



Response to changes in food palatability in tufted capuchin monkeys, *Cebus apella*

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Palatability of plant foods may change over time in relation to the concentration of toxic secondary metabolites. We investigated the behavioural response of capuchin monkeys to this type of change and assessed the influence of social conditions. Twenty-seven tufted capuchin monkeys were presented in Social or Individual conditions with a familiar palatable food (phase 1), with the same familiar food to which pepper had been added, making it unpalatable (phase 2), and with the same familiar palatable food of phase 1 (phase 3). Five sessions were carried out in each phase. The capuchins adapted quickly to the change in food palatability by reducing (phase 2) and increasing (phase 3) the amounts of food eaten. The unpalatable food prompted an increase in olfactory exploration and in food processing. The experimental conditions (Social versus Individual) did not influence consumption, or any of the other behaviours. In addition, capuchins were more often near subjects with food in phases 2 and 3 in which palatability changed than in phase 1. These findings show that capuchins readily adjust to changes in flavour and palatability of a familiar food and that sudden unpalatability has no carry-over effects. Therefore, capuchins behave differently towards a familiar food whose palatability has changed than they do towards novel foods.

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Some plants defend themselves from herbivorous animals with particular substances in their leaves, fruits and seeds (Janzen 1983; Cooper & Johnson 1984). Some of these secondary metabolites such as glucosides and alkaloids have a bitter taste (Garcia & Hankins 1975) which allows their detection at low concentrations (Steiner & Glaser 1984; Simmen 1994). Jones et al. (1978) showed that the levels of cyanogenic glucosides in various plants differ depending on geographical locality and that, as a consequence, they are eaten more in some areas than others. In addition, the concentration of toxic secondary metabolites (e.g. cyanogenic glucosides) changes in relation to plant age (McKey 1975; Janzen 1983), season (Ellis et al. 1977a, b) and plant tissue type (Cooper & Johnson 1984). For example, in different Amazonian forest types the composition and richness of mammal communities seem to be affected by the foliage phytochemistry, which is related to the nutrient content of the soil (Peres 1999). The success of a generalist species, which is likely to encounter familiar foods that have changed in flavour and faces the problem of avoiding those that are potentially toxic, depends on its flexible exploitation of the food resources.

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Primates adapt to changes in the environment by their behavioural flexibility (Box 1991). For social animals such as primates, Fairbanks (1975, page 182) has argued that 'there should be a selective advantage for individuals to be able to use social cues to assess food quality rather than having to rely on individual experience' and King (1994) has proposed that monkeys look for information by means of interactions with more knowledgeable individuals (see Whitehead 1986 for an example in mantled howling monkeys, *Alouatta palliata*). Although social learning would be particularly advantageous when foods are poisonous, several studies have shown that Japanese macaques, *Macaca fuscata*, do not learn to avoid a poisonous food by observing another's rejection of it (Hikami 1991; for a review see Visalberghi 1994) and instead rely on individual learning. Food avoidance is learnt faster when the food is novel than when it is familiar, and conversely extinction of avoidance is quicker when the food is familiar (Matsuzawa & Hasegawa 1983).

The responses to changes in flavour and/or palatability of foods and the social dynamics that might be prompted by them have never been studied. In the present study, we investigated these aspects of feeding in tufted capuchin monkeys by presenting them (individually or socially) with a food that changed flavour ('palatable–unpalatable–palatable') across phases of the experiment.

This species, which is widely distributed in South America, has a very broad diet consisting mainly of plant food, especially fruits, and a variety of invertebrates (see Kinzey 1997). To exploit the food sources available in varying environments, capuchins have to deal with novelty and to learn what they can feed upon. Wild capuchins, with the exception of small infants who remain near other individuals, encounter foods most of the time when not close to others (Phillips 1995). However, captive capuchins are more likely to accept and consume novel foods, at least during the first few encounters, when with their groupmates than when alone (Visalberghi & Fragaszy 1995; Visalberghi et al. 1998). In contrast, consumption of novel foods by infant capuchins does not seem to be influenced by their mothers or other adults (Fragaszy et al. 1997a).

