Taste responsiveness of chimpanzees (Pan troglodytes) and black-handed spider monkeys (Ateles geoffroyi) to eight substances tasting sweet to humans

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ABSTRACT

Using a two-bottle choice test of short duration, we determined taste preference thresholds for eight substances tasting sweet to humans in three chimpanzees (Pan troglodytes) and four black-handed spider monkeys (Ateles geoffroyi). We found that the chimpanzees significantly preferred concentrations as low as 100–500 mM galactose, 250 mM sorbitol, 0.5–2 mM acesulfame K, 0.5–2.5 mM allitame, 0.5 mM aspartame, 0.2–2 mM sodium saccharin, 0.001–0.2 mM thaumatin, and 0.0025–0.005 mM monellin over tap water. The spider monkeys displayed lower taste preference threshold values, and thus a higher sensitivity than the chimpanzees, with five of the eight substances (2–20 mM galactose, 20–50 mM sorbitol, 0.2–1 mM acesulfame K, 0.002–0.005 mM allitame, and 0.002–0.5 mM sodium saccharin), but were generally unable to perceive the sweetness of the remaining three substances (aspartame, thaumatin, and monellin). The ranking order of sweetening potency of the eight taste substances used here correlates significantly between chimpanzees and humans, but not between spider monkeys and humans. This is in line with genetic findings reporting a higher degree of sequence identity in the Tas1r3 genes coding for the mammalian heterodimer sweet-taste receptor between chimpanzees and humans compared to spider monkeys and humans. Taken together, the findings of the present study support the notion that taste responsiveness for substances tasting sweet to humans may correlate positively with phylogenetic relatedness. At the same time, they are also consistent with the notion that co-evolution between fruit-bearing plants and the sense of taste in animals that serve as their seed dispersers may explain between-species differences in sweet-taste perception.

1. Introduction

Substances tasting sweet to humans comprise an amazing diversity of chemical classes that ranges from simple amino acids over peptides, proteins, and carbohydrates to terpenoids, glycosides, flavonoids, saponins, sulfonyl amides and dihydrochalcones, to name but a few [31]. Considering that mammals have only one type of sweet-taste receptor, the TAS1R2-TAS1R3 heterodimer receptor [2], it is remarkable that this receptor is capable of binding such a wide array of structurally diverse ligands, although with different affinities. Recent studies have found that both allelic and copy number variation in the two sweet-taste receptor genes may explain the marked differences within and between species which have been reported for the ability to perceive and for the sensitivity to sweet-tasting substances [6]. Comparative studies of sweet-taste perception suggest that dietary specialization may plausibly explain between-species differences in taste perception [20]. Among New World primates, for example, the degree of frugivory has been found to positively correlate with sensitivity for food-associated carbohydrates [24]. Carnivorous species, such as cats, have been reported to lack a functioning sweet-taste receptor [29], possibly due to a diet-driven relaxed purifying selection pressure on the corresponding genes. Other studies suggest phylogenetic relatedness to underlie differences between species in their ability to detect certain taste substances. Among nonhuman primates, for example, the
sweet-tasting dipeptide derivatives L-aspartyl-(R)-α-methylphenethylamine and L-aspartyl-L-(O-tert-butyl)serine methyl ester have been reported to be detectable only for strepsirrhines and catarrhines, but not for platyrrhines [10]. Strepsirrhine primates, in contrast, have been shown to be less sensitive for sucrose compared to catarrhines [51]. It should be mentioned, however, that these two hypothetical explanations for the observed differences between species in the detectability of and sensitivity for sweet-tasting substances are not mutually exclusive but may complement each other.

