The role of novelty and fat and sugar concentration in food selection by captive tufted capuchins (*Sapajus apella)*

Benjamin Heuberger[1*], Annika Paukner[2,3], Lauren J. Wooddell[3,4], Matt Kasman[1,], Ross A Hammond[1,5,6]

[1]Center on Social Dynamics and Policy, Economics Studies Program, The Brookings Institution, Washington, DC, United States

[2]Nottingham Trent University, Nottingham, United Kingdom

[3]Laboratory of Comparative Ethology, National Institute of Child Health and Human Development, Poolesville, Maryland, United States

[4]Neuroscience and Behavior, California National Primate Research Center, Davis, California, United States

[5]Brown School, Washington University in St Louis, St Louis, Missouri

[6]Sante Fe Institute, Santa Fe, New Mexico

*Corresponding author:

The Brookings Institution
1775 Massachusetts Avenue NW
Washington, DC 20036
blheuberger@gmail.com
917-968-5982

Running title: Food selection behavior of capuchins

Abstract

Capuchins, like other primates, use feedback from sensory cues and digestion to make decisions about which foods to consume and which to avoid. However, little is known about how capuchins make consumption decisions when simultaneously presented with novel and familiar foods, or how food familiarity and macronutrient concentration together influence food choice, topics with potential implications for developmental and health research. In this study, we evaluated the role of familiarity, as well as fat and sugar concentration, in the food selections of captive tufted capuchins (*Sapajus apella*). In the first experiment, over ten sessions, subjects were assigned to either a group that chose between one familiar and one novel food item both high in fat or sugar (high condition), or to a group that chose between one familiar and one novel food item both low in fat or sugar (low condition). In the second experiment, subjects were divided into three groups, familiarized with a food over five feeding sessions, and then offered the familiarized food and a novel food that varied in fat or sugar for 10 sessions. When offered foods high in fat, capuchins showed no clear signs of neophobia, forming an initial preference for the novel food, rejecting foods less frequently, and selecting foods faster than when offered foods low in fat. These trends were generally not observed in response to foods with sugar. When presented with options that varied in macronutrient concentration, subjects showed an initial interest in the novel food irrespective of whether it was high in fat or sugar, yet formed a final preference for the higher-concentration item. Findings suggest that the concentration of fat or sugar in novel foods may be an important mediator of exploratory behavior, and that capuchins rely on immediate feedback from taste and other sensory cues to make consumption decisions.

Key words: Neophobia, neophilia, food preferences, capuchins

Introduction

The food preferences of capuchin monkeys (*Sapajus apella)* are shaped by both innate tendencies and individual experience. Capuchins, like some other species of non-human primates—including rhesus macaques (*Macaca mulatta:* Johnson, 2000) and chimpanzees (*Pan troglodytes:* Visalberghi, 2002)—are in part innately neophobic, showing caution in their exploration and consumption of novel foods (Addessi et al., 2004). Neophobia is thought to be evolutionarily advantageous to primates, acting as a protective mechanism from the potentially adverse consequences of toxins in unknown plants (Hladik & Simmen, 1996; Glander & Milton, 1982). Some previous studies have shown that wild capuchins react more slowly to and eat smaller quantities of novel foods than familiar foods (Sabbatini et al., 2007), and that adults are more neophobic than infants and juveniles (Fragaszy et al., 1997; Visalberghi et al., 2003a). However, capuchins are a generalist species with a diet in the wild ranging from fruit to arthropods (Visalberghi et al., 2003a) and face the "omnivore's dilemma," balancing the potential risks of unknown foods with the possible benefits of an adaptable diet capable of meeting their nutritional needs (Rozin, 1976). Novel foods are therefore not avoided unconditionally, but rather gradually explored (Glander & Milton, 1982). Furthermore, novel foods do not remain novel for an extended period of time, and capuchins can develop an enduring response to a novel food even after a relatively short number of exposures (Addessi et al., 2004).

The specific factors that may affect the exploration of novel foods—including perceived risk of predation, social facilitation (Visalberghi et al., 1998), age, and rank (Visalberghi et al., 2003a; Addessi et al., 2004)—are numerous and the subject of considerable investigation. One particularly salient set of factors concerns the palatability and macronutrient concentration of foods. Capuchins rely on feedback from food—in the form of taste, texture, and digestive consequences—to determine what is and is not safe to eat (Provenza et al., 1996). Flavor cues are an important driver of this selection behavior and preference formation. Visalberghi & Addessi (2000) found that when capuchins were presented with a familiar food that they knew to be palatable but had been made unpalatable with the addition of pepper, subjects adapted quickly by decreasing their consumption. When the food was subsequently made palatable again, consumption increased. These findings highlight the flexibility and adaptability of capuchins as well as their ability to learn from flavor signals. Capuchins and other primates also demonstrate a positive hedonic response to sweet tastes, responding in a favorable manner to sweet chemical compounds (Johnson, 2007; Nofre et al., 1996). This may be adaptive, as toxicity and sweetness are rarely correlated in plants encountered in the wild (Addessi et al., 2004).

