Gustatory responsiveness of West African Chimpanzees (Pan troglodytes verus) to seven substances tasting sweet to humans

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**Författare**

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**Sammanfattning**

Abstract

Comparative studies of taste perception have found that primates may differ markedly in their sensitivity for substances perceived as sweet by humans. These findings raise questions about the reason that may underlie these differences in sweet-taste sensitivity between species. The aim of the present study was to assess the taste responsiveness of chimpanzees (*Pan troglodytes verus*) to seven substances tasting sweet to humans and to compare the results with those of other primate species. Using a two-bottle preference test (1 min) I found that the taste preference thresholds of the chimpanzees for five food-associated carbohydrates ranged between 20-30 mM for sucrose, 20-50 mM for fructose, 60-80 mM for glucose, 50-80 mM for maltose, and 30-80 mM for lactose. Taste preference thresholds for two steviol glycosides ranged from 0.04-0.05 mM for stevioside, and 0.03-0.05 mM for rebaudioside A. The chimpanzees displayed clear preferences for all sweet-tasting substances presented. In line with data obtained in other primates, the taste preference threshold of the chimpanzees for sucrose was lower compared to the other carbohydrates presented and the taste preference thresholds for stevioside and rebaudioside A were lower compared to sucrose. In general, the taste sensitivity of the chimpanzees fell into the range of data reported in other nonhuman primate species. Interestingly, the taste preference thresholds of the chimpanzees reported here are similar to the taste detection thresholds obtained in humans, despite the fact that the former are only a conservative approximation of an animal’s taste sensitivity. This suggests that chimpanzees may be as sweet-taste sensitive as humans.

**Nyckelord**

Keyword
chimpanzees, fructose, lactose, glucose, maltose, rebaudioside A, stevioside, sucrose, taste preference threshold
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1 Abstract

Comparative studies of taste perception have found that primates may differ markedly in their sensitivity for substances perceived as sweet by humans. These findings raise questions about the reason that may underlie these differences in sweet-taste sensitivity between species. The aim of the present study was to assess the taste responsiveness of chimpanzees (Pan troglodytes verus) to seven substances tasting sweet to humans and to compare the results with those of other primate species. Using a two-bottle preference test (1 min) I found that the taste preference thresholds of the chimpanzees for five food-associated carbohydrates ranged between 20-30 mM for sucrose, 20-50 mM for fructose, 60-80 mM for glucose, 50-80 mM for maltose, and 30-80 mM for lactose. Taste preference thresholds for two steviol glycosides ranged from 0.04-0.05 mM for stevioside, and 0.03-0.05 mM for rebaudioside A. The chimpanzees displayed clear preferences for all sweet-tasting substances presented. In line with data obtained in other primates, the taste preference threshold of the chimpanzees for sucrose was lower compared to the other carbohydrates presented and the taste preference thresholds for stevioside and rebaudioside A were lower compared to sucrose. In general, the taste sensitivity of the chimpanzees fell into the range of data reported in other nonhuman primate species. Interestingly, the taste preference thresholds of the chimpanzees reported here are similar to the taste detection thresholds obtained in humans, despite the fact that the former are only a conservative approximation of an animal’s taste sensitivity. This suggests that chimpanzees may be as sweet-taste sensitive as humans.

2 Introduction

The primate taxon is a group of species which varies not only regarding their appearance, but also with regard to their feeding ecology. Among the primates, there are several different dietary specializations such as frugivores (fruit-eating) e.g. spider monkey (Ateles geoffroyi) (Laska et al., 1999b), folivores (leaf-eating) e.g. howler monkeys (Alouatta) (Ungar et al., 2016), herbivores (plant-eating) e.g. western lowland gorilla (Gorilla gorilla gorilla) (Remis et al., 2001), omnivores (plant- and animal-eating) e.g. baboon (Papio hamadryas anubis) (Laska et al., 1999b), insectivores (insect-eating) e.g. squirrel monkeys (Saimiri) (Ungar et al., 2016) and gummivores (plant exudate-eating) e.g. marmosets and tamarins (Callithrix) (Ungar et al., 2016). Therefore, comparative studies in primates are a suitable method to assess whether dietary specialization correlates with physiological features such as taste perception (Breslin 2013). Previous studies reported that sweet-tasting
carbohydrates are important for primates regarding their need for metabolic energy (Kare and Brand, 1986; Leonard and Robertson, 1992). Thus, it seems reasonable to assume that primates should be sensitive to these taste substances.