Studies on sweet-taste perception in nonhuman primates have so far mainly focused on sensitivity for food-related saccharides found in the diet of primates and taste preference thresholds – as a first and widely used approximation of an animal’s taste sensitivity [44] – for tastants such as sucrose, fructose, and glucose have been obtained in members of all major primate taxa (strepsirrhines: [51]; platyrrhines: [24]; catarrhines: [37]). The majority of studies on non-carbohydrate sweeteners, in contrast, usually only employed one, arbitrarily chosen, concentration of a given taste substance and therefore did not determine taste preference thresholds, and thus sensitivity, but only detectability at best (e.g. [9, 35, 42]). However, assessing the sensitivity for taste substances perceived as sweet by humans other than food-associated carbohydrates may allow us to gain further insight into the causes of between-species differences in taste perception and into the mechanisms underlying the evolution of the sense of taste. Additionally, they may allow us to draw further conclusions as to the structural properties of sweet-tasting ligands that may affect their affinity to the mammalian sweet-taste receptor.

It was therefore the aim of the present study to determine taste preference thresholds in two species of nonhuman primates for eight substances perceived as sweet by humans. They comprised members of six different chemical classes as well as both naturally occurring and artificial sweeteners and substances of high and low sweetening potency. Employing chimpanzees and spider monkeys allowed us to additionally address the question whether dietary specialization or phylogenetic relatedness may more plausibly explain between-species differences in the detectability of and sensitivity for sweet-tasting substances among primates.

2. Methods

2.1. Animals

We assessed taste responsiveness in two adult female and one adult male chimpanzees (Pan troglodytes) and one adult female and three adult male black-handed spider monkeys (Ateles geoffroyi). The chimpanzees were housed, together with one other individual, at Borås Zoo, Sweden, in a 750 m² indoor exhibit, with access to a 560 m² outdoor island with natural vegetation. They were 27, 33, and 48 years old at the start of the study. The spider monkeys were housed at the field station UMA Doña Hilda Ávila de O’Farrill of the Universidad Veracruzana, near the town of Catemaco, in the province of Veracruz, Mexico. They were housed in a series of enclosures exposed to natural light and ambient temperatures that were connected to each other via sliding doors. The spider monkeys were between 8 and 12 years old at the start of the study. With both species, we performed the tests in an enclosure adjacent to their indoor exhibit which held several compartments in which the animals were tested separately to avoid competition and distraction. All animals were trained to voluntarily enter the test compartments and were completely accustomed to the procedure described below. The animals were fed fresh fruit and vegetables (chimpanzees: three times per day; spider monkeys: one time per day). The chimpanzees were additionally provided with commercial primate chow and had ad libitum access to water. As spider monkeys do not normally drink from open water sources but meet their water requirements by consuming juicy fruits, they did not have access to water. With both species, no water deprivation schedule was adopted. The amount of food offered daily to the animals was such that leftovers were still present on the floor the next morning. Thus, it was unlikely that ravenous appetite affected the animals’ ingestive behavior.

2.2. Ethical note

The experiments reported here comply with the American Society of Primatologists’ Principles for the Ethical Treatment of Primates, and also with current Swedish and Mexican laws. The chimpanzee study was performed according to a protocol approved by Gothenburg’s Animal Care and Use Committee (Göteborgs djurförsöksättska nämnd, protocol #75–2016), and the spider monkey study was performed according to a protocol approved by the Ethical Board of the Federal Government of Mexico’s Secretariat of Environmental and Natural Resources (official permits no. 09/GS-2132/05/10).

2.3. Taste Stimuli

Eight substances tasting sweet to humans were used. The terms ‘high-potency’ and ‘low-potency’ mentioned below refer to a substance’s sweetening potency relative to sucrose and are used herein according to the following definition: a high-potency sweetener has a human taste detection threshold at least a factor of 10 lower than sucrose, whereas a low-potency sweetener has a human taste detection threshold higher than sucrose [53].