While sweet taste may be an indication of a lack of food toxicity in the wild, optimal foraging theory suggests that primates would choose high energy foods. In one experiment, Visalberghi et al. (2003b) offered capuchins all pairwise combinations of seven novel foods, finding that food preference rank was correlated with the glucose and fructose concentration of foods. However, Visalberghi et al. (1998) found that preference for novel foods was not associated with sugar concentration, but rather with total caloric value. Another study observed no association between food composition or caloric value and consumption (Sabbatini et al., 2007). Similar mixed findings have been seen among other primate species. Squirrel *(Saimiri sciureus)* and spider monkeys *(Ateles geoffroyi)* preferred foods based on total calorie value, regardless of carbohydrate or protein composition, while pigtail macaques (*Macaca nemestrina*) favored foods based on carbohydrate and fructose concentration, irrespective of total calorie value (Laska et al., 2000, 2001). More recent work in nutritional ecology has used novel analytical frameworks like nutritional geometry to challenge the theory of energy maximization and highlight the importance of nutritional balancing in the dietary strategies of some primate species (Felton et al., 2009; Righini, 2017).

The dichotomous choice paradigm—in which subjects are simultaneously presented two items and select one—is a useful technique to determine preference rank among a collection of foods that differ along salient dimensions. Dichotomous choice experiments have been used to examine how calorie and macronutrient concentration are associated with food preferences among a variety of both familiar foods (Laska et al., 2000, 2001) and novel foods (Visalberghi et al., 2003). However, we are unaware of any studies that have used this technique to observe the behavior of primates in response to the simultaneous presentation of a novel food and familiar food. Such an approach could provide some indication of how primates learn to incorporate novel foods into a familiar diet. In addition, it is still not well established how familiarity interacts with food properties—specifically macronutrient type (e.g., fat and sugar) and concentration—to influence food choice. In the current study, we systematically observed the behavioral responses of capuchins to foods that varied in fat or sugar concentration and explored how food familiarity and novelty affect choice. We conducted two experiments, described in sequential order below, using variations of the dichotomous choice paradigm.

Experiment 1

In experiment 1, we set out to answer two questions. First, how do capuchins choose between novel foods and familiar foods that are matched by fat or sugar concentration? Second, does behavior toward novel and familiar foods depend on fat or sugar concentration? We simultaneously presented subjects with a familiar high (or low) fat food item and a novel food item with equally high (or low) fat concentration. This experiment was then repeated with high and low sugar foods. We predicted that capuchins would initially choose and consume the familiar food item more frequently than the novel food item. We also predicted that over time, as subjects sampled the novel food, the two foods would be consumed with similar frequency because of their comparable macronutrient and caloric profiles. In addition, we hypothesized that exploration and consumption of the novel food item would happen faster in the high fat and sugar conditions than the low fat and sugar conditions.

Experiment 2

In experiment 2, we investigated the propensity of subjects to select and consume a novel food, as opposed to a familiar food, when the two foods vary in fat or sugar concentration. In other words, is neophobia or macronutrient concentration a stronger driver of consumption behavior, and how does this change over time? We familiarized subjects to a novel food item of either high or low macronutrient (fat or sugar) concentration through a series of five "exposure" sessions. In 10 subsequent "choice" sessions, we presented subjects with the familiarized food from the exposure sessions and a novel food item of either higher, lower, or equal macronutrient concentration. We predicted that capuchins would initially prefer the familiar over the novel food regardless of their relative fat or sugar concentration, but that ultimately, as subjects sampled the novel food, the food with higher fat or sugar concentration would be favored.

Methods:

Subjects and housing

Subjects were 18 tufted capuchin monkeys (*Sapajus apella*) studied from 2015-2016. All subjects were captive-born and housed at the Laboratory of Comparative Ethology at the NIH Animal Center in Poolesville, MD. All subjects were maternally reared and ranged in age from 3 to 34 years (mean age ± SE: 11.44 ± 1.82; see Table 1). Eight subjects (seven males, one female) were pair-housed in sets of quad cages (163 x 163 x 71 cm) furnished with perches and various enrichment. The remaining ten subjects were part of a social group that consisted of one adult male, four adult females, and five juveniles (<7 years old), and resided in two indoor runs (6.9 x 4.2 x 2.1 m) furnished with wood shavings, perches, and swings. Capuchins had *ad libitum* access to water and were provided enough biscuits twice per day such that they always had some leftover to consume at any time (Purina Monkey Chow #5045, St. Louis, MO). Fresh fruit (apples, oranges, bananas, or grapes) and scattered foraging enrichment (sunflower seeds, popcorn, peanuts, wheat, granola, or trail mix) were additionally provided once per day in the afternoon when testing had been completed. Subjects were relocated following the completion of experiment 1 and before the start of experiment 2 for unrelated management procedures. The social group was relocated to two outdoor runs (2.68 x 2.77 x 2.43 m each) with two inside quad cages (163 x 163 x 71 cm) used for testing. The social group was given approximately two months to acclimate to the new environment before experiment 2 testing began. The caged subjects were also relocated before experiment 2, but the housing conditions remain unchanged (Table 1).

All procedures adhered to the Guide for the Care and Use of Laboratory Animals, were approved by the National Institute of Child Health and Human Development Animal Care and Use Committee (IACUC approval number 15-064), and followed the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

[TABLE 1 HERE]

Separation procedure

We separated all subjects for testing. The pair-housed capuchins were tested in a steel and Plexiglass testing cage (45 x 40 x 48 cm) attached to one quadrant of the cage. Subjects in the social group were tested in a cubicle (86 x 76 x 79 cm) within one-half of their run. Separation procedures were identical for experiments 1 and 2.