The feeding habits of wild capuchins and the laboratory findings lead to the following predictions. (1) Capuchins will readily adapt to changes in flavour and palatability by decreasing or increasing food consumption. (2) They will adjust their feeding behaviour in the same way whether tested individually or socially, since socially tested capuchins will rely on their own experience and not on what they see the other group members doing. In addition, as shown by Rogers (1996, *in press*), we predict that (3) the social dynamics of access to food will differ according to food palatability and competition will be higher when the food is palatable.

METHODS

Subjects

We tested 27 capuchins (14 males and 13 females). They were all living in groups (group size 3–11), with the exception of one female who was paired with another female (not tested). Twenty-one were laboratory born (10 hand reared and 11 mother reared), two were wild born and confiscated when illegally traded and four were of unknown origin (probably wild born).

Therefore, 19 subjects (average age 10 years, range 2–31) were assigned to the Individual condition and tested alone, with the exception of two mothers that were tested with their infants (of 5 and 10 months of age). Eight subjects living in two groups ($N=3$ and $N=5$; average age 10 years, range 5–17) were assigned to the Social condition. In each group we assessed (on the basis of access to highly desirable food, e.g. peanuts) which were the two more dominant individuals over food and considered the others as subordinates. The dominant subjects were one male and one female in one group and two males in the other group. Rearing conditions and sex were balanced between conditions as much as possible; however, in the Social condition there were six males and two females.

Capuchin groups were housed in indoor–outdoor cages (11–25 and 22–25 m³, respectively). Testing occurred in cages measuring 1.7 × 1.9 m and 2.6 m high or 3 × 3 m and 2.5 m high. Cages were furnished with perches and slides; a variety of plastic toys and wooden blocks were given on a daily basis. All cages were connected by means

of sliding doors. Monkey chow, fresh fruits and vegetables were given once a day in the early afternoon. Every morning, grains, sunflower and pumpkin seeds were scattered on the floor bedding of the outdoor cage and three times a week monkeys received a mixture of cheese curd, vitamins, egg, bran, oats and sugar which all individuals liked very much. While the experiment was being carried out, this cheese mixture was not given during the normal feeding schedule since it was used for the experiment (see below).

Design

The experiment consisted of three phases of five 10-min sessions each. The cheese mixture was provided in phases 1 and 3, whereas the peppered cheese mixture was provided in phase 2. All subjects were tested once in each of the 15 sessions in the Individual or the Social condition. The total number of sessions (27 individuals × 15 sessions) was 405. For each subject the sessions of each phase were run on consecutive days, with a 1- or 2-day interval between phases.

Foods

The food presented in phases 1 and 3 consisted of equal volumes of cheese curd, oats and bran mixed together, hereafter called Food (note that it was similar to the cheese mixture the animals had in their usual diet). In phase 2, we added 6 g of white pepper to every 100 g of cheese mixture (hereafter called Pepper Food). The subjects had never tasted pepper before. The food was provided in balls weighing 8 g each; two balls for each subject. The food was placed on the green bottom of an open-topped Plexiglas box (20 × 22 cm and 20 cm high).

To assess whether the pepper, by altering the colour and/or odour of the food, provided a cue allowing the monkeys to discriminate the food without tasting, we tested 10 adult humans over 12 trials each. A trial consisted of simultaneous presentation of two balls, one of which contained pepper. In six trials, subjects were asked whether the balls differed in colour, and if so, which was darker. In the other six trials, they were allowed to smell (but not to see) the balls at a few cm distance and asked whether they had a different odour. No subject consistently (five or six times out of six) answered that the odour of the two balls was different. In contrast, five subjects consistently (in six trials out of six) distinguished between the balls by colour. Therefore, humans appeared able to discriminate the Pepper Food from the Food by colour, but not by odour. It should be noted, however, that simultaneous presentation facilitates discrimination and that in our experiment the monkeys were always presented with only one food at a time.

Procedure

For individual testing, we first separated the group into smaller units, and then allowed one individual to enter

the test cage. The subjects were already well accustomed to this separation procedure since it is used routinely in the laboratory for experimental purposes (see for example, Visalberghi & Frigaszy 1995). We tested subjects for one session per day, 5 days a week. Testing occurred indoors, between 1100 and 1500 hours before daily feeding. The experiment was videotaped and later scored in slow motion. The camera was focused on the box and the nearby area. Since the subject(s) could be out of the filmed field, at the tone of her stopwatch (every 10 s), the experimenter (E.A.) scored the behaviour of those subjects. The experiment was carried out between December 1997 and May 1998.

