Journal of Chemical Ecology, Vol. 25, No. 7, 1999

TASTE RESPONSIVENESS TO FOOD-ASSOCIATED ACIDS IN THE SQUIRREL MONKEY (*Saimiri sciureus*)

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(Received August 26, 1998; accepted March 14, 1999)

Abstract—The taste responsiveness of six adult squirrel monkeys to five food-associated acids was assessed in two-bottle preference tests of brief duration (5 min). In experiment 1 the monkeys were given the choice between tap water and defined concentrations of citric acid, ascorbic acid, malic acid, acetic acid, or tannic acid dissolved in tap water. In experiment 2 the animals were given the choice between a 50 mM sucrose solution and defined concentrations of the same acids dissolved in a 50 mM sucrose solution. With both procedures *Saimiri sciureus* significantly discriminated concentrations as low as 10 mM ascorbic acid and acetic acid, 5 mM citric acid and malic acid, and 0.2 mM tannic acid from the alternative stimulus. The results showed: (1) that squirrel monkeys respond to the same range of acid concentrations as other nonhuman primate species tested so far, (2) that *Saimiri sciureus* detects food-associated acids at concentrations well below those present in most fruits, and (3) that the responsiveness of this New World primate to acidic tastants was largely unaffected by the addition of a sweet-tasting substance. The results support the assumption that squirrel monkeys may use sourness and/or astringency of food-associated acids as a criterion for food selection.

Key Words—Gustatory preference thresholds, taste sensitivity, acidic compounds, squirrel monkey, *Saimiri sciureus*.

INTRODUCTION

The taste of most fruits is characterized by a mixture of sensations termed as sweet and sour by humans (Nagy and Shaw, 1980), and the food selection behavior of nonhuman primates suggests that they may use gustatory cues, and the relative salience of sweetness and sourness in particular, to assess palatability and nutritional value of a fruit (Clutton-Brock, 1977; Glaser, 1989). Thus, high sensitivity allowing the detection of both sweet- and sour-tasting substances should be important for frugivorous primates.

0098-0331/99/0700-1623$16.00/0

While the sense of taste has been investigated behaviorally and electrophysiologically in a number of primate species, most studies so far have concentrated on detectability of the four basic taste qualities, usually using acetic acid as the only, prototypic, sour stimulus. There is only sparse information as to the taste responsiveness of nonhuman primates for naturally occurring acids other than acetic acid.

Fruits usually contain a variety of acidic tastants (Ulrich, 1970), although ascorbic acid, citric acid, and malic acid are quantitatively predominant in most cases and may account for more than 90% of total acid content (Souci et al., 1989). Ascorbic acid plays essential roles in several physiological functions in mammals. Whereas many species of mammals synthesize their ascorbate requirements, all primate species examined so far are unable to do so (Milton and Jenness, 1987), and thus primates are thought to require a dependable dietary supply of ascorbic acid (Portman, 1970).

In addition to carbohydrates, citric acid and malic acid are the most common and abundant means of storing respiratory energy in fruits (Ulrich, 1970), and they represent an easily metabolizable source of energy for frugivorous primates (Gallina and Ausman, 1979). Furthermore, citric acid is known to act as an antirachitic agent in primates because it facilitates the absorption of calcium (Portman, 1970).

Acetic acid is also widely distributed in fruits, although usually only at low concentrations (Ulrich, 1970). However, it is a main product of fermentation, putrefying, and oxidation processes of plant material and thus is a potential indicator of the degree of ripeness of a fruit and concomitantly of its nutritional value (Lang, 1970).

Tannic acid also is present in a wide spectrum of plant matter, particularly in foliage, the skin and husks of fruits, and the bark of trees (Swain, 1979). It binds protein and amino acids and can prevent their absorption (Goldstein and Swain, 1965). Therefore, it seems adaptive for monkeys to be able to taste tannic acid in order to select food sources without too much of this substance. In humans, tannic acid elicits a characteristic astringent and—at high concentrations—bitter taste (Lyman and Green, 1990), and in rhesus monkeys tannic acid has been shown to be a major determinant of food selection (Marks et al., 1988).

Given the presumed importance of food-associated acids for food selection in primates, it was the aim of the present study to assess the gustatory responsiveness of squirrel monkeys—a frugivorous New World primate species—to ascorbic acid, citric acid, malic acid, acetic acid, and tannic acid, all important constituents of the natural diet in *Saimiri sciureus*.