Experiment 1 design

We randomly divided subjects into two testing groups (Table 1) that varied in the concentration (i.e., high or low) of macronutrients (fat or sugar) with age and sex balanced across groups.[1] The experimental paradigm was a dichotomous choice task: subjects in the "high" condition group were offered foods high in either fat (>45g fat/100g food) or sugar (>65g sugar/100g food), whereas subjects in the "low" condition group were offered foods low in either fat (< 5g fat/100g food) or sugar (< 5g sugar/100g food). Novel foods were unknown to the subjects, whereas familiar foods were part of their regular diets or regular enrichment. Novel foods were selected on the basis of how well they matched the general macronutrient profiles and caloric value of the familiar foods in their respective experimental condition. Familiar foods used in the experiment were selected from the limited number of food items that subjects had regular experience with and exposure to. When selecting among these familiar foods, we tried to ensure they had similar calorie content yet also fit within the sugar and fat requirements of our design. Each subject received 15 trials per day for 10 sessions. Experiment 1a consisted of foods that

[1] Due to time and resource constraints, we chose to employ a between-subjects, rather than within-subjects experimental design.

varied in fat concentration and experiment 1b consisted of foods that varied in sugar concentration (Table 2).

[TABLE 2 HERE]

Experiment 1 procedure

Subjects were tested separately. During each trial, an experimenter, who was separated from the subject by an opaque screen, placed an equal amount (each food item cut to approximately equivalent sizes of around 1 x 1 x 2 cm) of two foods onto a white testing board (30.48 x 20.32 cm). In experiment 1a, a familiar food item high or low in fat (low familiar: LF or high familiar: HF) and a novel food item high or low in fat (low novel: LN or high novel: HN) were presented. In experiment 1b, the food items presented varied in the amount of sugar they contained. The experimenter placed foods in one of the two locations (separated by 20.32 cm) with locations (left or right) randomized for each trial. Once the opaque screen was removed, a second experimenter used a stopwatch to measure latency to retrieve a single food item. Once a selection was made, the experimenter retrieved the other food to limit each trial to only one selection and prepared for the next trial. During the trial, experimenters looked toward the middle of the board to avoid cueing the subject. The inter-trial interval (ITI) was 10 seconds, during which time the capuchin could either reject (throw or drop) or consume (eat or lick) the food item. The experimenter recorded the behavioral response of the capuchin during the ITI. If the subject made no choice within 30 seconds, a new trial began after the 10-second ITI. "Null" responses were thus trials in which subjects made no choice, and "rejection" responses were those in which the subjects made a selection (retrieved the food item) but did not consume it. Each trial lasted until a selection had been made up to a maximum of 30 seconds, with 15 trials per day for 10 consecutive days (sessions).

Experiment 1 data analysis

We removed capuchin M1 from analysis because of unusual, erratic behavior and refusal to approach the food board. We conducted all statistical analyses by aggregating responses in the first three sessions (sessions 1-3, hereafter referred to as the “initial phase” – IP) and those in the last three sessions (sessions 8-10, referred to as the “final phase” – FP). This aggregation provided us with a larger sample of observations and allowed us to parsimoniously observe if any behavioral change or learning occurred over time.

In order to assess if subjects demonstrated phase-specific neophobic behavior and were disproportionately more likely to consume the familiar item or the novel item, we calculated the proportion of total consumptions that were of novel foods (as opposed to familiar foods) for each subject during the initial and final phases. To do this, we divided the number of novel consumptions by sum of novel and familiar consumptions across 45 trials (i.e., the number of trials in a phase). Null and rejection responses were dropped from this analysis in order to only consider trials in which a food item was consumed. We then used a one-sample Wilcoxon signed-rank test to determine if each group’s novel food selection rate in each phase was significantly different from chance (i.e., 50%).

To assess if behavior differed based on the macronutrient concentration (i.e., high or low) condition, we used a Mann-Whitney U test to compare the frequency of consumption behavior of the high condition group to that of the low condition group. Finally, to determine whether subjects made food selections more quickly in the high condition than low condition, we used a Mann-Whitney U test to compare latency across conditions.[2]

[2] The data that support the findings of this study are available from the corresponding author upon request.

Experiment 2 design

We divided the 18 subjects into three testing groups of six subjects each that varied in degree of fat or sugar concentration. Age and sex were balanced across groups. The experiment consisted first of five “exposure” sessions during which a single novel food was offered in each session in order to induce familiarity. This was done for two reasons: there were an insufficient number of foods already familiar to the subjects that met the macronutrient requirements of the experiment, and because—while outside the scope of this paper—we sought to observe the familiarization process itself. Subjects in group 1 received a low fat (or sugar) food (L1), subjects in group 2 received a high fat (or sugar) food (H1), and subjects in group 3 received a high fat (or sugar) food (H2). In the subsequent 10 “choice” sessions, the experiment consisted of dichotomous choice tasks. Group 1 was offered the choice between the familiarized low fat (or sugar) food (L1) and a novel high fat (or sugar) food (H2); group 2 was offered the familiarized high fat (or sugar) food (H1) and a novel high fat (or sugar) food (H2); and group 3 was offered the familiarized high fat (or sugar) food (H2) and a novel low fat (or sugar) food (L2). See Table 3 and Table 4 for further details.

[TABLE 3 HERE]

Experiment 2 procedure: exposure sessions

Procedures were similar to experiment 1. We tested capuchins separately. During each trial, one experimenter, who was separated from the subject by an opaque screen, placed a novel food in the middle of a testing board while another experimenter measured latency to retrieve the food item. Once retrieved, we recorded whether the food was rejected (thrown or dropped) or consumed (eaten or licked). If a food item was not selected within 30 seconds, a new trial began after the 10-

second ITI. Each monkey received 10 trials per day for five consecutive days (sessions). Based on previous work, we concluded that the number and length of exposure sessions would likely be sufficient for novel food familiarization (Visalberghi et al., 2003b).