Several studies have assessed the responsiveness of non-human primates to substances tasting sweet to humans (e.g. Glaser et al., 1996; Laska, 1996; Nofre et al., 1996; Simmen and Hladik, 1998; Simmen et al., 1999a). Notable differences in the taste sensitivity for sugars have been found between species of primates using the two-bottle preference test (Laska et al., 2001; Simmen and Hladik, 1998). These results raise the question if these differences in sweet-taste sensitivity are due to differences in the dietary specialization, allometric relationships, or phylogenetic relatedness (Simmen et al., 1999a; Simmen et al., 1999b; Simmen and Hladik, 1998).

Chimpanzees (Pan troglodytes) include a large variety of food items of both plant and animal origin into their diet. However, depending on season they spend 31-88 % of their feeding time foraging on various fruits (Wrangham, 1977). Fruits are rich in carbohydrates and are often low on other essential nutrients, such as minerals, fats and protein (Milton, 1999). This may explain why chimpanzees also feed on, for instance, leaves, seeds, flowers, underground storage organs, pith, insects, and small vertebrates (Hockings et al., 2010; McLennan, 2013; Morgan and Sanz, 2006; Potts et al., 2011; Watts et al., 2012). Nevertheless, chimpanzees are considered to be ripe fruit specialists (Wrangham, 1977). Previous studies reported that chimpanzees not only use visual and olfactory cues to select food items, but also gustatory cues. Chimpanzees inspect potential food items thoroughly and select individual fruits that contain low levels of fibre and higher contents of soluble carbohydrates (Conclin-Brittain et al., 1998). So far, only one previous study investigated the responsiveness of chimpanzees to sweet tastants, (Simmen and Charlot, 2003), in which the taste preference threshold for fructose of two chimpanzees was reported.

The five carbohydrates sucrose, glucose, lactose, maltose and fructose used in the present study are naturally occurring food-associated carbohydrates. Sucrose, glucose and fructose are the three quantitatively predominant soluble carbohydrates found in fruits (Kinghorn and Soejarto, 1986) and usually make up more than 90 % of the total sugar content in fruits (Nagy and Shaw, 1980). Lactose is the predominant carbohydrate found in milk which is the first diet of mammals. In primates, milk can contain lactose at concentrations as high as 6-9 g/100
ml depending on the species (Hinde and Milligan, 2011). Chimpanzee milk contains 7.4 g/100 ml of lactose, corresponding to a concentration of 216 mM (Hinde and Milligan, 2011). Maltose contributes to a sweet taste sensation when the animal is feeding on starch-containing plants during mastication and via enzymatic degradation starch is converted to sweet-tasting maltose (Beck and Ziegler, 1989).

The two glycosides stevioside and rebaudioside A used in the present study are two compounds found in the neotropical plant species Stevia rebaudiana which is endemic to Paraguay in South America, and belongs to the plant family Asteraceae (Soejarto, 2002). Stevioside and rebaudioside A are the two quantitatively predominant substances found in the leaves of the stevia plant and they are commercially used as low-calorie sweeteners (DuBois and Prakash, 2012). Further, both substances have been found to be 100-300 times sweeter than sucrose for humans. Depending on which reference concentration and psychophysical method was used, this number may vary (DuBois et al., 1991; Carakostas et al., 2012; Upreti et al., 2012). Nonetheless, when presented to humans at high concentrations, these two substances have been reported to have a bitter side taste (Schiffman et al., 1995).

There are, to my knowledge, no previous studies which assessed the responsiveness of chimpanzees to any of the sweet tastants mentioned above except fructose. It was therefore the aim of the present study to assess the taste responsiveness of chimpanzees to five carbohydrates (sucrose, fructose, lactose, maltose and glucose) and two steviol glycosides (stevioside and rebaudioside A) as well as to compare these results to those of other primate species. To this end, I determined the taste preference thresholds of Pan troglodytes verus for these seven substances.