Galactose (CAS# 59–23–4) is a low-potency, naturally occurring sweetener about 30% as sweet as sucrose to humans and chemically a monosaccharide and a constituent of the disaccharide lactose found in mammalian breast milk. It provides 4.0 kcal/g of energy. Sorbitol (CAS# 50–70–4) is a low-potency, naturally occurring sweetener about 60% as sweet as sucrose to humans and chemically a sugar alcohol. It is a sugar-substitute providing 2.6 kcal/g of energy. Acesulfame K (CAS# 55,589–62–3) is a high-potency, non-caloric artificial sweetener about 200 times sweeter than sucrose to humans and chemically a potassium salt of an oxathiazine and thus a sulfur- and nitrogen-containing compound. Alitame (CAS# 80,863–62–3) is a high-potency, non-caloric artificial sweetener about 2000 times sweeter than sucrose to humans and chemically a dipeptide composed of L-aspartic acid and L-alanine. Aspartame (CAS# 22,839–47–0) is a high-potency, non-caloric artificial sweetener about 200 times sweeter than sucrose to humans and chemically a methyl ester of the dipeptide built by the amino acids L-aspartic acid and L-phenylalanine. Sodium saccharin (CAS# 81–07–2) is a high-potency, non-caloric artificial sweetener about 300–400 times sweeter than sucrose to humans and chemically a protein found in the West African katemfe fruit (Thaumatroccus danielli). It provides 4.0 kcal/g of energy. Monellin (CAS# 9062–83–3) is a high-potency, naturally occurring sweetener about 800–2000 times sweeter than sucrose to humans and chemically a protein found in the fruit of the West African serendipity berry (Dioscoreophyllum cumminsii). It provides 4.0 kcal/g of energy. Four of these sweeteners (acesulfame K, aspartame, sodium saccharin, and thaumatin) have been reported to have a bitter side taste for humans when presented at high concentrations [41].

Acesulfame K and aspartame were obtained from Ter Hell & Co. (Hamburg, Germany), and thaumatin was obtained from Xi’an Sgonek Biological Technology Ltd. (Xi’an, China). All other substances were obtained from Sigma-Aldrich (Stockholm, Sweden). All substances were of the highest available purity (~99%).

2.4. Procedure

We used a two-bottle preference test of short duration [39]. The animals were allowed to drink for 1 min from a pair of simultaneously
presented graduated cylinders with metal drinking spouts. We performed three of such 1-min trials per day and animal, with intertrial intervals of approximately 30 min.

To determine taste preference thresholds, the animals were given the choice between tap water and defined concentrations of a sweetener dissolved in tap water. With all substances, testing usually started at a concentration that was approximately a factor of 100 above the known human taste detection threshold [49] and proceeded in 10-fold steps until an animal failed to show a significant preference. Subsequently, the animals were presented with intermediate concentrations (between the lowest concentration that was preferred and the first concentration that was not) in order to determine the preference threshold value more exactly. In cases where an animal did not display a preference with the starting concentration of a given taste substance, testing proceeded in 10-fold steps above the starting concentration until an animal showed a preference or until a concentration range of 1000 was covered. The order in which the eight sweeteners were tested was the same for all animals and testing with a new substance only started when testing with the previous one was completed.

We presented each pair of stimuli 10 times per individual animal, and the position of the stimuli was pseudo-randomized in order to counterbalance possible position preferences. Care was taken that an animal sampled both stimuli at least once during each trial. To maintain the animals’ motivation and willingness to cooperate, testing of the different stimulus concentrations with a given substance did not follow a strict order but was pseudo-randomized. This was true both within the three trials performed on a given testing day and between days.

2.5. Data analysis

For each animal, we recorded the amount of liquid consumed from each bottle, summed it for the ten trials with a given stimulus combination, converted it to percentages (relative to the total amount of liquid consumed from both bottles), and took 66.7% (i.e. 2/3 of the total amount of liquid consumed) as the criterion of preference. We chose this rather conservative criterion for reasons of comparability of data as the same criterion had been used in previous studies on sweet-taste responsiveness with other primate species [21–27, 33, 51], and in order to avoid misinterpretation due to a more liberal criterion. Additionally, we performed binomial tests and regarded an animal as significantly preferring one of the two stimuli if it reached the criterion of 66.7% and consumed more from the bottle containing the preferred stimulus in at least 8 out of 10 trials (binomial test, P < 0.05). Thus, we defined taste preference threshold as the lowest concentration at which the animals met both criteria mentioned above.