Experiment 2 procedure: choice sessions

Following the five exposure sessions, we conducted one choice session (of 15 trials per session) per day for 10 consecutive days (Table 4). Behind an opaque screen, an experimenter placed two foods onto the testing board: the food the subject had been offered during the exposure sessions (hereafter referred to as the familiarized food item), and a novel food item. As in the exposure sessions, another experimenter recorded latency to selection and the subject's behavioral response. If the subject made no choice within 30 seconds, a new trial began after the 10-second ITI.

[TABLE 4 HERE]

Experiment 2 data analysis

All analyses were done independently for the fat experiment (2a) and sugar experiment (2b). As in experiment 1, we performed statistical analyses on the initial and final phases of the 10 choice sessions, where the initial phase was an aggregation of the first three choice sessions (6-8), and the final phase was an aggregation of the last three sessions (13-15).

To assess differences in consumption rates of novel and familiarized food items, we determined the proportion of each subject's total consumptions that were of the novel food in each phase (choice sessions only). For each subject, we divided the number of novel consumptions across 45 trials (15 trials per session and 3 sessions per phase) by the number of trials in which a food was consumed. We only considered trials in which a food item was consumed and so the outcome variable was strictly dichotomous. Using a one-sample Wilcoxon signed-rank test, we determined if each group's novel food consumption rate in each phase differed from chance. We also evaluated the frequency of rejection and null responses, as well as latency to select novel and familiarized foods.

Results:

Experiment 1: consumption of novel foods

In experiment 1a (fat), subjects in the high condition were more likely than chance to consume novel items in both the initial and final phase (initial phase: median = 1.00, W+ = 36, z = 2.51, $p < 0.05$; final phase: median = 1.00, W+ = 36, z = 2.56, $p < .01$). Subjects in the low condition did not consume novel foods at a rate different than chance in either phase (initial phase: median = 0.46, W+ = 15, z = -0.83, NS; final phase: median = 0.40, W+ = 11, z = -1.30, NS).

In experiment 1b (sugar), subjects in the high condition were less likely to consume the novel food, but only in the initial phase (initial phase: median = 0.11, W+ = 3, z = -2.03, $p < 0.05$; final phase: median = 0.46, W+ = 14, Z = -0.49, NS). Novel selection rate among subjects in the low condition did not differ significantly from chance (initial phase: median = 0.33, W+ = 8, z = -1.66, p = .097); final phase: median = 0.12, W+ = 9, z = -1.55, NS).

Experiment 1: consumption by macronutrient condition

Capuchins in the high fat group were more likely to consume the novel food than capuchins in the low fat group in both the initial phase (U = 0, $N_1 = 8$, $N_2 = 9$, $p < 0.01$) and final phase (U = 2, $N_1 = 8$, $N_2 = 9$, $p < 0.01$) (Figure 1). They were also less likely to consume the familiar food than the low condition group in both the initial phase ($U = 5.5$, $N_1 = 8$, $N_2 = 9$, $p < 0 .01$) and final phase ($U = 0$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$).

There were no significant differences in frequency of novel food consumptions between the high sugar group and low sugar group in either the initial phase ($U = 31.5$, $N_1 = 8$, $N_2 = 9$, NS) or final phase ($U = 24.5$, $N_1 = 8$, $N_2 = 9$, NS). In the initial phase of experiment 1b, familiar foods were consumed at a higher median frequency by capuchins in the high sugar group than capuchins in the low sugar group ($U = 16.5$, $N_1 = 8$, $N_2 = 9$, $p = 0.06$). However, there were no differences in familiar food consumption in the final phase ($U = 31.5$, $N_1 = 8$, $N_2 = 9$, NS).

Figure 1: *Consumption frequency of novel and familiar food items among high (N = 8) and low (N = 9) macronutrient groups across experiment 1a (fat) and experiment 1b (sugar). Initial phase (IP) refers to sessions 1-3; final phase (FP) refers to sessions 8-10. X: median number of trials food consumed; boxes: 25-75 percentile; whiskers: lower and upper adjacent values defined as [Q1 – 1.5 x IQR] and [Q3 + 1.5 x IQR]; Group 1 (high condition).*

[FIGURE 1 HERE]

Experiment 1: rejections and null responses

In each the initial phase and final phase of the high fat condition, just two of eight subjects had a null response in more than 2% of trials, and only two rejected items more than 2% of the time. Frequency of null and rejection responses were similar in the high sugar condition; just two subjects had more than 4% of trials end in null or reject responses in each phase.

Although generally infrequent, rejections were more common in the low value conditions, and novel items were rejected more than familiar items. Across all sessions in experiment 1a (fat), 2.5% of all trials in the high condition were rejections (of which 86.7% were rejections of the novel item), compared to 29.4% of all trials in the low condition (of which 60.9% of rejections of the novel item). Similarly, in experiment 1b (sugar), 5.2% of trials in the high condition were rejections (of which 46.8% were rejections of the novel item), compared to 19% of trials in the low condition (of which 93.8% were rejections of the novel item).

Experiment 1: latency to retrieve food items

We measured the latency to retrieve food items regardless of whether they were consumed. In experiment 1a (fat), median (IQR) latency to retrieve food items in the high condition was 3.52 (2.94) seconds in the initial phase and 1.59 (2.51) seconds in the final phase. In the low condition, latency was 6.83 (2.84) seconds in the initial phase and 7.11 (3.73) seconds in the final phase. Subjects in the high condition group were quicker to initiate contact with a potential food item than subjects in the low condition group (initial phase: $U = 16$, $N_1 = 8$, $N_2 = 9$, $p = 0.05$; final phase: $U = 7.0$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$).