3 Material & methods

3.1 Animals and housing

The present study took place at Borås Zoo in Sweden and included three West African Chimpanzees (Pan troglodytes verus), one male, Jonathan, and two females, Pippi and Kankan. Pippi was 48, Kankan 33 and Jonathan 27 years old at the start of the study. They were housed together with an additional female which was not included in the study.

The chimpanzees were kept in both an indoor and an outdoor enclosure. During the nights they were kept indoors in a room measuring 450 m³ (70 m²) and during daytime they were kept in a room of 750 m³ (142 m²).
During daytime they were also allowed to go outside on an island with natural vegetation measuring 560 m$^2$. A narrow corridor connected the daytime enclosure and the outdoor enclosure and next to it, there was a small room measuring 100 m$^3$ (12 m$^2$) which was the room Jonathan and Pippi were tested in.

The chimpanzees were fed three times a day with a large variety of vegetables and fruits such as carrots, tomatoes, cucumber, salad, onions, strawberries, blueberries, grapes, oranges, and apples. In addition, the chimpanzees were fed commercial primate chow pellets once a day and provided with water *ad libitum*.

![Figure 1. The female chimpanzee Kankan included in the study at Borås Zoo.](image)

### 3.2 Taste stimuli

Seven sweet-tasting substances were used in this study, the five carbohydrates sucrose (CAS# 57-50-1), glucose (CAS# 50-99-7), lactose (CAS# 63-42-3), maltose (CAS# 6363-53-7) and fructose (CAS# 57-48-7), and the two steviol glycosides stevioside (CAS# 57817-89-7) and rebaudioside A (CAS# 58543-16-1). The five carbohydrates were obtained from Sigma-Aldrich Sweden AB, Stockholm, Sweden. The two steviol glycosides were obtained from Shanghai Xunxin Chemical Co. (Shaoxing, China), and Xinghua Green Biological Preparation Co. (Jiangsu, China). All substances were of the highest purity available (≥99.5%).

### 3.3 Experimental set-up

A two-bottle preference test of short duration (1 min) was used to determine the taste preference thresholds of the chimpanzees (Richter and Campbell, 1940). Three different drinking stations were built and placed in three different places of the enclosure, one for each test subject. The
reason for this was to avoid distraction and competition between the individuals. The drinking stations will be referred to as 1, 2 and 3. Drinking station 3 was placed on a gate in the daytime enclosure where Kankan was tested. The other two drinking stations were placed in the smaller room between the daytime enclosure and the outdoor enclosure. The smaller room was divided in two compartments and one drinking station was placed in each compartment. Jonathan and Pippi were tested in the two-compartment room at drinking station 1 and 2, respectively (Fig.2).

Figure 2. The daytime enclosure with drinking station 3 and the smaller compartments with drinking stations 1 and 2.

The drinking stations were constructed in a way so that the chimpanzees were not able to see the content in the bottles (Fig 3.).

Figure 3. Drinking station from the experimenter’s side, without bottles (left), and from the animal’s side, with drinking spouts pointing towards the animal (right).
3.4 Experimental procedure

Firstly, the chimpanzees were familiarised with the bottles and trained to participate in the two-bottle preference test. The training started in February 2016. In the beginning the carbohydrate sucrose dissolved in tap water was used as well as juice to make the chimpanzees interested in the bottles. Each individual was also trained to go to his/her own drinking station in every test. When data collection started in May 2016, the animals had learned to cooperate and the carbohydrates were presented in the following order: sucrose, glucose, lactose, maltose, fructose, stevioside, rebaudioside A. For testing the three chimpanzees in parallel, a couple of caretakers aided in every test.

In each trial the chimpanzees were simultaneously presented with two graduated bottles of 700 mL with metal drinking spouts for 1 minute. One bottle contained tap water and the other bottle contained a solution of one of the sweet-tasting substances diluted with tap water at a given concentration. The bottles were weighed before and after each trial and the consumption of liquid was calculated for each bottle.

