the same time, as was the case in our study. Further research in this area is needed.

Both in Phases 1 and 2, capuchins' preferences negatively correlated with foods' fiber content. For species such as capuchins, without particular adaptations for the digestion of structural carbohydrates [38], foods with high fiber content are of little importance as an energy source. Moreover, many cebines have a relatively short transit time of food through the digestive tract, which might prevent them from having a diet rich in structural carbohydrates [38]. In fact, during times of seasonal scarcity of fruit, capuchins turn to nuts, insects, and other types of animal protein rather than to leaves [39–41]. Fiber content can be detected via the texture and toughness of the food [9]. When eating, capuchins discard portions rich in fiber by processing food items between lips and incisors or by chewing the food and spitting out the tougher parts. However, it should be mentioned that often fiber content is higher in foods that are low in sugar and energy contents. This was the case in our study, where glucose and energy contents (but not fructose content) were negatively correlated with fiber content. Therefore, we cannot establish the contribution to food preference of each of these characteristics. Experiments with a larger number of foods and/or with foods whose characteristics are independent from one another should be undertaken [27].

Finally, although after the experience with the foods received during treatment capuchins changed their preferences, the social or individual condition in which individuals encountered the foods during treatment did not affect differently their change in food preferences. On the contrary, in Phase 2, subjects' preferences were more alike than in Phase 1. Similarly, when eight different novel foods were repeatedly presented to capuchins, acceptance was not affected by having encountered the food alone or with group members [42]. Both studies indicate that the food preferences acquired in solitary or social contexts are alike,

and that social learning is not a *conditio sine qua non* for their similarity.

In conclusion, our experimental results demonstrate that (1) individual experience based on the feedback obtained from different foods guides the establishment of preferences towards novel foods and that (2) individual experience is sufficient to determine food preferences similar to those individuals may acquire when together with group members eating the same foods. Our results broaden the findings already available for familiar foods [5,6] and provide an empirical insight about how an individual makes up its mind when encountering and tasting new food sources. Finally, our findings support Milton's [22] observations about the typical species' diet acquired by captive spider monkeys released in the wild and can be of use in theoretical models of foraging behavior [43].

Acknowledgements

We thank F. Natale and V. Truppa for statistical advice. We also thank Amy Galloway and the two anonymous referees for their useful comments. We are grateful to the Bioparco for hosting the laboratory where the experiment was carried out, to our keepers S. Catarinacci and M. Bianchi for their help, and to the CNR that provided E. Adessi with a fellowship.

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