Median (IQR) selection latency of the high condition group in experiment 1b (sugar) was 2.69 (2.27) seconds in the initial phase and 2.06 (2.22) seconds in the final phase. In the low condition, latency was 4.45 (2.29) seconds in the initial phase and 2.32 (1.9) seconds in the final phase. Difference in latency between conditions was not statistically significant.

Experiment 2: consumption of novel foods

For all three groups across both experiment 2a and 2b, the median number of trials in which the novel food was consumed was higher in the initial phase than the final phase, while the number in which the familiarized food was consumed was lower (Table 5).

For group 1 in the fat condition (L1 exposure; L1/H2 choice), the proportion of consumed foods that were novel was greater than chance in the initial phase, but not the final phase (initial phase: median = 0.80, W+ = 21, z = 2.10 $p < 0.05$; final phase: median = 0.69, W+ = 17, z = 1.26, NS). This same pattern was observed in the sugar condition (initial phase: median = 0.92, W+ = 21, z = 2.10, $p < 0.05$; final phase: median = 0.69, W+ = 16.5, z = 1.16, NS).

Among group 2 (H1 exposure; H1/H2 choice), novel food consumption was not significant in the initial phase and final phase—in both the fat condition (initial phase: median = 0.72, W+ = 13, z = 1.35, NS; final phase: median = 0.48, W+ = 12, z = 0.21, NS) and the sugar condition (initial phase: median = 0.84, W+ = 18, z = 1.47, NS; final phase: median = 0.64, W+ = 15, z = 0.84, NS).

Group 3 (H2 exposure; H2/L1 choice) novel food consumption was not different than chance in the initial or final phase in either the fat condition (initial phase: median = 0.47, W+ = 8, z = -0.42, NS; median = 0.38, W+ = 2, z = -1.68, p = 0.09) or sugar condition (initial phase: median = 0.28, W+ = 5, z = -1.05, NS; final phase: median = 0.21, W+ = 3.5, z = -1.37, NS).

Group 1 and 3 both chose between a high value food and a low value food. In the initial phase of both experiment 2a and 2b choice sessions, Group 1, for whom the high value food was novel, chose this food at a higher rate than Group 3, to whom the same food had been familiarized in the exposure sessions (fat condition: $U = 5$, $N_1 = N_2 = 6$, $p < 0.05$; sugar condition: $U = 3$, $N_1 = N_2 = 6$, $p < 0.05$). This same trend was observed in the final phase (fat condition: $U = 4$, $N_1 = N_2 = 6$, $p < 0.05$; sugar condition: $U = 5.5$, $N_1 = N_2 = 6$, $p < 0.05$). See Table 5 for more details.

[TABLE 5 HERE]

Experiment 2: rejections and null responses

For subjects in Group 1 and 2 in the fat condition, who received a novel high fat item in the choice session, rejections accounted for 2% and 7.5% of all trials, respectively, of which 38% and 29% were rejections of the novel item. Group 3 rejected 4.5% of all trials on average, of which 23% were rejections of the novel item. In the sugar condition, subjects in Group 1 and 2 rejected foods in 5% and 7% of trials, respectively; 38% and 28.5% of Group 1 and 2 rejections were on the novel item. Null responses accounted for less than 2% of all trials regardless of group in the high fat condition. In the high sugar condition, null responses accounted for 7.5% of responses for Group 1 and 2 and 3% of responses for Group 3.

Experiment 2: selection latency

Selection latency was not significantly different between novel and familiarized items. In both experiment 2a and 2b—with the exception of Group 3 novel item latency—median latency across all choice sessions ranged from 0.95 seconds to 1.5 seconds. Group 3, which was simultaneously offered a low value novel food and high value familiarized food in the choice sessions, had a median latency of 2.02 seconds for novel items and 1.27 seconds for familiarized items in experiment 2b, and a median latency of 2.11 seconds for novel items and 1.20 seconds for familiarized items in the experiment 2a. There were no significant differences between overall latency in the initial and final phases in either experiment 2a or 2b.

Discussion:

In two experiments, we used a dichotomous food choice paradigm to observe associations between food properties—familiarity and fat or sugar concentration—and the tendency of captive capuchins to select and consume food items. Overall, our findings did not support the hypothesis that capuchins are neophobic when presented with a familiar and novel food, although there were notable differences between the fat and sugar conditions. When two foods with similarly high macronutrient concentration were presented to subjects in experiment 1, the novel food was initially consumed at a higher rate than the familiar food in the fat condition, whereas the opposite was observed in the sugar condition. Both of these initial preferences disappeared over time. Even though subjects in the high sugar condition consumed the novel food at a lower rate than chance in the initial phase, they did show some level of initial exploration of the novel food: most consumed the novel food at least once over the first few exposures of the first session and continued to do so in about 10% to 20% of trials across all sessions, while also rejecting novel foods infrequently. A pattern of early exploration and interest in the novel food was supported by the results from experiment 2, which showed that when capuchins were familiarized with a food high in fat or sugar and then offered a choice between this familiarized food and a novel food of a similar macronutrient profile, they initially selected the two items at similar rates.