Behavioural data were collected at 10-s intervals with instantaneous focal sampling (Individual condition) and scan sampling (Social condition). Several exclusive categories of interaction with the food were recorded: (1) eating; (2) nibbling (characterized by the ingestion of no food or very little of it); (3) sniffing; (4) rubbing; (5) holding (with no consuming or sniffing). At the end of each session the leftovers were carefully collected from the cage floor and their amount (g) estimated. Eating and the amount of leftovers provide information about consumption, whereas, nibbling, sniffing, rubbing and holding refer to a more cautious and exploratory approach to food.

In addition, in the Social condition the following interactions were scored with scan sampling: interest in another's food (scored when an individual came close to and/or looked at, and/or sniffed at a piece of food held or eaten by another individual); stealing, or attempting to steal another's food. Proximity (less than 20 cm) with other individual(s) was scored when at least one of the individuals in proximity was showing a food-related behaviour. Overt agonistic interactions (threat, lunge) were noted ad libitum.

One of us (E.A.) collected the data and scored them from videotapes. Intraobserver reliability was calculated on 15% of the social and the individual sessions; the index of concordance assessed for each behaviour ranged between 99 and 96%.

Analysis

We calculated the mean number of behavioural samples in every session for each subject and analysed them by nonparametric statistics. Within each condition (Individual and Social) the scores obtained in the three phases were compared by the Friedman ANOVA; then, we used the Wilcoxon signed-ranks test to assess differences between phases. To assess whether the scores obtained in the five sessions of each phase differed, we used the Friedman ANOVA; in addition the behavioural scores of the last session of a phase were compared with those of the first session of the following phase by means of the Wilcoxon signed-ranks test. We also compared Individual and Social conditions with the Mann-Whitney *U* test. Social interactions, which were rare, are reported as descriptive results. All statistical tests are two tailed.

RESULTS

General Results

Overall, on average capuchins ate at least one sample in 91.1% of the sessions of phase 1, 71.8% of the sessions of phase 2, and 97% of the sessions of phase 3. (Note that in phases 1 and 3 subordinate individuals sometimes did not have access to food, which was monopolized by the dominant group members; see below.)

Sniffing occurred in 38 sessions of phase 2 (when the food was unpalatable) and in 3 and 11 sessions of phases 1 and 3, respectively ($\chi^2=38.9$, $P<0.01$). When capuchins sniffed the Pepper Food, they then ate it in 33% of the sessions and did not eat it in 36.8%. In contrast, in phases 1 and 3 sniffing was always followed by eating.

Individual Condition

The mean number of samples scored for all the different behaviours was statistically different across phases (for all the statistical values not reported in the text, see Table 1). Within each phase, eating was not statistically different across the five sessions (Friedman test: phase 1: $\chi^2=2.4$; phase 2: $\chi^2=2.7$; phase 3: $\chi^2=8.1$; NS). In phase 2, capuchins consumed only a small amount of the Pepper Food. They did not vomit, nor did they systematically make facial expressions of disgust when tasting the Pepper Food. In addition, they tended to manipulate, explore and hold the Pepper Food significantly more than they did the Food. In phase 3, when presented again with the Food, their behaviours towards it reverted back to values not significantly different from those of phase 1.

Capuchins responded immediately to the changes in flavour occurring between sessions 5 (Food) and 6 (Pepper Food) and between sessions 10 (Pepper Food) and 11 (Food) (Fig. 1, Table 2). They ate significantly less in the first session of phase 2 than in the last session of phase 1 and significantly more in session 11 than 10. Overall, the other manipulative/exploratory behaviours follow the opposite trend, increasing when food consumption decreased and vice versa. Holding was not significantly different in the sessions considered.

