Gustatory Responses of the Hamster *Mesocricetus auratus* to Various Compounds Considered Sweet by Humans

VICKTORIA DANILOVA, 1 GÖRAN HELLEKANT, 1 JEAN-MARIE TINTI, 2 AND CLAUDE NOFRE 2

1Animal Health and Biomedical Sciences, The University of Wisconsin-Madison, Madison, Wisconsin 53706; and 2Université Claude Bernard, Faculté de Médecine Alexis Carrel, 69372 Lyon, France

Danilova, Vicktoria, Göran Hellekant, Jean-Marie Tinti, and Claude Nofre. Gustatory responses of the hamster *Mesocricetus auratus* to various compounds considered sweet by humans. *J. Neurophysiol.* 80: 2102–2112, 1998. The taste of 30 compounds was studied in the golden hamster with three different methods: single-fiber recordings, two-bottle preference (TBP), and conditioned taste aversion (CTA) tests. On the whole, the results showed that the sense of taste in the hamster differs in many respects from that in humans because, of 26 tested compounds known as sweet to humans, 11 had no taste or tasted differently. The results also supported the notion that activity in S-fibers elicits liking and activity in Q- or H-fibers rejection. Specifically hierarchical cluster analysis of 36 single fibers from the chorda tympani proper nerve separated N-, H-, and S-clusters consisting of 11 sucrose-, 14 NaCl-, and 11 citric-best fibers. Ace-K, cyananosuasan, N-4-cyanophenyl-N'-cyanoguanidineacetate (CCGA), d-tryptophan, N-3,5-dichlorophenol-N'-α-methylbenzylguanidineacetate (DMGA), saccharin, SC-45647, and suosan stimulated only the S-fibers, were significantly preferred in TBP tests, and generalized to sucrose in the CTA tests. Ethylene glycol stimulated the N-fibers in addition to the S-fibers. This explains its generalization to sucrose in CTA. Its toxicity may contribute to its rejection in TBP tests. Sodium cyclamate stimulated a few N-but no S-fibers, which may explain the nondiscriminatory TBP and CTA results. Glycine elicited its largest response in the S-fibers, although it also stimulated other fibers. The resulting mixed taste sensation may explain why it was not preferred in TBP, although it generalized to sucrose in the CTA.

METHODS

**Chemicals**

Table 1 lists the solutions used in the electrophysiological and behavioral experiments. Twenty-six of these compounds are sweet to humans, as indicated in the right column. Figure 1 presents the structure of some of the more unusual sweeteners.

The compounds were dissolved in distilled water for the two-bottle preference (TBP) and conditioned taste aversion (CTA) experiments and in artificial hamster saliva for electrophysiological experiments. The composition of the artificial saliva was based on the composition of pilocarpine-stimulated natural hamster saliva (Rehnberg et al. 1992) and was made from 6.6 mM NaHCO₃, 15 mM KCl, 28 mM KHCO₃, pH 8.5. Because 10 mM quinine hydrochloride (QHCl) did not dissolve in the saliva, it was dissolved in distilled water. Precipitation also prevented the use of d- and l-asparagine over 24-h periods in the TBP tests.

**Electrophysiology**

The recordings were obtained from the chorda tympani proper (CT) nerve of nine golden hamsters, *Mesocricetus auratus*, of both sexes, 7- to 10-mo old. Anesthesia was initiated with 0.1 ml im Innovar followed by 0.1 ml pentobarbital sodium, 15 mg/ml im
and then was maintained with pentobarbital intravenously as needed. The trachea was cannulated, and body temperature, heart, and respiratory rates were continuously monitored.

The right CT was dissected free from the point where it joins the lingual nerve to the tympanic bulla, where it was cut. Single-fiber impulses were recorded with an impulse-amplitude analyzer, which displayed adjustable upper and lower levels. It triggered a pulse when a nerve impulse exceeded the lower but not the upper level. These pulses were processed by an IBM-PC computer. The custom-made software controlled stimulus delivery and stored intervals between pulses together with information on the presented stimulus.