To account for cases in which the animals rejected a taste stimulus, we took 33.3% (i.e. 1/3 of the total amount of liquid consumed) as the criterion of rejection. Accordingly, we regarded an animal as significantly rejecting a taste stimulus if it stayed below the criterion of 33.3% and consumed less from the bottle containing the rejected stimulus in at least 8 out of 10 trials (binomial test, P < 0.05).

Preliminary analyses of the data indicated that there were no systematic differences in choice behavior and liquid consumption between the three 1-min trials performed on a given day. Intraindividual variability of the amount of liquid consumed across the ten 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.

3. Results

3.1. Chimpanzees

Taste preference thresholds of the three chimpanzees were found to be 100–500 mM for galactose, 250 mM for sorbitol, 0.5–2 mM for acesulfame K, 1 mM for alitame, 0.5–2.5 mM for aspartame, 0.2–2 mM for sodium saccharin, 0.001–0.2 mM for thaumatin, and 0.0025–0.005 mM for monellin (Fig. 1). All three animals failed to show a significant preference for the lowest concentrations presented, suggesting that the preference for higher concentrations of a given taste substance was indeed based on the chemical nature, i.e. the sweetness of the stimuli. With none of the eight stimuli did the animals display any rejection responses, suggesting that the bitter side taste reported by humans at high concentrations of four of the sweeteners [41] did not affect the chimpanzees’ consumptive behavior, even at the highest concentrations tested.

With six of the eight substances, interindividual variability of taste preference threshold values was low and ranged between zero (i.e. all three animals displaying the same taste preference threshold with a given substance) and a dilution factor of 5 between the most- and the least-responsive animal. Thaumatin was a notable exception in this respect, with threshold values varying by a dilution factor of 200 between the most- and the least-responsive animal.

3.2. Spider monkeys

Taste preference thresholds of the four spider monkeys were found to be 2–20 mM for galactose, 20–50 mM for sorbitol, 0.1–1 mM for acesulfame K, 0.002–0.005 mM for alitame, and 0.002–0.5 mM for sodium saccharin. With aspartame, only two out of four animals showed a significant preference for the highest of the four concentrations tested (20 mM) and were indifferent towards the other concentrations (2, 0.2, and 0.02 mM). The other two animals significantly rejected the aspartame concentrations of 20 and 2 mM (both animals) and even 0.2 mM (one animal) and were indifferent to the lowest concentration tested (0.02 mM). With thaumatin, only one animal significantly preferred the highest of the four concentrations tested (0.1 mM) and was indifferent towards the other concentrations (0.01, 0.001, and 0.0001 mM). Two animals displayed a significant rejection of the two highest thaumatin concentrations (0.1 and 0.01 mM) and were indifferent towards the two lower ones. The remaining animal did neither display a preference nor a rejection towards any of the four thaumatin concentrations. With monellin, only one animal showed a significant preference for one of the four concentrations tested (0.001 mM) and was indifferent towards the other concentrations. The other three animals significantly rejected the highest two concentrations (0.01 and 0.001 mM) and were indifferent towards the lowest concentration of monellin (0.0001 mM) tested. With all three substances for which only one or, in the case of aspartame, only two animals showed a significant preference for a sweetener, it was always the same individual.

Similar to the chimpanzees, all four spider monkeys failed to show a significant preference (or rejection) for the lowest concentrations presented, suggesting that the preference for (or rejection of) higher concentrations of a given taste substance was indeed based on the chemical nature of the stimuli, i.e. their sweetness in case of preference, and their bitterness in case of rejection.

With four of the five substances for which all four spider monkeys displayed a preference, interindividual variability of taste preference threshold values was low and ranged between a dilution factor of 2.5 (with alitame and sorbitol) and a dilution factor of 10 (with galactose) between the most- and the least-responsive animal. Sodium saccharin was a notable exception in this respect, with threshold values varying by a dilution factor of 250 between the most- and the least-responsive animal.