Of the two infants tested with their mother, the younger one (5 months old) never ate the food whereas the 10-month-old one ate more in phases 1 and 3 than in phase 2. His mother never prevented him from taking the Pepper Food. In phases 1 and 3, on the other hand, she did not allow him to take the Food from her mouth or hand. Notwithstanding her refusal, on two occasions he succeeded in taking food from her. No systematic pattern (phases 1 and 3 versus phase 2) was found in the number of times in which the mother or the infant ate first.

Social Condition

We first present the data as a whole by reporting what individuals did on average. Then, since we noticed striking interindividual differences, we compare the behaviour of the dominant and subordinate individuals. Within each phase, the average number of samples of eating scored in the five sessions was not statistically

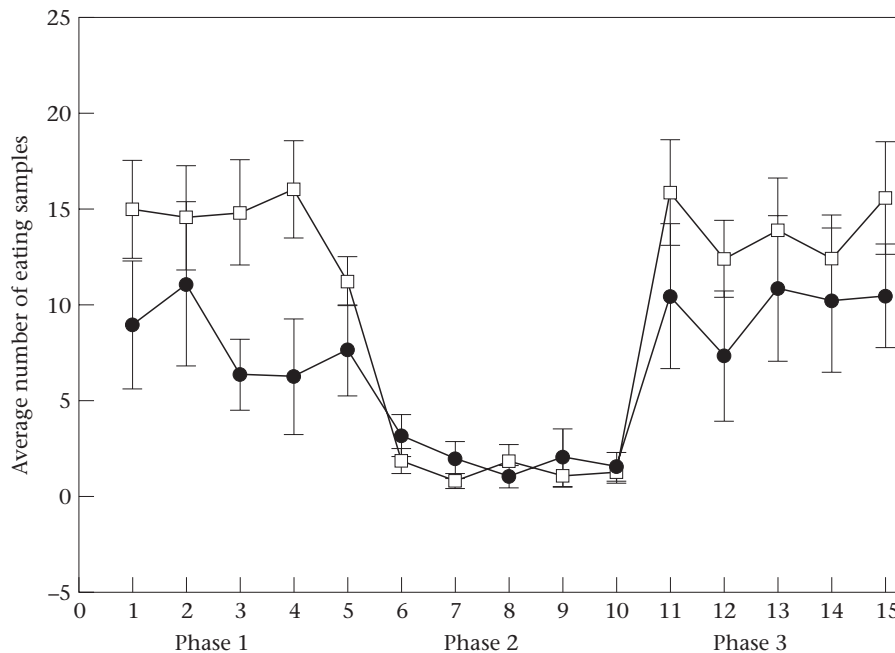
Table 1. Number of focal or scan samples ($\bar{X}\pm\text{SE}$) in which various behaviours occurred and the amount of food not eaten in phase 1 (normal food), phase 2 (food flavoured with pepper) and phase 3 (normal food)

Condition†	Phase 1	Phase 2	Phase 3	Friedman ANOVA χ^2	Wilcoxon T Phase 1 versus 2	Wilcoxon T Phase 2 versus 3	Wilcoxon T Phase 1 versus 3
Individual (N=19)							
Eating	69.4±10	6.1±2.1	73.1±11.9	29.0***	0***	0***	81.0
Leftovers (g)	0.8±2.1	15.6±1.8	1.2±3.2	34.8***	0***	0***	18.5
Nibbling	0.2±0.2	6.9±3.0	0.1±0.1	22.7***	0**	0**	81.0
Sniffing	0.4±0.2	5.3±0.9	0.6±0.2	25.3***	2.5***	0***	28.5
Rubbing	0.2±0.1	3.1±1.5	0.1±0.1	7.0*	5.0*	2.2*	81.0
Holding	12.7±2.0	5.0±1.7	12.1±2.7	7.6*	24.0**	38.0*	85.0
Social (N=8)							
Eating	40.4±12.5	9.5±4.6	49.5±17	7.0*	3.0*	5.0	12.0
Leftovers (g)	0	14.2±0.2‡	0				
Nibbling	0	18.5±2.2	0	16.0***	0*	0*	
Sniffing	0	3.0±0.9	0	14.0***	0*	0*	
Rubbing	0	20.0±8.5	0	14.0***	0*	0*	
Holding	2.5±1.1	31.1±7.6	2.6±1.6	10.1**	0*	3.0*	7.5

†Capuchins were tested individually or in a group.