The solutions were delivered over the anterior part of the tongue by a computerized system described earlier (Hellekant and Roberts 1995). Each stimulus lasted for 5 s with 40-s rinsing time between stimulations. Hamster artificial saliva rinsed the tongue between stimulations (Rehnborg et al. 1992). The stimuli and rinses were maintained and delivered at constant temperature (34°C).

The spontaneous activity before each stimulation was deducted from the responses. We define here spontaneous activity as the impulse activity preceding the stimulation during rinsing of the tongue with artificial saliva for 5 s. A cluster was considered to be responsive to a stimulus if the nerve impulse rate during the first 5 s of stimulation was larger than 2 times SD of the spontaneous activity of the cluster. Cluster and multidimensional (MDS) analyses were performed on the responses of 36 fibers to 31 stimuli (SYSTAT for Macintosh, Version 5.2). The hierarchical cluster analysis measured the intercluster similarity with the use of the Pearson correlation coefficient, and the cluster analysis proceeded according to the average linkage method.

To facilitate comparisons with data from other species and studies, the responses of CT fibers to the four basic stimuli (NaCl, citric acid, QHCl, and sucrose) were used to categorize each fiber by its best stimulus (Frank 1973) and to calculate the breadth of responsiveness ($H$) for each fiber. $H$ was calculated according to the formula $H = -K p_i \log p_i$, where $K$ is a scaling constant (1.6) and $p_i$ is the proportional response each of the four basic stimuli (Smith and Travers 1979).

**TBP experiments**

A total of 28 adult hamsters of both sexes, housed individually, served as subjects. Each stimulus was tested with seven animals. Their intake of water and a stimuli was recorded during four consecutive 24-h periods with graduated cylinders switched and Roberts (1995). Each stimulation lasted for 5 s with 40-s rinsing time between stimulations. Hamster artificial saliva rinsed the tongue between stimulations (Rehnborg et al. 1992). The stimuli and rinses were maintained and delivered at constant temperature (34°C).

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**CTA experiments**

Twelve conditioned and eight control adult hamsters of both sexes served as subjects. Their consumption was measured as num-
FIG. 1. Structures of SC-45647, N-4-cyanophenylguanidineacetate (CGA), cyanosuosan, N-3,5-dichlorophenyl-N'- (S)-α-methylbenzylguanidineacetate (DMGA), N-4-cyanophenyl-N'-cyanoguanidineacetate (CCGA), TGC, N-4-cyanophenyl-carbamoyl-(R, S)-3-amino-3-(3,4-methylenedioxyphenyl) propionic acid (CAMPA), N- (S)-2-methylhexanoyl-L-glutamyl-5-amino-2-pyridinecarbonitrile (MAGAP), N-1-naphthoyl-L-glutamyl-5-amino-2-pyridinecarbonitrile (NAGAP), N-4-cyanophenylcarbamoyl-L-aspartyl-(R)-α-methylbenzylamine (CAM), and N-4-azidophenyl-N'-diphenylmethylguanidineacetate (ADGA).

RESULTS

Single-fiber responses in hamster chorda tympani

Figure 2 shows an example of the nerve impulses recorded from single CT taste fiber HA94M25E classified as an S-fiber by the hierarchical analysis below. We present here only the number of licks from 16 different bottles mounted in a carousel. Each lick broke an infrared beam positioned between the animal and the bottle in use and triggered one count by the computer. The first lick started a timer that presented the bottle for 30 s.

After a session in which the hamsters were trained to drink water through the apparatus, the animals were water deprived for 24 h and then offered 0.2 M sucrose solution (conditioning stimulus). After consumption of sucrose, 1.5 ml of 0.3 M LiCl (unconditioning stimulus) was injected intraperitoneal within 5–15 min. The control animals underwent the same routine as conditioned animals but without LiCl injections. After a 1-day recovery period we tested if the animals were successfully conditioned. If they drank as much sucrose as before first conditioning, we again injected them with LiCl. Two to four injections were necessary to produce conditioning.