4. Discussion

The results of the present study demonstrate that chimpanzees and spider monkeys differ markedly in their responsiveness to substances tasting sweet to humans. With five of the eight sweeteners (galactose, sorbitol, acesulfame K, alitame, and sodium saccharine), the spider monkeys displayed lower taste preference thresholds and thus a higher
sensitivity than the chimpanzees. With the remaining three sweeteners (aspartame, monellin, and thaumatin), however, the spider monkeys were generally unable to detect them whereas the chimpanzees clearly perceived their sweetness.

4.1. Between-species comparisons of taste preference thresholds

Table 1 summarizes the taste preference thresholds for the sweet-tasting saccharides galactose and sorbitol in different mammal species. With both substances, the spider monkeys displayed markedly lower thresholds and thus a higher taste sensitivity than the chimpanzees. Black-and-white ruffed lemurs, the only other nonhuman primate
species tested with galactose and sorbitol so far, are also less sensitive than the spider monkeys but more sensitive than the chimpanzees for these two tastants. Similarly, pygmy marmosets are clearly less sensitive for galactose than the spider monkeys. These findings support the notion that the ability to perceive the sweetness of both galactose and sorbitol is present in all major taxa of primates (catarrhines, platyrhines, and strepsirrhines). The spider monkeys’ taste preference thresholds are also lower compared to those obtained with non-primate mammals such as cattle, rats, mice, and pigs. With both galactose and sorbitol, the taste preference thresholds of the spider monkeys are in the same range as the taste detection thresholds obtained with human subjects. This is remarkable considering that taste preference thresholds provide only a conservative approximation of an animal’s ability to detect a taste stimulus [44] whereas taste detection thresholds, obtained using sophisticated signal detection methods, can be regarded as a valid limit of human taste sensitivity. This suggests that spider monkeys are probably at least as sensitive for these two naturally occurring low-potency sweeteners as humans are.

Table 2 summarizes the taste preference thresholds for the artificial sweeteners acesulfame K, alitame, aspartame and sodium saccharin in different mammal species. With acesulfame K, the taste preference threshold values of spider monkeys and chimpanzees overlap with each other, and are higher than the taste detection thresholds of human subjects. The only other primate species tested so far with acesulfame K, the gray mouse lemur, failed to display a preference for this sweetener. The threshold values of non-primate mammals such as cattle, pig, and mouse for acesulfame K also overlap with those of the two primate species tested here.

With alitame, the threshold values of the spider monkeys overlap with those reported for human subjects, and both species are more sensitive for this artificial sweetener than the chimpanzees. Here, too, the gray mouse lemur, the only other nonhuman primate species tested so far, failed to display a preference for this substance. The pig, the only non-primate mammal tested with alitame so far, displayed a markedly higher taste preference threshold, and thus a lower sensitivity compared to both spider monkeys and human subjects.

With aspartame, the chimpanzees displayed higher threshold values compared to human subjects, and two of the four spider monkeys tested here preferred only the highest concentration of this artificial sweetener whereas the remaining animals failed to detect it at all. Four catarrhine primate species (sooty mangabey, white-eyelid mangabey, Japanese macaque, and rhesus macaque) all displayed threshold values for aspartame that were similar to those of the chimpanzees. Strepsirrhine primates such as the mongoose lemur and the gray mouse lemur, in contrast, failed to show a preference for this artificial sweetener. Similarly, non-primate mammals such as cattle, pig, mouse, rat, and golden hamster all failed to display a preference for aspartame.

With sodium saccharin, the spider monkeys displayed lower taste preference thresholds than the chimpanzees, but both were clearly less sensitive for this artificial sweetener compared to human subjects. The only two strepsirrhine primates tested so far (gray mouse lemur and black-and-white ruffed lemur) both failed to detect sodium saccharin. Non-primate mammals such as cattle, pig, rabbit, and golden hamster, are all markedly less sensitive than both spider monkeys and chimpanzees. Mice and rats, although displaying taste preference threshold values for sodium saccharin that overlap with those of the two primate species tested here, have been reported to display only a weak preference for this artificial sweetener.