‡The value refers to the total amount of food left by the whole group/number of group members. Note that the standard error is based on one data point for each group.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

**Figure 1.** Number of samples ($\bar{X}\pm\text{SE}$) in which eating was scored in the Individual condition (□) and in the Social condition (●) across: phase 1, Food (sessions 1–5); phase 2, Pepper Food (sessions 6–10); and phase 3, Food (sessions 11–15).

different (Friedman test: phase 1: $\chi^2=3.4$; phase 2: $\chi^2=6.9$; phase 3: $\chi^2=5.7$; NS), whereas eating differed between phases (see Table 1). Rubbing, sniffing, nibbling and holding increased significantly from phases 1 to 2 (Table 1). As in the Individual condition, in phase 3, when presented again with the Food, the capuchins' behaviours reverted back to values not significantly different from those of phase 1.

Dominant individuals ate significantly more than subordinates only in phase 1. The overall patterns for dominant and subordinate individuals were similar

except that dominants held food significantly more in phase 3 (Table 3).

An individual interacting with food provides group members with opportunities to be in its proximity and, possibly, to assess indirectly the food's palatability on the basis of that individual's behaviour with the food. If this is the case, proximity scores should be higher in the session(s) after the change in flavour. Proximity was not more frequent in phase 1 than 2 (total number of samples, $N=30$ and 31 , respectively; $Z=0$) but was more frequent in phase 3 ($N=50$) than in phase 1 ($Z=2.1$,

Table 2. Number of focal or scan samples in which various behaviours occurred and the amount of food not eaten ($\bar{X}\pm\text{SE}$) in the last session of phase 1 (session 5; normal food) and in the first session of phase 2 (session 6; food flavoured with pepper), in the last session of phase 2 (session 10) and in the first session of phase 3 (session 11; normal food)

Condition‡			Wilcoxon <i>T</i>		Wilcoxon <i>T</i>	
	Session 5	Session 6	5 versus 6	Session 10	Session 11	10 versus 11
Individual (N=19)						
Eating	11.4±1.4	1.8±0.7	2.5***	0.8±0.5	16.5±2.8	0***
Leftovers (g)	0	14.4±0.8	0****	16.2±0.3	0.3±0.3	0****
Nibbling	0	1.0±0.1	0†	1.5±0.7	0	0*
Sniffing	0	1.2±0.3	0**	1.1±0.2	0.1±0.1	0**
Rubbing	0	0.6±0.4	54.0	0.6±0.3	0	0*
Holding	3.2±0.8	1.8±0.9	30.5	1.3±0.6	1.8±0.8	35.0
Social (N=8)						
Eating	7.6±2.4	3.1±1.1	8.5	1.5±0.8	10.5±3.8	3.0†
Leftovers (g)	0	12.6±4.9§		14.9±7.8§	0	
Nibbling	0	2.6±1.0	0*	5.8±0.4	0	0*
Sniffing	0	0.5±0.4		0.4±0.2	0	0
Rubbing	0	2.1±1.0	0†	3.6±1.8	0	0*
Holding	0.4±0.2	6.4±2.8	1.0*	4.1±1.8	0.3±0.2	2.0*

‡Capuchins were tested individually or in a group.

§The value refers to the total amount of food left by the whole group/number of group members. Note that the standard error is based on one data point for each group

† $P<0.1$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$.

Table 3. Number of scan samples in which various behaviours ($\bar{X}\pm\text{SE}$) were scored for dominant and subordinate individuals tested in a group in phase 1 (normal food), phase 2 (food flavoured with pepper) and phase 3 (normal food)

	Phase 1	Mann-Whitney <i>U</i> ($N_1=N_2=4$)	Phase 2	Mann-Whitney <i>U</i> ($N_1=N_2=4$)	Phase 3	Mann-Whitney <i>U</i> ($N_1=N_2=4$)
Eating						
Dominant	66.0±14.9	1.0*	13.0±9.4	8.0	79.3±26.7	3.0
Subordinate	14.8±8.5		6.0±2.2		19.8± 5.9	
Nibbling						
Dominant	0		20.3±8.3	6.5	0	
Subordinate	0		16.8±7.4		0	
Sniffing						
Dominant	0		2.3±1.1	5.5	0	
Subordinate	0		3.8±1.5		0	
Rubbing						
Dominant	0		13.3±9.3	7.5	0	
Subordinate	0		26.8±14.9		0	
Holding						
Dominant	3.8±1.8	3.0	19.0±12.3	3.0	5.3±2.7	2.0*
Subordinate	1.3±1.3		43.3±4.9		0	

* $P<0.05$.