The CTA test was carried without water deprivation. Each animal was tested with three cycles that each included distilled water, sucrose, and sweeteners presented at random.

The level of drinking differed between animals. To use the results from different animals, the consumption of sweeteners had to be normalized to a “standard.” For each animal we considered the average number of licks of water during three cycles as the standard and assigned it the value 100%. Then for each hamster, consumption of all stimuli was expressed in percentage of this standard. The data were then averaged for the control and conditioned animals.

With the use of a $t$-test for independent samples we analyzed the difference in consumption by control and conditioned animals. A $P < 0.01$ value was considered a significant difference in the statistical analysis.

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GUSTATORY RESPONSES OF HAMSTER TO SWEETENERS

FIG. 2. Recordings from the chorda tympani (CT) S-cluster fiber HA94M25E. Onset and offset of stimuli are shown as changes in bar code.

a part of the recordings from this unit. However, it is evident that sucrose, suosan, N-4-cyanophenyl-N’-cyanoguanidineacetate (CCGA), SC-45647, N-4-cyanophenylguanidineacetate (CGA), cyanosuasan, N-3,5-dichlorophenyl-N’-(S)-

α-methylbenzyguanidineacetate (DMGA), and to some extent NaCl gave a response, but citric acid, QHCl, alitame, superaspartame, N-(S)-2-methylhexanoyl-L-glutamyl-5-amino-2-pyridinecarbonitrile (MAGAP), N-1-naphthoyl-L-glutamyl-5-amino-2-pyridinecarbonitrile (NAGAP), N-4-cyanophenylcarbamoyl-L-aspartyl-(R)-α-methylbenzylamine (CAM), and sodium cyclamate did not.

Figure 3 shows an overview of the responses to all compounds in all 36 CT fibers. The legend included in Fig. 3 relates the area of the circles with the nerve responses over the first 5 s of stimulation. Open circles indicate a suppression of the nerve activity during a stimulation. The fibers were ordered along the y-axis in groups, starting with the fibers responding best to NaCl, followed by the fibers mainly stimulated by citric acid and QHCl and finally a group of sucrose-best fibers.

The breadth of tuning (H) for the NaCl-best fibers was 0.23 (SE = 0.05), for citric acid-best 0.66 (SE = 0.04), and for sucrose-best 0.41 (SE = 0.07). This shows that the NaCl-best fibers are more narrowly tuned than the other types.

Hierarchical cluster analysis

The responses of the 36 CT fibers in Fig. 3 were subjected to a hierarchical cluster analysis. Our analysis distinguished three major clusters consisting of 11 S-fibers, 14 N-fibers, and 11 H-fibers. The result is represented as a dendogram in Fig. 4 with the identity number of the fiber and response category on the basis of its best response to the four basic solutions listed on the left side.

Average response profiles

Figure 5 shows the average response profiles of these three clusters. The stimuli were listed along the x-axis, and the average impulse activity measured over 5 s was plotted along the y-axis. The error bars illustrate the SE of these averages. We will present each cluster.

N-cluster. This cluster included 14 units and was the largest one. Figure 5A shows that the N-cluster was characterized by strong responses to NaCl but also to ethylene glycol. These fibers did not respond to bitter compounds. Among the compounds that taste sweet to humans, only Na-cyclamate, ethylene glycol, and glycine elicited a strong response in these fibers; responses to other stimuli were not significant. The average spontaneous activity of the 14 N-cluster fibers was 9.39 (SE = 1.92) imp/5 s.

H-cluster. Figure 5B shows the average response profile of 11 units. Citric acid elicited the best response, and QHCl and L-asparagine gave significant responses. NaCl also stimulated this cluster, although responses were not strong. Most compounds sweet to humans did not stimulate the H-cluster fibers, with exception of ethylene glycol, glycine, and D-asparagine. The average spontaneous of the H-cluster was 4.02 (SE = 0.77) imp/5 s.