Wild primates are cautious in their approach toward and consumption of novel foods (Visalberghi et al., 2003a; Sabbatini et al., 2007; Visalberghi et al., 2002). Although some research has found that captive primates show signs of food neophobia as well (Visalberghi and Fragaszy, 1995), our observations are generally consistent with Englerova et al. (2019), Forss et al. (2015), and others that document limited or no neophobia and even signs of neophilia among those in captivity. Social facilitation may account for some of the observed neophilic behavior in the high value conditions of experiment 1 and across all three groups in experiment 2. Previous studies have found that capuchins are more likely to approach and consume a novel food presented in a social setting than a solitary setting (Visalberghi et al., 1998; Visalberghi & Addessi, 2000). Local group food norms have also been shown to be a strong predictor of foraging behavior in some wild primates (van de Waal et al., 2013). In our experiments, all subjects were visible to others during testing, and they had direct physical contact when they were returned to their pair mate or group. This setup may have allowed subjects to ascertain the safety of novel foods through observation and olfactory cues, thereby diminishing any preexisting caution and encouraging exploratory behavior. Future analysis could explore whether subjects tested first are more neophobic than those tested later.

Importantly, our findings suggest that reactions to novel foods may be dependent on macronutrient concentration. We found that capuchins showed some behaviors consistent with neophobia—including longer selection latency, more food rejections, and less frequent consumption of novel foods—only when offered a choice between two food items that were both low in fat or sugar. Similarly, Johnson (2007) observed that rhesus monkeys demonstrated neophobic behavior in response to a novel no-sugar food but not toward a novel high-sugar food. Primates may use specific sensory cues (e.g., olfactory, visual, tactile) to infer food palatability, toxicity, and macronutrient concentration, which may explain their willingness to consume foods. In the wild, for example, ethanol concentrations in ripening fruits can be detected by primates via olfactory receptors and often correlate positively with soluble sugar concentration, while some toxic plants contain distinct odors that discourage consumption (Dominy et al., 2001; Dominy, 2004; Nevo and Valenta, 2018). Indeed, effectively utilizing available cues is an evolutionarily advantageous strategy, reducing the risk of consuming potentially poisonous substances encountered in the wild while also promoting safe consumption (Johnson et al., 1975).

Some previous literature has found that primates choose foods that maximize their caloric intake, whether captive (Laska et al. 2000; Visalberghi et al., 2003b) or wild (Emerson and Brown, 2012). We found that controlling for calories, on average capuchins will choose and consume foods that are highest in sugar concentration. High fat foods were also preferred to low fat foods but were also somewhat higher in calories because it is difficult to find low fat foods that have the same calorie content as high fat foods. Preferential consumption of foods high in fat and sugar was observed within the first few exposure sessions of experiment 2, which may suggest preference formation is largely immediate rather than a more gradual reinforcement learning process. Simple sugars, including fructose and sucrose, are found in fruits like those in this study and provide clear and direct sensory reward in the form of sweetness. It is less well-understood how and if fats, typically characterized by a more neutral taste profile, provide similar immediate, positive sensory feedback. In addition to the potential taste mechanisms of fats, primates may respond positively to their odorant and tactile cues (Hladik and Simmen, 1996). Despite favoring the food higher in fat or sugar concentration, capuchins in group 1 and 3 in experiment 2 still consumed a non-trivial amount of the lower-value foods when they were simultaneously presented. This finding suggests that capuchins seek to maintain variety in their consumption even while maintaining a clear preference for one food. Indeed, Addessi (2008) found that capuchins were faster to consume foods and ate more when presented with a varied selection of multiple food items than a monotonous selection of just a single food type.

Our study is not without limitations, including our relatively small sample size (n=18) and lack of controls for food characteristics that could potentially affect behavior, including smell, color, and texture. Although we sought to minimize the calorie difference, high fat foods were somewhat higher in calories than low fat foods due to the limited selection of foods that vary in fat concentration but have similar calories. Capuchins may also have been conditioned or more willing to accept foods from handlers because of their comfort and familiarity with these individuals, whose presence could implicitly indicate foods are safe for exploration (Forss et al., 2015). Future research should examine how responses toward novel and familiar foods vary by age, such as a comparison of the behavior of juveniles and adults, which we were unfortunately unable to do due the small sample size. To better understand relative preferences, a continuous measure of consumption (e.g., measuring the amount of food consumed in each trial) would also be beneficial. Our setup was also limited to the simultaneous presentation of only two food items. Additional work should explore how and if behavior changes as a function of the number of options available.

Our results suggest that fat and sugar concentration in food is an important moderator of neophilia and neophobia in captive capuchins. The ability of capuchins to quickly discriminate between foods based on macronutrient concentration, engage in exploratory behavior when cues suggest it is safe to do so, and maintain dietary variety are all behaviors consistent with optimal foraging theory. Further examination into the specific sensory cues that drive these behaviors may help disentangle the mechanisms that shape food choice in primates.

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References

Addessi, E., Galloway, A. T., Birch, L. & Visalberghi, E. (2004). Taste perception and food choices in capuchin monkeys and human children. *Primatologie: Revue Publiee Sous l'egide de la Societe Francophone de Primatologie*, *6*, 101.

Addessi, E. (2008). Food variety-seeking in tufted capuchin monkeys (*Cebus apella*). *Physiology & Behavior*, *93*, 304-309. https://doi.org/10.1016/j.physbeh.2007.09.001

Dominy, N. J., Lucas, P. W., Osorio, D. & Yamashita, N. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *10*(5), 171-186. https://doi.org/10.1002/evan.1031

Dominy, N. J. (2004). Fruits, fingers, and fermentation: the sensory cues available to foraging primates. *Integrative and Comparative Biology*, *44*(4), 295-303. https://doi.org/10.1093/icb/44.4.295

Emerson, S. E., & Brown, J. S. (2012). Using giving-up densities to test for dietary preferences in primates: an example with Samango monkeys (*Cercopithecus (nictitans) mitis erythrarchus*). *International Journal of Primatology*, *33*(6), 1420-1438. https://doi.org/10.1007/s10764-012-9631-2