$P<0.02$) or phase 2 ($Z=2.0$, $P<0.03$). However, in the first sessions of phases 2 and 3, that is, in the sessions in which the change in flavour occurred, proximity was not more frequent than average (12 and 6 times versus an average per session of 7.4).

Aggression, apparently elicited by the presence of the food, was observed 11, 5 and 4 times in phases 1, 2 and 3, respectively. In 10 cases it involved dominant individuals directing aggression towards subordinate ones; in six cases it was between dominant individuals and in four cases it was between subordinate individuals.

In the Social condition capuchins ate less food in session 6 than in 5 (Table 2). All the other behaviours towards food increased in frequency in session 6 and

nibbling and holding did so significantly. From sessions 10 to 11, eating increased but not significantly so, whereas the frequencies of nibbling, rubbing and holding decreased significantly.

Comparison Between Individual and Social Conditions

Figure 1 shows eating across sessions for the two conditions. Although capuchins in all phases had more eating samples in the Individual than in the Social condition, these differences are not significant (phase 1: $U=44.5$, $N_1=19$, $N_2=8$; phase 2: $U=46$, $N_1=19$, $N_2=8$; phase 3: $U=47$, $N_1=19$, $N_2=8$; NS; Table 1).

In phases 1 and 3, nibbling, sniffing and rubbing were absent in the Social condition. In phase 2, these behaviours were present and two of them were scored significantly more in the Social than in the Individual condition (nibbling: $U=24.5$, $N_1=19$, $N_2=8$, $P<0.01$; rubbing: $U=31$, $N_1=19$, $N_2=8$, $P<0.05$); an opposite tendency, which did not reach significance, was observed for sniffing ($U=47.5$, $N_1=19$, $N_2=8$, NS). In phases 1 and 3, holding was significantly more frequent in the Individual than in the Social condition ($U=14$, $N_1=19$, $N_2=8$, $P<0.001$; $U=26$, $N_1=19$, $N_2=8$, $P<0.01$, respectively), whereas the opposite was true in phase 2 ($U=17.5$, $N_1=19$, $N_2=8$, $P<0.01$).

DISCUSSION

Capuchins have been described as a successful genus (Fragaszy et al. 1990), whose ecology and diet are extremely adaptable (Kinzey 1997). In our experiment they undoubtedly showed behavioural flexibility when facing negative as well as positive changes in the palatability of a familiar food. In particular, regardless of their social status, capuchins responded to the pepper by drastically decreasing consumption, while increasing behaviours related to visual and olfactory exploration. They tried to process the food, possibly to make it more palatable, by manipulating it as if trying to get rid of something, they rubbed it in their hands and on substrates and, on a few occasions, brought it to the tap and rinsed it under running water. After these processing attempts, they tasted the food again. Similar behaviours are commonly performed towards toxic butterflies and caterpillars (*Amata phegea*, *Zygaena filipendulae*; E. Addressi, unpublished data) and with frogs (Izawa 1978).

As expected, capuchins responded to a flavour change in familiar food in the first session in which the change occurred; and within each phase, consumption did not differ across sessions. This pattern was similar regardless of the test conditions (Individual versus Social). Marked differences in food consumption between dominant and subordinate monkeys were evident when the food was palatable, even if overt aggression was rare. In contrast, as found by Rogers (1996, in press) for less preferred foods, capuchins did not compete when the food was unpalatable, nor did they differ in food consumption.