These findings support the notion that both catarrhine and platyrhine, but not strepsirrhine primates, are able to perceive the sweetness of acesulfame K, alitame, and sodium saccharin, whereas only non-primate mammals such as cattle, pig, mouse, rat, and golden hamster all failed to display a preference for aspartame.

Please note that the values cited for *Homo sapiens* are taste detection thresholds, and not taste preference thresholds.
catarrhine, but not platyrhine and strepsirrhine primates are able to detect the sweetness of aspartame.

Table 3 summarizes the taste preference thresholds for the sweet-tasting proteins thaumatin and monellin in different mammalian species. With both substances, the chimpanzees displayed markedly higher threshold values and thus a lower taste sensitivity compared to human subjects. Three of the four spider monkeys tested here failed to show any preference for both proteins and the remaining animal preferred only the highest concentration tested. The only other primate species tested so far with thaumatin and monellin (red-handed tamarin and gray mouse lemur) both failed to display a preference. These findings support the notion that the ability to perceive the sweetness of both thaumatin and monellin may be restricted to catarrhine primates whereas both platyrhine and strepsirrhine primates may generally be unable to do so.

All three non-primate mammals tested so far with these sweet-tasting substances, the pig, mouse, and golden hamster, also failed to display any preference for thaumatin and monellin.

4.2. Sweetening potency and the sweet-taste receptor

Sweet-tasting substances are known to differ markedly in their sweetening potency [49]. Six of the eight substances used in the present study (acesulfame K, alitame, aspartame, monellin, sodium saccharin, and thaumatin) are considered as “high-potency” sweeteners as their human taste detection thresholds are at least a factor of 10 lower than that of sucrose whereas two substances (galactose and sorbitol) are “low-potency” sweeteners as their human taste detection thresholds are higher than that of sucrose [53]. Using their taste preference threshold for sucrose (20 mM, [37]) as the reference point, the chimpanzees of the present study displayed exactly the same dichotomy as they, too, had lower thresholds compared to sucrose with the other six sweeteners. Accordingly, the ranking order of sweetening potency of the eight taste substances used here correlates significantly between chimpanzees and humans (Spearman $r_s = 0.85$, $p < 0.01$). Although the spider monkeys also had higher taste preference thresholds for the monosaccharide and the sugar alcohol than for sucrose (3 mM, [24]) and lower thresholds compared to sucrose with three of the six high-potency sweetener, they generally failed to perceive aspartame, monellin, and thaumatin. Accordingly, the ranking order of sweetening potency of the eight substance used here did not correlate significantly between spider monkeys and humans (Spearman $r_s = 0.10$, $p > 0.05$).

| Species                  | Thaumatin (mM) | Monellin (mM) | Ref. |
|-------------------------|----------------|---------------|-----|
| Hominid primates        |                |               |     |
| Pan troglodytes verus   | 0.001 – 0.2    | 0.0025 – 0.005 | [1] |
| Homo sapiens            | 0.00006 – 0.0001| 0.000002 – 0.00009 | [2] |
| Platyrhine primates     |                |               |     |
| Ateles geoffroyi        | 0.001 (1/4)    | 0.1 (1/4)     | [1] |
| Saginus midas           | No pref.       | No pref.      | [3] |
| Strepsirrhine primates  |                |               |     |
| Microcebus murinus      | No pref.       | No pref.      | [4] |
| Non-primates            |                |               |     |
| Menocricetus auratus    | No pref.       | No pref.      | [5] |
| Mus musculus            | No pref.       | No pref.      | [6, 7] |
| Not available           | No pref.       | No pref.      | [8] |

[1] Present study; [2] van Gemert [49]; [3] Hellekant et al. [15]; [4] Schilling et al. [42]; [5] Danilova et al. [4]; [6] Bachmanov [1]; [7] Matsunami and Amrein [30]; [8] Glaser et al. [12]

Please note that the values cited for Homo sapiens are taste detection thresholds, and not taste preference thresholds. ‘No pref.’ indicates that no preference was shown over water in two-bottle preference tests. The numbers in round brackets indicate how many out of the total number of animals tested displayed a preference for the substance.