Englerova, K., Klement, D., Frynta, D., Rokyta, R., & Nekovarova, T. (2019). Reactions to novel objects in monkeys: what does it mean to be neophobic? *Primates*, *60*(4), 347-353. https://doi.org/10.1007/s10329-019-00731-2

Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., Wallis, I. R., & Lindenmayer, D. B. (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology*, *20*(4), 685-690. https://doi.org/10.1093/beheco/arp021

Forss, S. I., Schuppli, C., Haiden, D., Zweifel, N., & Van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology*, *77*(10), 1109-1121. https://doi.org/10.1002/ajp.22445

Fragaszy, D., Visalberghi, E., & Galloway, A. (1997). Infant tufted capuchin monkeys' behaviour with novel foods: opportunism, not selectivity. *Animal Behaviour*, *53*(6), 1337-1343. https://doi.org/10.1006/anbe.1996.0368

Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *American Journal of Physical Anthropology*, *25*(S3), 1-18. https://doi.org/10.1002/ajpa.1330250503

Hladik, C. M., & Simmen, B. (1996). Taste perception and feeding behavior in nonhuman primates and human populations. *Evolutionary Anthropology: Issues, News, and Reviews*, *5*(2), 58-71. https://doi.org/10.1002/(SICI)1520-6505(1996)5:2<58::AID-EVAN5>3.0.CO;2-S

Johnson, C., Beaton, R., & Hall, K. (1975). Poison-based avoidance learning in nonhuman primates: Use of visual cues. *Physiology & Behavior*, *14*(4), 403-407. https://doi.org/10.1016/0031-9384(75)90003-7

Johnson, E. (2000). Food-neophobia in semi-free ranging rhesus macaques: Effects of food limitation and food source. *American Journal of Primatology*, *50*(1), 25-35. https://doi.org/10.1002/(SICI)1098-2345(200001)50:1<25::AID-AJP3>3.0.CO;2-D

Johnson, E. C. (2007). Rhesus macaques (*Macaca mulatta*) are not neophobic toward novel food with a high sugar content. *American Journal of Primatology*, *69*(5), 591-596. https://doi.org/10.1002/ajp.20364

Laska, M., Salazar, L. T. H. & Luna, E. R. (2000). Food preferences and nutrient composition in captive spider monkeys, *Ateles geoffroyi*. *International Journal of Primatology*, *21*(4), 671-683. https://doi.org/10.1023/A:1005517421510

Laska, M. (2001). A comparison of food preferences and nutrient composition in captive squirrel monkeys, *Saimiri sciureus*, and pigtail macaques, *Macaca nemestrina*. *Physiology & Behavior*, *73*(1), 111-120. https://doi.org/10.1016/S0031-9384(01)00439-5

Nevo, O. & Valenta, K. (2018). The ecology and evolution of fruit odor: implications for primate seed dispersal. *International Journal of Primatology*, *39*(3), 338-355. https://doi.org/10.1007/s10764-018-0021-2

Nofre, C., Tinti, J. M., & Glaser, D. (1996). Evolution of the sweetness receptor in primates. II. Gustatory responses of non-human primates to nine compounds known to be sweet in man. *Chemical Senses*, *21*(6), 747-762. https://doi.org/10.1093/chemse/21.6.747

Provenza, F. D. (1996). Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *Journal of Animal Science*, *74*(8), 2010-2020. https://doi.org/10.2527/1996.7482010x

Righini, N. (2017). Recent advances in primate nutritional ecology. *American Journal of Primatology*, *79*(4), 1-5. https://doi.org/10.1002/ajp.22634

Rozin, P. (1976). The selection of foods by rats, humans, and other animals. *Advances in the Study of Behavior*, *6*, 21–76. https://doi.org/10.1016/S0065-3454(08)60081-9

Sabbatini, G., Stammati, M., Tavares, M. C. H., & Visalberghi, E. (2007). Response toward novel stimuli in a group of tufted capuchins (*Cebus libidinosus*) in Brasilia National Park, Brazil. *American Journal of Primatology*, *69*(4), 457-470. https://doi.org/10.1002/ajp.20365

Van de Waal, E., Borgeaud, C. & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), 483-485. https://doi.org/10.1126/science.1232769

Visalberghi, E. & Fragaszy, D. (1995). The behaviour of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. *Animal Behaviour*, *49*(4), 1089-1095. https://doi.org/10.1006/anbe.1995.0137

Visalberghi, E., Valente, M., & Fragaszy, D. (1998). Social context and consumption of unfamiliar foods by capuchin monkeys (*Cebus apella*) over repeated encounters. *American Journal of Primatology*, *45*(4), 367-380. https://doi.org/10.1002/(sici)1098-2345(1998)45:4%3C367::aid-ajp4%3E3.0.co;2-u

Visalberghi, E. & Addessi, E. (2000). Response to changes in food palatability in tufted capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *59*(1), 231-238. https://doi.org/10.1006/anbe.1999.1297

Visalberghi, E., Myowa Yamakoshi, M., Hirata, S., & Matsuzawa, T. (2002). Responses to novel foods in captive chimpanzees. *Zoo Biology*, *21*(6), 539-548. https://doi.org/10.1002/zoo.10057

Visalberghi, E., Janson, C. H., & Agostini, I., (2003a). Response toward novel foods and novel objects in wild *Cebus apella*. *International Journal of Primatology*, *24*(3), 653-675. https://doi.org/10.1023/A:1023700800113

Visalberghi, E., Sabbatini, G., Stammati, M., & Addessi, E. (2003b). Preferences towards novel foods in *Cebus apella*: the role of nutrients and social influences. *Physiology & Behavior*, *80*(2), 341-349. https://doi.org/10.1016/j.physbeh.2003.08.004