With the five carbohydrates (sucrose, glucose, lactose, maltose, fructose) testing started at a concentration of 200 mM and proceeded with 100 mM, 50 mM, 20 mM and 10 mM until the individual failed to show a significant preference for a concentration. Thereafter, the individuals were presented with intermediate concentrations, in order to determine the taste preference threshold more accurately. Regarding stevioside and rebaudioside A, testing started at a concentration of 1 mM and continued with 0.1 mM and 0.01 mM and subsequently intermediate concentrations. The reason for presenting stevioside and rebaudioside A at such low concentrations was due to the fact that they are known to taste a lot sweeter than the carbohydrates to human subjects. The lowest concentration of a sweet-tasting substance that the animals preferred over the bottle with tap water was considered as the taste preference threshold value.

However, the concentrations were not presented in a strict descending order but instead presented pseudo-randomized. The reason for this was to keep the animals motivated and willing to participate in the tests. Also, the bottle containing a sweet-tasting solution was not placed on the same side in every trial, but rather in a pseudo-randomized sequence on either the left or the right side, in order to avoid a preference for a certain side. This procedure was also performed during the training period before data collection started. The animal had to sample each bottle at least once in order to count it as a complete trial.
Four to six such 1-minute trials were performed each testing day per animal, if possible, two in the morning, two after lunch and two in the afternoon. The number of trials performed with each individual depended on the willingness of the animal to participate in the testing.

3.5 Data analysis

Each animal was presented with a set of a given concentration of a taste substance and tap water for ten trials. The amount of liquid consumed from each of the two bottles summed over ten trials was calculated and converted to percentages. A two-tailed binomial test was performed for each experiment (over 10 trials) and to determine the taste preference threshold two criteria had to be met. Firstly, the taste preference value in percent had to be >66.7 % as well as the taste stimulus had to be preferred over the water in at least 8 out of 10 trials (P <0.05). For each concentration of a tested substance. The mean value across the three individuals was built by summing up the individual values and dividing them by the number of animals.

4 Results

4.1 Carbohydrates

The taste preference threshold regarding sucrose was 20 mM for both Jonathan and Kankan and 30 mM for Pippi (P <0.05, binomial test) (Fig. 4). The mean taste preference threshold for sucrose was calculated to be 20 mM for the three chimpanzees combined. With glucose, the taste preference threshold was 80 mM for both Jonathan and Kankan and 60 mM for Pippi (P <0.05, binomial test) (Fig. 4). The mean taste preference threshold for all three chimpanzees combined was 80 mM for glucose. The taste preference threshold for lactose was 80 mM for both Pippi and Kankan and 30 mM for Jonathan (P <0.05, binomial test) (Fig. 4). The mean taste preference threshold regarding lactose including all three chimpanzees combined was 80 mM. Regarding maltose, the taste preference threshold was 50 mM for both Jonathan and Pippi and 80 mM for Kankan (P <0.05, binomial test) (Fig. 4). The mean taste preference threshold for maltose for the three chimpanzees combined was 80 mM. The taste preference threshold for fructose was 50 mM for Kankan, 40 mM for Jonathan and 20 mM for Pippi (P <0.05, binomial test) (Fig. 4). The mean taste preference threshold for all three chimpanzees combined regarding fructose was 40 mM.
Figure 4. Taste preferences of the three chimpanzees when tested with sucrose, glucose, lactose, maltose and fructose presented along with tap water. Each data point represents the mean value of 10 trials of 1 min per individual. The horizontal lines at 66.7 % and 50 % illustrate the criterion of preference and the chance level, respectively.
4.2 Steviol glycosides

The taste preference threshold concerning stevioside was 0.05 mM for Pippi and Kankan, and 0.04 mM for Jonathan (P < 0.05, binomial test) (Fig. 5). The mean taste preference threshold combined for all three chimpanzees was 0.05 mM for stevioside. The taste preference threshold regarding rebaudioside A was 0.05 mM for Jonathan, 0.04 mM for Pippi and 0.03 mM for Kankan (P < 0.05, binomial test) (Fig. 5). The mean taste preference threshold for all three chimpanzees combined was 0.03 mM for rebaudioside A.