In the Social condition the capuchins did not seem to take advantage of the behaviour of group members. Food consumption was not affected by seeing a sudden change (increase or decrease) in the amount of food eaten by others. Proximity was more frequent in phase 3, but neither in phase 3 nor in phase 2 did it preferentially occur in the session in which the food had just changed flavour, that is, when the behaviour of conspecifics might provide useful indirect information about the food's palatability. Behaviours performed to prevent another individual from eating the Pepper Food were never observed, not even in the mother–infant pair (see also Visalberghi & Frigaszy 1996). This mother allowed her 10-month-old infant to take her food and, by default, acquire information about it (see Frigaszy et al. 1997b). It can be

argued that throughout this pattern of interactions, infants might acquire information about food from the food itself. However, on the basis of the behaviour of infants towards group members in experiments in which novel foods (Fragaszy et al. 1997a) and food difficult to process (pecan nuts) were presented to capuchin monkeys, Frigaszy et al. (1997b, page 198) concluded that 'we cannot determine from these findings whether infants are also seeking information', and not only seeking food. Therefore, regardless of age, the argument suggested by King (1994) that monkeys look for information by means of interactions with more knowledgeable individuals, not to mention the idea of active provision of information, has not yet been shown for capuchins. Rather, the available findings support the view that individuals, infants included, find out about food palatability on their own and do not rely on what others do.

The lack of social influences in learning about unpalatable food (phase 2) is in agreement with the findings that monkeys do not learn from others to avoid poisonous foods (for a review, see Visalberghi 1994) and supports Visalberghi & Frigaszy's (1996) view that social learning requires a behaviour to be performed (e.g. eating) while the absence of the behaviour (e.g. not eating) is not likely to lead to social learning, unless behaviours that are cognitively demanding (e.g. active teaching) are also present.

During the experiment we presented a food whose external features were familiar to the subjects. The lack of social learning in phase 3 is in agreement with Visalberghi & Frigaszy's (1995) study which showed that the consumption of familiar foods did not increase when other group members were also eating, whereas the consumption of novel foods did.

Therefore, two lines of inquiry, that is, the experiments on food aversion learning in Japanese macaques (Hikami 1991) and our capuchin experiment with unpalatable food, show a primacy of individual learning versus social learning as a way of getting information about foods in these monkey species. The line of inquiry with novel foods (Visalberghi & Frigaszy 1995) might contradict this view only if new experiments clarify whether this facilitatory effect is due to (1) companions eating the same novel food, (2) companions merely eating a food, or (3) a nonspecific reduction of neophobia. The latter phenomenon has been suggested by Greenberg (1990) who showed that in novel feeding situations birds (warblers, *Dendroica castanea* and *D. pensylvanica*) tested in groups learned quicker because the presence of companions reduced their neophobia.

Overall, capuchins' responses towards the Pepper Food were extremely consistent. On the one hand, they kept tasting the food (nibbling or eating it at least once) across sessions; but when it was peppered they did not consume it. On the other hand, they ate all the food when it became palatable once again. This pattern is very different from that characterizing the well-studied phenomenon of food aversion learning. In food aversion learning, (1) the ingestion of a food that is matched with strong negative experience(s), such as gastrointestinal illness, leads to the complete avoidance of the noxious food,

(2) the avoidance is based on information other than gustatory and persists when the food is no longer noxious, and (c) the avoidance learning process is quicker when the food is novel (Garcia et al. 1955; Garcia & Koelling 1966; for a review of primate studies see Visalberghi 1994). In contrast, in the capuchins' response to changes in flavour: (1) ingestion was necessary to prevent consumption (they tasted the Pepper Food before refusing it); (2) the food was eaten again when the pepper was removed; and (3) the familiarity of the food did not prevent an immediate drastic reduction in consumption. Therefore, it is evident that ours is not an experimental paradigm to test food aversion learning.

Our paradigm appears suited to investigate the behavioural responses to changes in flavour and palatability, such as those likely to occur in many plant sources exploited by primates (Jones et al. 1978; Janzen 1983; Cooper & Johnson 1984). These changes, which cannot be easily noticed from outside (but which are detectable by taste and/or smell), make a food unpalatable (not highly toxic or lethal), and again make it palatable when that food source is renewed (e.g. when young leaves appear, or when the same species of plant is encountered elsewhere, etc.). By adding pepper to a palatable food we simulated these changes. Further experiments are needed to assess whether this paradigm is suited for other species.

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