S-cluster. Figure 5C shows massive responses to some but not all of the compounds sweet to humans. Thus all compounds from dulcin to glycine elicited a significant response according to our criteria for a response. The remaining sweeteners from NHDHC to MAGAP did not elicit any activity; responses to cyclamate and N-4-cyanophenylcarbamoyl-(R,S)-3-amino-3-(3,4-methylene dioxyphenyl) propionic acid (CAMPA) were insignificant. The latter applies also to the activity recorded during stimulation with NaCl, citric acid, and L-asparagine. For all S-fibers the average spontaneous activity before stimulation was 14.2 (SE = 4.2) imp/5 s.

Multidimensional scaling

On the basis of a correlation matrix of the stimuli and to present the relationships between stimuli used, we performed multidimensional scaling. The spatial representation of the
FIG. 3. An overview of the response profiles of 36 single CT fibers with the use of topographical method. The area of the circles represents impulse activity over the first 5 s of stimulation. Open circles, inhibition; absence of a mark shows that data are missing. The stimuli were arranged along the x-axis in order of salty, sour, bitter, and sweet. The fibers were arranged along the y-axis in groups: NaCl-, acid-, and sucrose-best fibers.

similarities among 30 stimuli is shown in Fig. 6. The stress value is 0.072.

Sucrose, suosan, cyansuosan, CAMPA, CGA, TGC, dulcin, acesulfame-K, saccharin, SC-45647, CCGA, DMGA, D-tryptophan, and D-asparagine formed a tight group separate from the other stimuli. Another group included NaCl together with cyclamate and ethylene glycol. Citric acid, L-asparagine, and QHCl were segregated from sweeteners and sodium salts by dimension 2. The closeness between QHCl and citric acid is evident. The nine stimuli that elicited no response are scattered between the groups; eight of these compounds are sweet to humans.

Results of TBP tests

Figure 7 presents the results with TBP in hamsters with the compounds arranged in order of increasing intake. Except for L-tryptophan, all compounds used in the TBP tests taste sweet to humans. Some compounds were presented in two or three concentrations (see Table 1).

On the basis of the intake all stimuli can be divided into three groups. One group was significantly rejected. It comprised ethylene glycol and L-tryptophan. The second group was neither preferred nor rejected as indicated by the statistical test showing that the intake of the two bottles did not
Results of CTA tests

Figure 8 shows the extent of generalization between intake of sucrose and one of the compounds listed along the x-axis according to the procedure described under METHODS. The circles (control hamsters) and squares (conditioned hamsters) illustrate the number of licks for each compound expressed in percentage of number of licks when offered plain water. In the control group the means varied from 82% (for suosan) to 134% (for glycine).

In Fig. 8 the stimuli were arranged from the most rejected to the least rejected compound by the conditioned hamsters. As expected the consumption of sucrose was most suppressed (13.9% of water intake) followed by all the compounds that elicited a response in the S-fibers ($P < 0.01$). As in previous figures these compounds are highlighted in Fig. 8.

DISCUSSION

The aim of this study was to investigate how a number of compounds, known as sweet to humans, taste to the hamster. We used three different approaches in our attempts to elucidate this: single-fiber recordings from the CT nerve, TBP and CTA tests.

It seems that together these three techniques can provide us with information how a tantastic tastes to an animal species. The electrophysiological method provides information as to whether a compound has taste or not. If a compound does not elicit any impulse activities in the taste nerve, it has no taste. If single-fiber responses are obtained, comparisons of these responses with those of other compounds reveal how similar their tastes are.

The TBP method shows how much the hamsters prefer the compounds over water but gives no information about the taste quality of the stimuli. On the other hand, our assumption is that compounds with a sucroselike taste are liked by hamsters.

The CTA technique here showed to what extent the hamsters generalized from their aversion to sucrose to the other stimuli. From this we conclude that the amount of suppression mirrors the taste similarities between the compound in question and sucrose.

Table 2 summarizes the results of all experiments and draws conclusions about the taste of each compound in the hamsters.