![Stevioside vs. Water](image1)
![Rebaudioside A vs. Water](image2)

Figure 5. Taste preferences of the three chimpanzees when tested with stevioside and rebaudioside A presented against tap water. Each data point represents the mean value of 10 trials of 1 min per individual. The horizontal lines at 66.7 % and 50 % illustrate the criterion of preference and the chance level, respectively.

5 Discussion

All seven substances tasting sweet to humans were clearly preferred over water by the chimpanzees. Further, the taste preference thresholds of the chimpanzees ranged from 20-30 mM for sucrose, 20-50 mM for fructose, 60-80 mM for glucose, 50-80 mM for maltose, and 30-80 mM for lactose. Taste preference thresholds for two steviol glycosides ranged from 0.04-0.05 mM for stevioside, and 0.03-0.05 mM for rebaudioside A.

5.1 Comparison of the sweet-tasting carbohydrates

Table 1 compares the taste preference thresholds of the chimpanzees for the five food-associated carbohydrates found in the present study to all published data reported in other primate species. Except for sucrose, there
is in general only little information concerning taste responsiveness in nonhuman primates regarding naturally occurring food-associated sugars. Within the Hominoidea, chimpanzees are the only species except for humans which have been tested with all five naturally occurring food-associated sugars.

The chimpanzees tested here have a mean taste preference threshold of 20 mM for sucrose. Several nonhuman primate species have been tested for sucrose and the taste preference thresholds range between 10-20 mM for the majority of them. However, some species have extremely high taste preference thresholds, that is, a lower taste sensitivity compared to the chimpanzees. For instance, the cotton-top tamarin (Saginus oedipus) belonging to the Platyrhini and the mongoose lemur (Eulemur mongoz) belonging to the Strepsirrhini have a taste preference threshold of 125 mM for sucrose. Further, the sunda slow lori (Nycticebus coucang) also belonging to Strepsirrhini primates has a taste preference threshold as high as 330 mM for sucrose. In contrast, black-handed spider monkeys (Ateles geoffroyi) belonging to the Platyrhini have a taste preference threshold of 3 mM for sucrose, which is a higher taste sensitivity for sucrose compared to the chimpanzees.

The chimpanzees have a mean taste preference threshold of 40 mM for fructose. Nonhuman primates within the Hominoidea that have been tested for fructose in addition to chimpanzees are western lowland gorillas (G. gorilla gorilla) and bornean orangutans (Pongo pygmaeus). The chimpanzees show a higher taste sensitivity for fructose compared to the western lowland gorilla which has a taste preference threshold of 75 mM for fructose. However, the chimpanzees show a lower taste sensitivity compared to the bornean orangutan, which has a taste preference threshold of 15 mM for fructose and is also one of the lowest taste preference thresholds noted in primates for fructose. Additionally, the mongoose lemur (E. mongoz) has a taste preference threshold as high as 110 mM which is the highest taste preference threshold for fructose found in primates.

The mean taste preference threshold of the chimpanzees for glucose was found to be 80 mM. Few nonhuman primate species have been tested for glucose. However, a couple of species have taste preference thresholds ranging between 20-25 mM, belonging both to the Cercopithecidae and the Platyrhini primates. Furthermore, the black-handed tamarin (Saginus midas niger) belonging to the Platyrhini has been reported to have a taste preference threshold as high as 330 mM, that is, a much lower taste sensitivity for glucose compared to the chimpanzees.
As in the case with glucose, only few nonhuman primate species have been tested for maltose. The mean taste preference threshold of the chimpanzees is 80 mM for maltose. Of those primate species tested for maltose, the squirrel monkey (*Saimiri sciureus*) belonging to the *Platyrrhini* has the highest taste preference threshold of 90 mM, which does not differ notably from the taste preference threshold of the chimpanzees. The remaining taste preference thresholds of nonhuman species tested ranged between 10-50 mM for maltose.