These findings are in line with genetic studies that demonstrated a high degree of sequence identity at the nucleotide level in both the Tas1r2 gene (99%) and the Tas1r3 gene (98%) between humans and chimpanzees [28]. The degree of sequence identity between humans and New World primates such as squirrel monkeys and pygmy marmosets, in contrast, was found to be clearly lower (92% and 90% with Tas1r2, and 89% and 88% with Tas1r3, respectively). This may plausibly explain why the TAS1R2-TAS1R3 heterodimer taste receptor of the New World spider monkeys of the present study may have a lower binding affinity for some of the ligands used here that taste sweet to humans. In the case of aspartame, one of the high-potency sweeteners that the spider monkeys generally failed to detect, Li et al. [28] identified 9 variant sites in the Tas1r2 gene and 32 variant sites in the Tas1r3 gene that distinguish taste and non-taster species. Computer-assisted modeling of the taste receptor structure suggests that variation at a secondary, allosteric binding site of the TAS1R2 protein is the most likely origin of differences in the perception of sweetness of aspartame.

High molecular mass sweeteners such as peptides and proteins are thought to recognize a binding site at the mammalian sweet-taste heterodimer receptor that is different from the binding site of low molecular mass sweeteners [47]. In this context it should be noted that aspartame is a methyl ester of a dipeptide and thus chemically similar to the other two sweeteners that the spider monkeys generally failed to detect, the proteins thaumatin and monellin. Interestingly, one of the four spider monkeys tested here displayed a preference for all three aforementioned high-potency sweeteners at the highest concentration tested (Fig. 2). This suggests that interindividual variation in the amino acid sequence of the TAS1R2-TAS1R3 heterodimer, presumably at the level of single nucleotide polymorphisms [52], may be sufficient to increase the binding affinity between the sweet-taste receptor and its ligand to allow for at least some perception of its sweetness, though at concentrations that are markedly higher than those of species that readily detect it.

Both the present findings and genetic studies support the notion that the degree of phylogenetic relatedness may underlie differences between species in their ability to detect certain substances tasting sweet to humans. However, it should be considered that thaumatin has so far only been found to naturally occur in the west African katemfe fruit (Thaumatococcus danielli), and monellin only in the fruit of the west African serendipity berry (Dioscoreophyllum cumminsii). This raises the possibility that Old World primates such as the chimpanzee, but not New World primates such as the spider monkey, may have been exposed to these sweet-tasting proteins over an evolutionarily relevant period of time and thus may have evolved a correspondingly modified TAS1R2-TAS1R3 receptor allowing their perception [18]. In line with this notion, only Old World, but not New World primates have been found able to perceive the sweetness of brazzein, a protein found in the fruit of the African oublie plant (Penadiplandra brazzeana) [13]. Co-evolution between fruit-bearing plants and the sense of taste in animals that serve as their seed dispersers has repeatedly been suggested as a mechanism underlying between-species differences in the sense of taste both in primates [46, 48] as well as in non-primate frugivores [50]. However, a recent study showed that steviol and rebaudioside A, the two sweet-tasting diterpene glycosides of Stevia rebaudiana, are perceived as sweet by both Old World primates such as chimpanzees and black-and-white ruffed lemurus and by New World primates such as spider monkeys [33], despite the fact that this plant is endemic to South America. This suggests that between-species differences in the ability or inability to perceive sweet-tasting substances do not necessarily require that a co-evolution between animal and plant species has occurred.