Compounds that did not stimulate CT fibers

The electrophysiology identified compounds that did not stimulate any of the CT fibers. These were l-tryptophan and eight sweeteners: alitame, aspartame, CAM, MAGAP, NAGAP, NHDHC, superaspartame, and thaumatin.

These sweeteners were neither preferred nor rejected over water in TBP experiments, and their consumption was not suppressed in CTA experiments. Thus we conclude that alitame, aspartame, CAM, MAGAP, NAGAP, NHDHC, superaspartame, and thaumatin in concentrations used here do not taste sweet for hamsters.

It is unlikely that these compounds might stimulate S-fibers in glossopharyngeal or superior laryngeal nerves. However, the population of sucrose-best fibers in these two nerves is small, and sucrose is a rather ineffective stimulus
Fig. 5. Average response profiles of N-cluster (A), H-cluster (B), and S-cluster (C) of hamster CT fibers. Error bars are SE. Hatched columns, salts; open columns, acids; shaded columns, bitter compounds; black columns, sweeteners. Numbers within parentheses show number of fibers tested with each compound.
for the glossoopharyngeal or superior laryngeal nerves (Dickman and Smith 1988; Hanamori et al. 1988). Hamster CT neurons provide the main information about sweeteners’ and sodium salts’ tastes, whereas NG neurons play a major role in description of bitter and acid stimuli (Frank and Nowlis 1989). Thus we can conclude that the results of the three methods are congruent and that these compounds are tasteless to hamsters.

![Figure 6](image1.png)

**FIG. 6.** Distribution of 30 stimuli in a 3-D space resulting from multidimensional scaling. Distribution was calculated with Pearson correlation coefficient between stimuli across 36 CT fibers. Kruskal stress value is 0.072.

![Figure 7](image2.png)

**FIG. 7.** Results of the two-bottle preference (TBP) test. Data were averaged for 7–9 hamsters individually tested during 4 consecutive days. Sweeteners eliciting responses in S-cluster fibers are in bold type. Error bars are SE. Line shows preference ratio level 0.5. *, significant difference from preference ratio 0.5.
Figure 7 shows that L-tryptophan was avoided in the TBP experiments, indicating an aversive taste sensation. It is possible that L-tryptophan stimulates Q-fibers in the glossopharyngeal nerve. Results of previous CTA experiments support this conclusion because hamsters show reciprocal generalization between 50 mM L-tryptophan and 1 mM HCl (Yamamoto et al. 1988). Thus it is likely that L-tryptophan has to the hamster a slight quinine/acidlike taste, the same as it has to humans (Haefeli and Glaser 1990; Schiffman 1976).

Compounds that stimulated any CT fibers except S-cluster fibers

The rest of the stimuli elicited significant responses in single CT fibers. The electrophysiology distinguished stimuli that did not elicit responses in S-fibers from those which did. As mentioned we distinguished three clusters. This corroborates previous studies (Frank 1973, 1988), which showed similar clusters.

The compounds that did not stimulate the S-fibers included cyclamate and L-asparagine. Cyclamate, which was in form of sodium salt, stimulated the N-fibers, was neither preferred nor rejected in TBP test, and was not avoided in CTA experiments. The conclusion is supported by the finding that 25 mM cyclamate generalizes to NaCl in CTA (Nowlis et al. 1980). However it was also shown that 25 mM cyclamate generalizes to sucrose in CTA (Nowlis et al. 1980). When we tested 25 and 50 mM cyclamate in TBP tests, the animals did not prefer it. This indicates that, even if S-fibers would respond to higher concentrations of cyclamate, the responses of N-fibers of CT would determine the reaction of the whole organism. Thus hamsters may taste 10 mM cyclamate as similar to NaCl.

L-Asparagine stimulated only the H-fibers, and its consumption was not suppressed in CTA. We suggest that, to hamsters, L-asparagine tastes similar to acids.

Compounds that stimulated more than S-cluster fibers

The next group of compounds included sweeteners that stimulated more than one cluster: D-asparagine, glycine, and ethylene glycol. We suggest that different clusters of fibers provide information about different taste qualities.