The taste preference threshold of the chimpanzees for lactose was 80 mM. Again, few nonhuman species have been tested for lactose with regard to their taste preference thresholds. However, as stated for glucose, the black-handed tamarin (*S. midas niger*), again, has the highest taste preference threshold of the nonhuman species tested, with a concentration of 250 mM. Additionally, the pygmy marmoset (*Cebulla pygmaea*) has a taste preference threshold of 125 mM and the squirrel monkey (*S. sciureus*) a taste preference threshold of 100 mM, both belonging to the *Platyrrhini* primates. On the other hand, the lowest taste preference threshold, that is, the highest taste sensitivity, reported for lactose has been reported in the black-handed spider monkey (*A. geoffroyi*) with 10 mM, also belonging to the *Platyrrhini*.

Humans and chimpanzees do not differ markedly in their taste sensitivity. However, when comparing the taste thresholds of the chimpanzees to those of humans one must keep in mind that the values for humans are so called taste detection thresholds and not taste preference thresholds. The two-bottle method as used in the present study only allows for determining a taste preference threshold and is therefore a conservative estimate of the chimpanzees’ taste sensitivity whereas the psychophysical signal detection methods used for human testing allow for determining a taste detection threshold which is indeed the lowest concentration that humans can detect. Therefore, it is quite possible that the chimpanzees can still detect lower concentrations of a sweet tastant in the two-bottle preference test but these concentrations may be so weak that they do not display a preference anymore.
Table 1. Taste preference thresholds (mM) of the food-associated carbohydrates, sucrose, fructose, glucose, maltose and lactose in the tested chimpanzees and in various other primate species, based on published data. Note that the values for *H. sapiens* are taste detection thresholds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sucrose</th>
<th>Fructose</th>
<th>Glucose</th>
<th>Maltose</th>
<th>Lactose</th>
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<td><em>Aotus trivirgatus</em></td>
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<td><strong>Strepsirrhini</strong></td>
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<td><em>Varecia variegata variegata</em></td>
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<td>18.5</td>
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<td><em>Microcebus coquereli</em></td>
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The taste preference thresholds for sucrose in the three chimpanzees tested in the present study were overall lower compared to those for the other four sweet-tasting carbohydrates. This is in line with the vast majority of nonhuman primate species that have been tested with carbohydrates other than sucrose (see Table 1). Three species of Cercopithecoid primates, pigtail macaque (Macaca nemestrina), bonnet macaque (Macaca radiata) and Japanese macaque (Macaca fuscata) are as sensitive for maltose as they are for sucrose. This can be explained by the notion that taste sensitivity for maltose is linked to an evolutionary adaptation of the gustatory system in order to be able to generate nutritional energy from feeding on starch-rich plants (Laska, 2000). Old world monkeys are considered as herbivores and they feed on leaves, seeds and fruits. The three Macaca species mentioned above are known to feed on starch-rich plants (Nishi et al., 2016). Similar to these Macaca species, granivorous rodents, such as mice and rats show the same pattern which makes sense considering that they also feed on starch-rich grains (Laska, 1997).

5.2 Comparison of the two steviol glycosides

Table 2 compares the taste preference thresholds of the chimpanzees for the two substances stevioside and rebaudioside A which are commercially used as low-calorie sweeteners. The taste preference threshold for stevioside and rebaudioside A has previously only been established in A. geoffroyi and V. variegata variegata. However, for humans, the taste detection thresholds of these two substances have been reported. Chimpanzees are more taste sensitive to both stevioside and rebaudioside A compared to V. variegata variegata, that is, they have a lower taste preference threshold. Regarding A. geoffroyi, the taste sensitivity for stevioside is the same as in the chimpanzees, whereas the chimpanzees are less taste sensitive for rebaudioside A compared to A. geoffroyi, that is, they have a higher taste preference threshold. Human taste detection thresholds were one order of magnitude lower than those of the chimpanzees. However, one should keep in mind that the difference in taste perception between humans and chimpanzees might not be that big because taste preference thresholds are only a conservative estimate of a species’ taste sensitivity.