Most studies in nonhuman primates on the ability to detect sweet-tasting substances other than carbohydrates have so far employed only one, arbitrarily chosen, concentration (e.g. [8, 9, 35, 42]). In the present study, in contrast, we assessed the animals’ responsiveness to a range of stimulus concentrations that spanned three orders of magnitude. The usefulness of this approach is not only evident by our findings concerning the ability of individual spider monkeys to perceive the
sweetness of certain sweeteners at high concentrations that their conspecifics fail to detect, but also by our findings concerning a possible bitter or otherwise unpleasant side taste of some of the taste substances. Four of the high-potency sweeteners used in the present study (acesulfame K, alitame, aspartame, sodium saccharin, and thaumatin) have been reported to have a bitter side taste for humans when presented at high concentrations [41]. Whereas the chimpanzees did not display a rejection response with any of the eight sweeteners used here (Fig. 1), at least some of the spider monkeys significantly rejected the highest concentrations of aspartame (2 out of 4 animals), sodium saccharin (1 out of 4), and thaumatin (2 out of 4 animals) (Fig. 2). This suggests that spider monkeys, similar to humans, may perceive a bitter or otherwise unpleasant side taste with these high-potency sweeteners when presented at high concentrations, even when, or perhaps because they are unable to perceive their sweetness. Interestingly, three of the four spider monkeys also significantly rejected the highest concentration of monellin, a high-potency sweetener for which no unpleasant side taste has been reported so far by humans. Considering that the TAS2R bitter taste
receptors of primates have also been reported to display allelic variation [19], this may explain both individual and between-species differences in the responsiveness to ligands that taste bitter to humans. Electrophysiological studies in nonhuman primates demonstrated that certain sweet-tasting substances, including acascufame K and saccharin, also bind to bitter taste receptors when presented at high concentrations and, accordingly, elicit activity in bitter-best fibers and, presumably, cause a bitter side taste [5, 16].

It is commonly agreed that the degree of preference that an animal displays in a two-alternative choice taste test reflects the degree of attractiveness of a taste stimulus [44]. It was therefore interesting to note that the chimpanzees of the present study consistently showed a lower degree of preference (rarely above 80%) compared to the spider monkeys (generally above 90%) with high concentrations of all five sweeteners that both species were able to perceive (see Figs. 1 and 2). Exactly the same pattern was found in previous studies that compared sweet-taste responsiveness of chimpanzees and spider monkeys with the five food-associated carbohydrates sucrose, fructose, glucose, maltose, and lactose [27] and with the two sweet-tasting glycosides stevioside and rebaudioside A [33]. This raises the question as to possible reasons that may underly this between-species difference in attractiveness of sweet-tasting substances. Considering that sweet taste is thought to be indicative of an easily metabolizable source of energy [38] it is not surprising that all primate species tested so far display a clear preference for food-associated carbohydrates [48], usually close to 100% when presented with high concentrations of sucrose (e.g. squirrel monkeys, [21]; pigtail macaques, [23]; olive baboons, [27]; black-and-white ruffed lemurs, [51]).

Although dietary specialization has repeatedly been suggested to explain between-species differences in sweet-taste sensitivity (e.g. [20, 29]), it is currently not known whether this may also account for differences among primate species in sweet-taste attractivity. Squirrel monkeys and spider monkeys, for example, differ markedly in their dietary habits, with the former including a considerably lower proportion of fruits into their diet compared to the latter [14], but nevertheless both species show the same high degree of preference (close to 100%) for high concentrations of sweet-tasting carbohydrates. Unfortunately, most studies on sweet-taste responsiveness in nonhuman primates so far only reported taste preference threshold values, but not the corresponding dose-response curves which would allow us to further elucidate a possible correlation between the degree of sweet-taste attractivity and dietary specialization.

The chimpanzees of the present study were kept on a vegetable-based rather than on a fruit-based diet. Thus, they were definitely not exposed to the high concentrations of sweet-tasting carbohydrates that are typical for cultivated fruits. Although it is not exactly intuitive to assume that a captive diet that is restricted in food-associated carbohydrates would lower the attractiveness of sweet-tasting substances, we cannot exclude the possibility that this may have affected the comparatively low degree of preference towards sweeteners displayed by the chimpanzees in the present study. Here, too, further studies are needed to assess possible effects of captive diets on taste preferences.

Taken together, the findings of the present study support the notion that taste responsiveness for substances tasting sweet to humans may correlate positively with phylogenetic relatedness. At the same time, they are also consistent with the notion that co-evolution between fruit-bearing plants and the sense of taste in animals that serve as their seed dispersers may explain between-species differences in sweet-taste perception.

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