D-Asparagine elicited responses in the S- and H-fibers. Unfortunately TBP data are missing, but the hamsters generalized from sucrose to D-asparagine, which indicates that it exerts a mixed sucrose- and acidlike taste.

Glycine stimulated fibers in every cluster. Thus it elicits a mixed taste. The suppression of its consumption in CTA suggests that its taste has a sucrose-like component. This conclusion is supported by earlier studies showing reciprocal generalization between 0.1 M sucrose and 0.6 M glycine (Nowlis et al. 1980; Yamamoto et al. 1988). On the other hand the complexity of its taste is demonstrated by its generalization to HCl (Nowlis et al. 1980). Because neither preference nor rejection was recorded in the TBP experiments here, it is likely that the effects on S- and H-fibers balanced each other.

Ethylene glycol is a highly toxic compound. Consequently postigestive signals may explain the discrepancy between the generalization to sucrose in our CTA tests and the rejection in the TBP experiments. On the other hand, ethylene glycol stimulated both the N- and S-fibers (Fig. 3). It is
possible that the strong response in N-fibers was the cause for the rejection because hamsters reject NaCl in TBP tests (Hettinger and Frank 1990). Ethylene glycol also generalized to sucrose in our CTA experiments. This can be explained by its substantial response in the S-fibers. Thus it has both a sucrose- and NaCl-like taste to hamsters.

Compounds that stimulated only S-cluster fibers

The last group of stimuli included compounds that stimulated only S-cluster fibers. Hamsters liked all these compounds in TBP experiments. The CTA experiments separated these sweeteners into two groups. The consumption of ace-K, cyanosuosan, CCGA, d-tryptophan, DMGA, saccharin, SC-45647, and suosan was suppressed, indicating that the hamsters generalized from sucrose to these compounds. Thus these compounds taste like sucrose.

The consumption of CGA, dulcin, and TGC was not suppressed in CTA. Although both dulcin and TGC evoked significant responses in the S-fibers, these responses were smaller than those of the other sweeteners (Fig. 5C). It is possible that we used concentrations of dulcin (1.6 mM) and TGC (0.16 mM) that were too low. CGA was the only compound that gave contradictory results. Because of several circumstances, one of these being lack of compound, we were unable to repeat the CTA tests for CGA.

CAMPA presents a special case. In CTA and TBP experiments with low concentration (28 μM), the hamsters showed no reaction. However, 10× higher concentration of CAMPA was preferred in the TBP. This is in contrast to all the other compounds tested with more than one concentration in TBP tests (Table 2). Furthermore, CAMPA at 28 μM stimulated four of nine S-cluster fibers, although the average response was not significant. MDS analysis positioned it together with stimuli that taste like sucrose. This indicates that the concentration of CAMPA used for electrophysiology was below the behavioral threshold for hamsters. At higher concentrations it might be sweet to hamsters.

These results further support the hypothesis that activity in S-fibers stimulates intake (Rehberg et al. 1990) and activity in Q-fibers rejection. The results show that, by combining single-fiber nerve recordings and TBP and CTA methods, it is possible to gain insight on how an unknown compound may taste to an animal species. The results of all compounds can be explained by the assumption that activity in S-fibers will evoke a preference and activity in H-/Q-fibers rejection, whereas the behavioral effects of N-fiber activity are species related.

Address for reprint requests: G. Hellekant, Animal Health and Biochemical Sciences, The University of Wisconsin–Madison, 1655 Linden Dr., Madison, WI 53706-1581.