Table 1: *Age, sex, housing, and experimental condition. In Experiment 1, the "High" ("Low") condition group was offered foods high (low) in either fat or sugar concentration as shown in Table 2. For the feeding schedule of Groups 1-3 in Experiment 2, refer to Table 4.*

Subject	**Age (years)**	**Sex**	**Housing**	**Experiment 1 Condition**	**Experiment 2 Condition**
M1	4	M	Social group	High	Group 3
M2	9	M	Social group	High	Group 2
M3	4	F	Social group	High	Group 1
M4	13	F	Social group	High	Group 3
M5	17	F	Social group	High	Group 3
M6	8	M	Pair	High	Group 3
M7	11	M	Pair	High	Group 3
M8	5	F	Social group	High	Group 1
M9	12	M	Pair	High	Group 2
M10	3	M	Social group	Low	Group 1
M11	11	F	Social group	Low	Group 1
M12	23	M	Social group	Low	Group 1
M13	13	M	Social group	Low	Group 1
M14	3	F	Social group	Low	Group 2

M15	34	F	Social group	Low	Group 2
M16	9	M	Pair	Low	Group 2
M17	11	M	Pair	Low	Group 3
M18	16	F	Pair	Low	Group 2

Table 2: *Macronutrient concentration of foods used in experiment 1*[3] *(HF = high fat/sugar familiar food; HN = high fat/sugar novel food; LF = low fat/sugar familiar food; LN = low fat/sugar novel food).*

Experiment 1a (Fat manipulation)					**Experiment 1b (Sugar manipulation)**				
Food	**Type**	**Kcals /100g**	**Sugar /100g**	**Fat /100g**	**Food**	**Type**	**Kcals /100g**	**Sugar /100g**	**Fat /100g**
Sunflower seed	HF	584	2.6	51.4	Raisin	HF	310	69	0
Almond	HN	607	3.6	53.6	Dried mango	HN	314	75	0.78
Popcorn	LF	337	1.1	4.2	Wheat	LF	339	0	2.5
Sourdough pretzel	LN	393	<3.6	3.6	All bran	LN	380	2.76	2.63

[3] Nutrition information can be obtained at: https://www.myfooddiary.com/foods/

Table 3: *Fat and sugar concentration of foods used in experiment 2.*

Experiment 2a (fat manipulation)					**Experiment 2b (sugar manipulation)**				
Food	**Type**	**Kcal /100g**	**Sugar /100g**	**Fat /100g**	**Food**	**Type**	**Kcal /100g**	**Sugar /100g**	**Fat /100g**
Toasted rice	L1	370	7.4	0	Rice cake	L1	400	0	0
Roasted pistachio	H1	533	6.7	46.7	Pitted date	H1	325	70	0
Roasted cashew	H2	607.1	10.7	50	Dried cranberry	H2	325	67.5	0

Table 4: *Design layout for experiment 2. L1 = low value fat or sugar item (toasted rice and rice cake, respectively); H1 = high value fat or sugar item (roasted pistachio or pitted date, respectively); H2 = high value fat or sugar item (roasted cashew or dried cranberry, respectively).*

	Exposure Sessions (1-5)					**Choice sessions (6-15)**			
	Session 1	**Session 2**	**Session 3**	**Session 4**	**Session 5**	**Session 6**	**Session 7**	**Session 8…**	**Session 15**
Group 1	L1	L1	L1	L1	L1	L1, H2	L1, H2	L1, H2	L1, H2
Group 2	H1	H1	H1	H1	H1	H1, H2	H1, H2	H1, H2	H1, H2
Group 3	H2	H2	H2	H2	H2	H2, L1	H2, L1	H2, L1	H2, L1

Table 5: *Median (IQR) number of trials (out of 45) per phase in which a novel or familiar food was consumed, by group. (IP = initial phase; FP = final phase. L = low macronutrient value food; H1 = high macronutrient value food 1; H2 = high macronutrient value food 2. Exp = exposure sessions; Ch = choice sessions. N = 6 for each group.)*

		Experiment 2a (fat manipulation)			**Experiment 2b (sugar manipulation)**		
		Group 1 (L exp, L/H2 Ch)	**Group 2 (H2 exp, H1/H2 Ch)**	**Group 3 (H2 exp, H2/L Ch)**	**Group 1 (L exp, L/H2 Ch)**	**Group 2 (H2 exp, H1/H2 ch)**	**Group 3 (H2 exp, H2/L ch)**
Novel food consumption	**IP**	34 (3)	32 (22)	21.5 (18)	39.5 (9)	37.5 (19)	10.5 (11)
	FP	29.5 (27)	21 (24)	18 (15)	30.5 (7)	27 (25)	7.5 (20)
Familiar food consumption	**IF**	9.5 (3)	12.5 (16)	23.5 (22)	3.5 (9)	7 (20)	21.5 (11)
	FP	14 (24)	23 (22)	25.5 (15)	14.5 (5)	18 (24)	30 (19)

Figure 1. Consumption frequency of novel and familiar food items among high (N=8) and low (N=9) macronutrient groups across Experiment 1a (fat) and Experiment 1b (sugar). Initial phase (IP) refers to sessions 1-3; final phase (FP) refers to Sessions 8-10. X: median number of trials food consumed; boxes: 25-75 percentile; whiskers: lower and upper adjacent values defined as [Q1-1.5 x IQR] and [Q3 + 1.5 x IQR]; Group 1 (high condition). IQR, interquartile range.