Because most, but not all primate species tested so far reject substances that taste sour and/or astringent to humans (Glaser and Hobi, 1985), a two-bottle preference test of brief duration (5 min) was employed. This methodology makes it possible to directly measure preferences for or aversions to tastants and largely rules out the influence of postingestive factors on the animal's ingestive behavior. Tap water (experiment 1) or a sucrose solution (experiment 2), both as solvent for the acids and as the alternative stimulus, allowed me to additionally address the question of whether adding a sweet-tasting substance would affect the monkeys' responsiveness to the acids.

METHODS AND MATERIALS

Animals. Testing was carried out with three male and three female adult squirrel monkeys (*Saimiri sciureus*) weighing 0.8–1.2 kg and ranging from 4 to 8 years of age. This social group was housed in a 10-m^3 enclosure, which could be subdivided by sliding doors to allow temporary separation of animals for individual testing, and was maintained on a 12L : 12D cycle at 20–24°C. Animals were fed marmoset pellets (Ssniff) and fresh fruit and vegetables ad libitum but were deprived of water overnight before testing on the following morning. The amount of food offered daily to the animals was such that leftovers were still present on the next morning and thus it was unlikely that ravenous appetite affected the animals' ingestive behavior in the tests.

Procedure. Taste responsiveness to ascorbic acid, citric acid, malic acid, acetic acid, and tannic acid (reagent grade, Merck) was assessed in a two-bottle preference test. Twice each day, approximately 3 and 1 hr before feeding, the animals were separated and allowed 5 min to drink from a pair of simultaneously presented graduated 100-ml cylinders with metal drinking tubes.

In experiment 1, the monkeys were given a choice between tap water and defined concentrations of the acids dissolved in tap water. In experiment 2, the monkeys were given a choice between a 50 mM sucrose solution and defined concentrations of the acids dissolved in a 50 mM sucrose solution. In both experiments testing usually started at a concentration of 100 mM and proceeded in the following steps: 50, 20, 10, 5, 2, 1 mM, etc., until the animals failed to show a significant preference or aversion. With tannic acid, testing started at a concentration of 5 mM and proceeded in the same manner as for the other substances. Higher concentrations were additionally tested with ascorbic acid (400 and 200 mM) and acetic acid (200 mM) in order to evaluate whether such an increase in stimulus intensity would lead to an even more pronounced behavioral response.

Each pair of stimuli was presented 10 times, and the position of the stimuli was randomized in order to counterbalance possible position preferences. All animals had served in previous studies with the same methodology (Laska, 1994, 1996, 1997) and were completely accustomed to the procedure.

The experiments reported here comply with the "Principles of Animal Care" (publication No. 86-23, revised 1985 of the NIH) and also with current German laws.

Data Analysis. For each animal, the amount of liquid consumed from each bottle was recorded, summed for the 10 test trials with a given stimulus combination, converted to percentages (relative to the total amount of liquid consumed from both bottles), and 66.7% (i.e., 2/3 of the total amount of liquid consumed) was taken as criterion of preference. This rather conservative criterion was chosen for reasons of comparability of data because the same criterion had been used in previous studies with the same methodology and individuals (Laska, 1994, 1996, 1997), and in order to avoid misinterpretation of data due to a too liberal criterion.

Additionally, two-tailed binomial tests (Siegel and Castellan, 1988) were performed and an animal was only regarded as significantly preferring one of the two alternative stimuli if it reached the criterion of 66.7% and consumed more from the bottle containing the preferred stimulus in at least 8 of 10 trials (binomial test, $P < 0.05$).

Preliminary analysis of the data indicated that there were no reliable differences in choice behavior and liquid consumption between the male and female subjects and between the first and the second presentation of the day. Intraindividual variability of the amount of liquid consumed across the 10 test trials with a given stimulus combination was low and averaged less than 20%. Thus, a theoretically possible bias in the overall preference score due to excessive drinking in aberrant trials did not occur. Therefore, the data for the males and females obtained in the 10 test trials were combined and reported as group means with standard deviations.

Preliminary tests showed that the animals rejected the solutions containing detectable concentrations of the acids. Following convention, the results are nevertheless expressed as percentage of preference for the tastant and not for the solvent. Accordingly, 33.3% (i.e., 1/3 of the total amount of liquid consumed) was taken as criterion of avoidance.