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REFERENCES


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TABLE 2. Summary table for the results of the all experiments in hamsters

<table>
<thead>
<tr>
<th>Response in S fibers</th>
<th>Grouped together in MDS</th>
<th>Reaction in TBP Test</th>
<th>Result in CTA Test</th>
<th>Conclusion About Taste</th>
</tr>
</thead>
<tbody>
<tr>
<td>l-Asparagine</td>
<td>NS; also in H fibers</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet, may be similar to citric acid</td>
</tr>
<tr>
<td>t-tryptophan</td>
<td>No response</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet</td>
</tr>
<tr>
<td>NHDHC</td>
<td>No response</td>
<td>—</td>
<td>No preference</td>
<td>Not sweet</td>
</tr>
<tr>
<td>CAM</td>
<td>No response</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet</td>
</tr>
<tr>
<td>Alitame</td>
<td>No response</td>
<td>—</td>
<td>No preference</td>
<td>Not sweet</td>
</tr>
<tr>
<td>Aspartame</td>
<td>No response</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet</td>
</tr>
<tr>
<td>Superaspartame</td>
<td>No response</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet</td>
</tr>
<tr>
<td>NAGAP</td>
<td>No response</td>
<td>—</td>
<td>No preference</td>
<td>Not sweet</td>
</tr>
<tr>
<td>Thaumatin</td>
<td>No response</td>
<td>—</td>
<td>No preference</td>
<td>Not sweet</td>
</tr>
<tr>
<td>MAGAP</td>
<td>No response</td>
<td>—</td>
<td>No preference</td>
<td>Not sweet</td>
</tr>
<tr>
<td>ADGA</td>
<td>—</td>
<td>—</td>
<td>No suppression</td>
<td>Not sweet</td>
</tr>
<tr>
<td>Cyclamate</td>
<td>Response in N fibers</td>
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<td>No preference</td>
<td>Not sweet, may be similar to NaCl</td>
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<td>Response in 4/9 fibers*</td>
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<td>Preference</td>
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<td>Dulcin</td>
<td>Response (not strong)</td>
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<td>Preference</td>
<td>Sweet not like sucrose</td>
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<td>Response (not strong)</td>
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<td>Preference</td>
<td>Sweet not like sucrose</td>
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<td>d-Tryptophan</td>
<td>Response</td>
<td>Yes</td>
<td>Preference</td>
<td>Sweet like sucrose</td>
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<td>Saccharin</td>
<td>Response</td>
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<td>Preference</td>
<td>Sweet like sucrose</td>
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<tr>
<td>Ethylene glycol</td>
<td>Response; also in N fibers</td>
<td>—</td>
<td>Aversion</td>
<td>Mixed taste, sweet like sucrose and may be similar to NaCl</td>
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<td>Response</td>
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<td>Preference</td>
<td>Mixed taste, sweet like sucrose</td>
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<tr>
<td>d-Asparagine</td>
<td>Response; also in H fibers</td>
<td>—</td>
<td>—</td>
<td>Mixed taste, sweet like sucrose and may be similar to citric acid</td>
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<tr>
<td>Suosan</td>
<td>Response</td>
<td>Yes</td>
<td>Preference</td>
<td>Sweet like sucrose</td>
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<td>CCGA</td>
<td>Response</td>
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<td>Preference</td>
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</tr>
<tr>
<td>Sucrose</td>
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<td>DMGA</td>
<td>Response</td>
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<td>Preference</td>
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</tr>
<tr>
<td>Cyanosuosan</td>
<td>Response</td>
<td>Yes</td>
<td>Preference</td>
<td>Sweet like sucrose</td>
</tr>
<tr>
<td>CGA</td>
<td>Response</td>
<td>Yes</td>
<td>Preference</td>
<td>Sweet like sucrose</td>
</tr>
<tr>
<td>SC-45647</td>
<td>Response</td>
<td>Yes</td>
<td>Preference</td>
<td>Sweet like sucrose</td>
</tr>
<tr>
<td>Glycine</td>
<td>Responses in all fibers</td>
<td>Yes</td>
<td>Preference</td>
<td>Mixed taste, not only sweet like sucrose taste</td>
</tr>
</tbody>
</table>

MDS, multidimensional analysis; NS, not significant; see Table 1 for other definitions. * Low concentration; ** high concentration.


Tinti, J. M., Nofre, C., and Dubrozzard, D. Studies on sweeteners requiring the simultaneous presence of both NO\(2\)/CN and COO\(\) groups. Naturwissenschaften 65: 148, 1981.