Considering that chimpanzees are endemic to Africa and the stevia plant to South America, it is unlikely that chimpanzees have encountered this
plant throughout their evolutionary history. However, as shown in Table 2, nonhuman primates belonging to the Hominoidea, the Platyrrhini, and the Strepsirrhini suborders, respectively, are able to detect these two steviol glycosides. Consequently, a plausible explanation for the fact that primate species of all these taxa are able to detect these two substances may be that this was also the case regarding their common ancestor. However, another plausible explanation could simply be that a co-evolution between animal and plant species has not been necessary to occur regarding the ability or inability to perceive sweet-tasting substances between different species. This explanation is supported by previous studies which reported that the artificial sweeteners aspartame and neotame are only detectable for Catarrhine primates but not for Prosimian and Platyrrhine primates (Glaser et al., 1992). A further explanation could be that plant species containing substances that are structurally similar to those of stevioside and rebaudioside A have co-evolved with catarrhine and prosimian primates. This, in turn, may have resulted in modifications of the receptors responsible for sweet taste in the primates and thus allowed for the recognition and binding of stevioside and rebaudioside A to the sweet-taste receptors (Niklasson et al., 2017).

Table 2. Taste preference thresholds (mM) for stevioside and rebaudioside A in V. variegata variegata, P. troglodytes verus, A. geoffroyi, and H. sapiens. Note that values for H. sapiens are taste detection thresholds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stevioside</th>
<th>Rebaudioside A</th>
<th>Reference</th>
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<tbody>
<tr>
<td><strong>Hominoidea</strong></td>
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<td><em>Pan troglodytes verus</em></td>
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<td><strong>Plathyrrhini</strong></td>
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<tr>
<td><em>Ateles geoffroyi</em></td>
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<td>0.01</td>
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<tr>
<td><strong>Strepsirrhini</strong></td>
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<tr>
<td><em>Varecia variegata variegata</em></td>
<td>0.1</td>
<td>0.1</td>
<td>4</td>
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</tbody>
</table>

1Present study; 2 van Gemert (2011); 3 Niklasson et al. (2017); 4 Sandra Niklasson (2015) Master thesis.

5.3 Ethical and societal considerations

The experiments reported here comply with current Swedish laws and the Guide for the Care and Use of Laboratory Animals (National Institutes of Health Publication no. 86-23, revised 1996). This study was approved by Gothenburg’s Animal Care and Use Committee (Göteborgs djurförsöksetiska nämnd, protocol #75-2016.
The experiments conducted in the present study were all performed depending on the willingness of the chimpanzees to cooperate. The animals were not in any way forced to partake and could leave the drinking stations at all times. The substances used in the present study were all safe and approved for human consumption and were not considered as harmful to the chimpanzees in any of the presented concentrations. The caretakers were present during every test session and monitored the health and behaviour of the chimpanzees on a daily basis, during the test period.

Studies like the present one provide knowledge about taste perception of captive animals which can help to improve their welfare and it gives information on how to improve their diet. For instance, with such information, obesity may be avoided in chimpanzees which is a common health condition among captive chimpanzees. When the chimpanzees are keen on sweet tastes, this makes it easier to modify the diet so that they are not so keen on eating certain stuff.

5.4 Conclusions

All three chimpanzees included in the present study displayed a clear preference for all seven sweet-tasting substance presented. Further, the chimpanzees did not differ markedly in their taste sensitivity from humans, however it is important to distinguish between taste preference threshold as for chimpanzees, and taste detection threshold as for humans. Hence, it is possible that the chimpanzees detect even lower concentrations of the sugars used in the present study. The chimpanzees displayed a lower taste preference threshold for sucrose compared to glucose, lactose, maltose and fructose. This result is in line with studies on other primates. In addition, the chimpanzees in the present study displayed a preference for both stevioside and rebaudioside A, which is interesting as the stevia plant is endemic to South America and the chimpanzees to Africa. To better understand how the gustatory sense has evolved among primates and how preferences for food-associated sugars correlate with dietary specialization, more studies are needed on gustatory responsiveness including different primate species and different food-associated substances.

6 Acknowledgement

I want to thank my supervisors Matthias Laska and Daniel Roth who gave me the opportunity to perform this study and I am truly grateful to the caretakers at Borås Zoo who trained the Chimpanzees to willingly participate in the testing and who assisted me throughout the whole study.
7 References


Figure 1, 2 and 3. Ownership by Desirée Sjöström.