RESULTS

Experiment 1. Figure 1 shows the mean performance of the six squirrel monkeys in the two-bottle preference tests with tap water used both as solvent for the acids and as the alternative stimulus. All six animals significantly discriminated concentrations as low as 10 mM ascorbic acid and acetic acid, 5 mM citric acid and malic acid, and 0.2 mM tannic acid from tap water, and in some cases single individuals even scored slightly lower values. All animals rejected detectable concentrations of all acids tested and in no case showed a preference for an acid. However, all animals failed to reject the lowest concentrations presented, suggesting that the avoidance of higher concentrations was indeed based on taste perception. In most cases, interindividual variability of scores was low for both sub- and suprathreshold concentrations tested (cf. SDs in Figure 1).

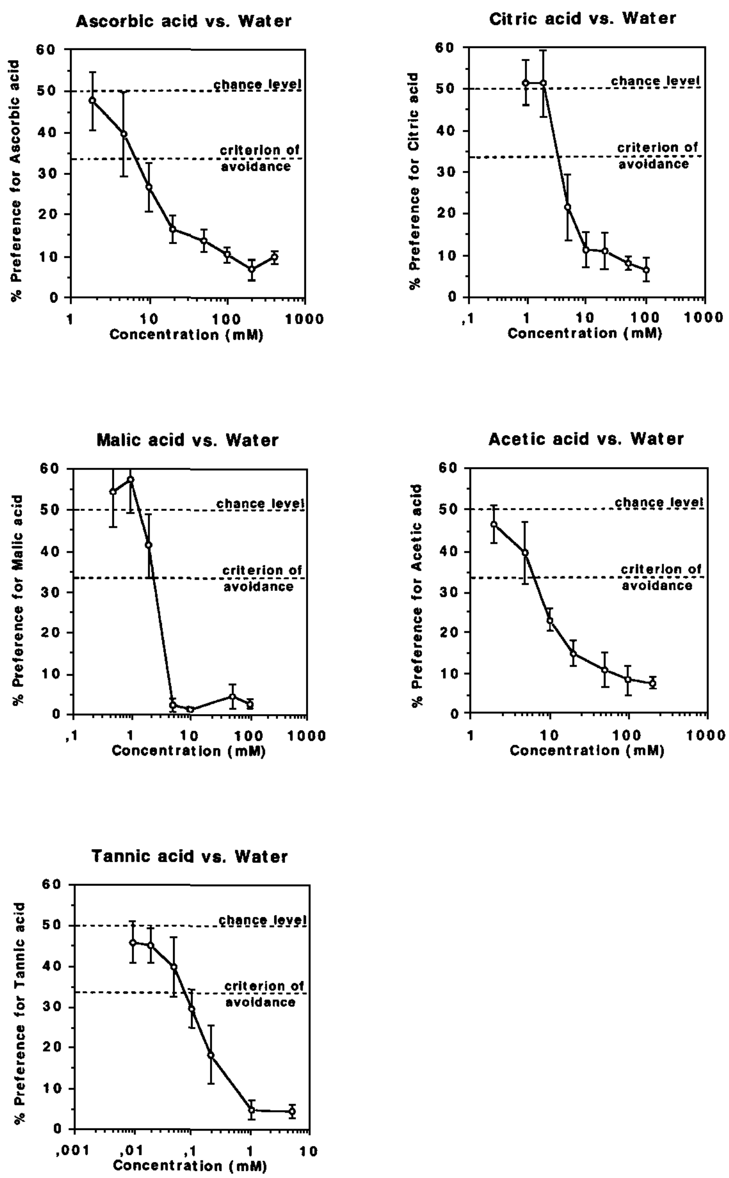

FIG. 1. Taste responsiveness of six squirrel monkeys to ascorbic acid, citric acid, malic acid, acetic acid, and tannic acid dissolved in tap water and tested against tap water as alternative stimulus. Each point represents the mean value (±SD) of 10 test sessions of 5 min per animal.

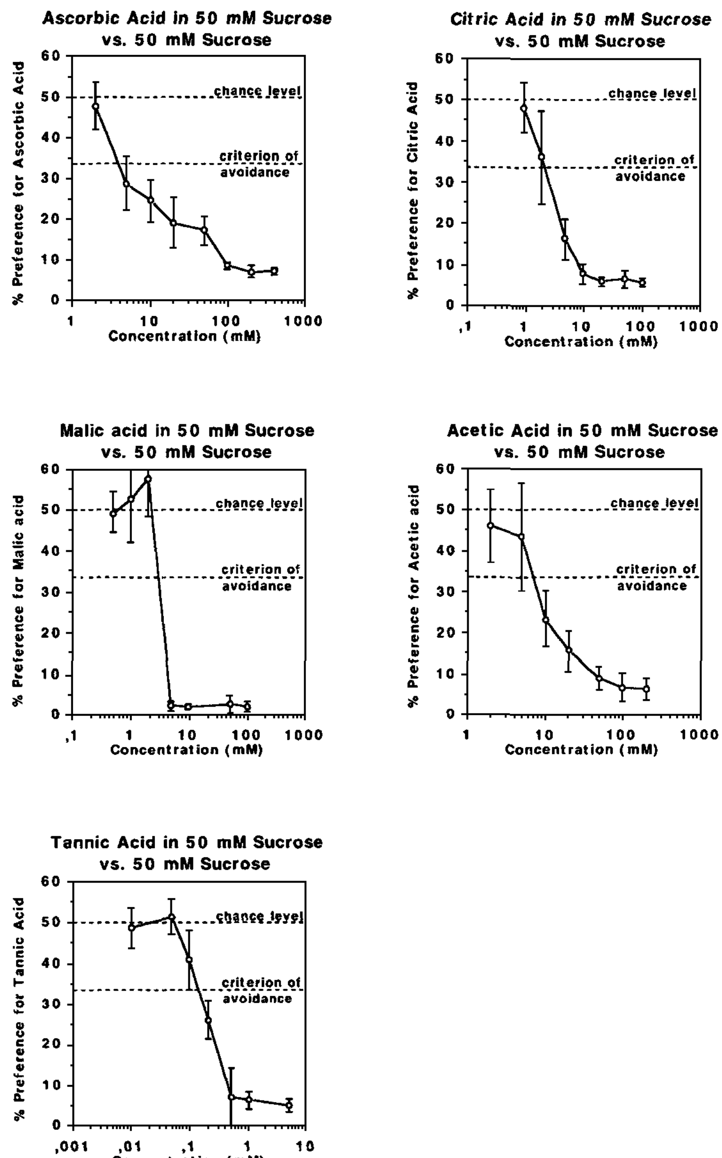

FIG. 2. Taste responsiveness of six squirrel monkeys to ascorbic acid, citric acid, malic acid, acetic acid, and tannic acid dissolved in a 50 mM sucrose solution and tested against a 50 mM sucrose solution as alternative stimulus. Each point represents the mean value (±SD) of 10 test sessions of 5 min per animal.

Experiment 2. Figure 2 shows the mean performance of the six squirrel monkeys in the two-bottle preference tests with a 50 mM sucrose solution used both as solvent for the acids and as the alternative stimulus. In accordance with the findings from experiment 1, all six animals significantly discriminated concentrations as low as 10 mM ascorbic acid and acetic acid, 5 mM citric acid and malic acid, and 0.2 mM tannic acid from the alternative stimulus, and again in some cases single individuals even scored slightly lower values. Despite the sweet-tasting—and thus highly attractive—solvent used in this experiment, all acids were rejected at detectable concentrations by all animals. The lowest acid concentrations presented, however, were consumed at equal amounts compared to the alternative stimulus, suggesting that the avoidance of higher concentrations was indeed based on perception of the acidic tastants. In most cases, interindividual variability of scores was low as can be inferred from the SDs in Figure 2.

DISCUSSION

The results of this study can be regarded as a first and conservative approximation of the gustatory sensitivity squirrel monkeys for food-associated acids. Table 1 compares the taste responsiveness of *Saimiri sciureus* obtained here with the few data available from other primate species. Squirrel monkeys responded to the same range of concentrations as other nonhuman primates tested so far. The finding that the preference thresholds found here were only about one order of magnitude higher than the detection thresholds established in humans (ASTM, 1973) is remarkable considering that the sophisticated psychophysical signal detection methods employed with human subjects are likely to be more sensitive compared to the simple two-bottle preference test used with the monkeys. This supposition is supported by findings from Pritchard et al. (1995), who reported taste thresholds obtained with a conditioning paradigm in *Macaca mulatta* to be lower than those obtained with a preference test. This suggests that the sensitivity of *Saimiri sciureus* for food-associated acids might indeed match, if not exceed, that of *Homo sapiens*.

The reliability of the data reported here is supported by the fact that very similar values for citric acid and acetic acid were obtained with a single squirrel monkey in an earlier study (Glaser and Hobi, 1985) and the same methodology but a slightly different criterion.

The acid concentrations detected by the squirrel monkeys are well below those present in most fruits (Souci et al., 1989) or other parts of plants that are consumed by this species (Albach et al., 1981; Milton and Jenness, 1987). Thus, it seems reasonable to assume that the sourness and/or astringency elicited by the acids in their natural diet enter into the food selection behavior of *Saimiri sciureus*.

TABLE 1. TASTE RESPONSIVENESS TO FOOD-ASSOCIATED ACIDS IN SQUIRREL MONKEYS AND OTHER PRIMATE SPECIES

	Conc. (mM)				
Species[a]	Ascorbic acid	Citric acid	Malic acid	Acetic acid	Tannic acid
Saimiri sciureus[1]	10	5	5	10	0.2
Microcebus murinus[2,5]				8	*0.2*
Loris tardigradus[2]				17	
Nycticebus coucang[2]				6	
Galago senegalensis[2]				4	
Cebuella pygmaea[2]		6		6	
Saguinus midas niger[2]		4		4	
Aotus trivirgatus[2]		4		8	
Saimiri sciureus[2]		8		8	
Ateles geoffroyi[3]	5				
Macaca fascicularis[6]	*10*	*10*	*10*	*10*	*10*
Homo sapiens[4]	1	0.4	0.4	0.8	0.006

[a]Behavioral thresholds: [1]present study, [2]Glaser (1986), [3]Laska et al. (unpublished), and [4]ASTM (1973). *Electrophysiological responses:* [5]Hellekant et al. (1993) and [6]Plata-Salaman et al. (1995).

At detectable concentrations, all acids tested were rejected by the squirrel monkeys. This behavioral response is in accordance with reports of their natural feeding behavior (Baldwin, 1985) and with most of the few experimental studies that presented other primate species with acidic tastants (Glaser, 1986). So far, only one New World primate species, the owl monkey (*Aotus trivirgatus*), has been reported to prefer citric acid and acetic acid over tap water at low but detectable concentrations (Glaser and Hobi, 1985), and thus to show an inverted U-shaped function of preference, which also has been described in humans and some nonprimate mammal species (Kare, 1971). The authors hypothesize this preference for acidic tastants as an evolutionary adaptation of this species to avoid competition pressure between sympatric frugivores for sweet-tasting fruits.

A final aspect of the present study is the finding that the responsiveness of *Saimiri sciureus* to acidic tastants was largely unaffected by the addition of a sweet-tasting substance. The preference threshold values obtained in both experiments were identical and the degree of rejection at suprathreshold concentrations did not differ markedly between experiments 1 and 2, suggesting that the monkeys perceived an acid similarly when dissolved in tap water or in a sucrose solution. Numerous psychophysical studies have shown that both the intensity and the quality of a taste stimulus, as perceived by humans, is modified by including that stimulus in a mixture (McBride, 1989). However, there are conflicting findings with regard to the nature and degree of this modification: Suppression and enhancement of one tastant by another have been reported to occur in the perception of taste mixtures (Gregson and McGowen, 1963), although the former seems to be the rule (Schifferstein and Frijters, 1993). In a recent study, Stevens (1996) reported that sucrose has only a small masking effect on citric acid in humans, a finding which is in accordance with the responsiveness shown by the squirrel monkeys.

Considering that frugivorous species must make complex decisions in order to select a nutritionally balanced and nontoxic diet from among the available plants that may vary greatly in their chemical composition, it makes sense for such a species to be able to detect constituents of a potential food that presumably are critical for food choice as well in a taste mixture as when presented singly. This idea concurs with electrophysiological recordings from gustatory neurons in the primary taste cortex of the cynomolgus monkey (*Macaca fascicularis*) that have shown sour-best cells to be less susceptible to mixture suppression than, for example, sugar-best cells (Plata-Salaman et al., 1996).

Taken together, the results of the present study support the assumption that squirrel monkeys may use sourness and/or astringency of food-associated acids as a criterion for food selection.

Acknowledgments—I would like to thank Inno Stangl for his help in collecting data, and the Deutsche Forschungsgemeinschaft for financial support (La 635/6-1).

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