14 Manunta, P., Hamilton, B. P., Pruce, E., and Hamlyn, J. M., High dietary sodium raises plasma levels of ouabain in normal man. Abstr. 14th Scientific Meeting of the International Society of Hypertension, Madrid, Spain, 14–18 June 1992. J. Hypertension *10*, Suppl. 6 (1992) 96.
15 Manunta, P., Evans, G., Hamilton, B. P., Gann, D., Resau, J., and Hamlyn, J. M., A new syndrome with elevated plasma ouabain and hypertension secondary to an adrenocortical tumor. Abstr. 14th Scientific Meeting of the International Society of Hypertension, Madrid, Spain, 14–18 June 1992. J. Hypertension *10*, Suppl. 6 (1992) 27.
16 Mathews, W. R., DuCharme, D. W., Hamlyn, J. M., Harris, D. W., Mandel, F., Clarke, M. A., and Ludens, J. H., Mass spectral characterization of an endogenous digitalislike factor from human plasma. Hypertension *17* (1991) 930–935.
17 Sweadner, K. J., Isozymes of the Na^+/K^+-ATPase. Biochim. biophys. Acta *988* (1989) 185–220.

0014-4754/92/11-12/1102-05$1.50 + 0.20/0

Research Articles

Speed and consistency of human decisions to swallow or spit sweet and sour solutions[1]

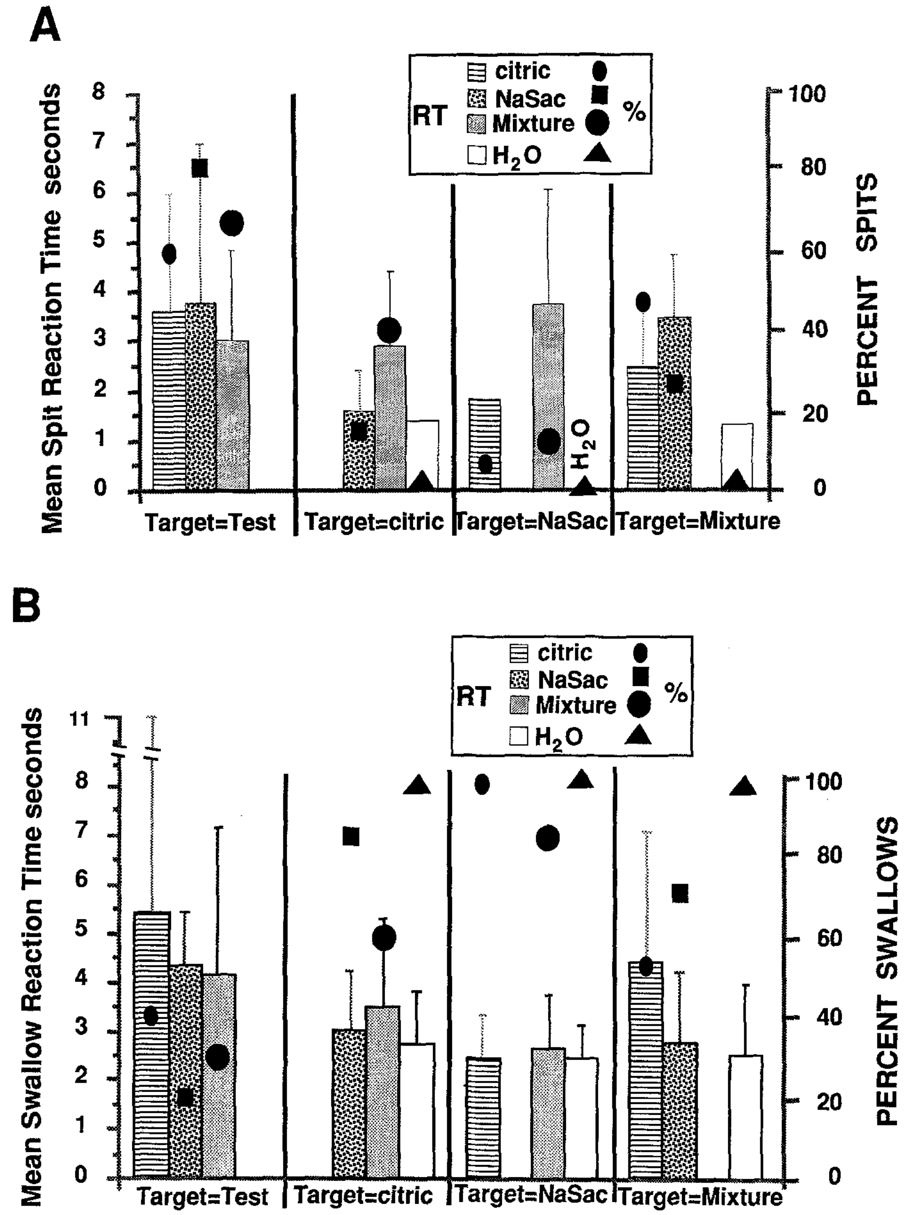
J. D. Delconte, S. T. Kelling and B. P. Halpern

Department of Psychology, Field of Physiology and Department of Applied and Engineering Physics, and Section of Neurobiology and Behavior, Cornell University, Ithaca (New York 14853-7601, USA)
Received 7 June 1991; accepted 14 July 1992

Abstract. Measurements of the frequency and speed of spitting or swallowing citric acid, sodium saccharin, or mixture solutions, using the taste of one of them as the definition of what was to be spit, revealed that 'correct' spits occurred on ≥ 70% of trials with equal reliability and latency among the liquids, indicating that recognition-based rejection decisions in adult humans are as rapid and consistent for an arbitrary sweet taste as for a sour or mixed taste.
Key words. Taste; decisions; reaction time; sour; sweet; mixture spit; swallow.

The gustatory characteristic of regional or national human diets differ widely, but the children of individuals from one region, when brought up in another locale, will usually adopt the cuisine of their new habitat if they are regularly exposed to it, and may find the diet of their parents' homeland unacceptable[2–5]. These observations indicate that much human taste-dependent preference and rejection is experientially based. It is generally assumed that the primary means through which this experience acts is learning[6–9] (although learning-independent effects of prenatal experience on gustatory structure and function have also been demonstrated in a mammal[10]). Despite these experience-based differences in what are considered acceptable foods and beverages, a fundamental consistency in human taste preferences is often stated. The claim is that sweet things will be selected or accepted, while others, especially sour or bitter, will be rejected[11,12]. It is argued that sour things, for example, will be much more likely to be immediately damaging than sweet things[13,14]. When adults nonetheless accept or select sour items and reject sweet ones, this is taken to be a learned reversal of the 'natural' human pattern[15].

If 'natural', unlearned human behavior is to reject sour tasting substances and select sweet items, rejection of a sour tasting substance should be faster or more reliable than rejection of a sweet item, even in adults who have learned to accept particular regional cuisines. It is known that simple taste reaction time, i.e., detection that any taste is present, is generally more rapid for acids than for sweeteners[16,17]. Faster or more reliable rejection would be predicted because taste-dependent behavior that rapidly and consistently removes from the oral cavity substances that are usually dangerous should be maximized through natural selection. We tested this hypothesis by providing 15 paid, screened[18], volunteer subjects (age 21 ± 6 years {mean ± SD}, 7 female) with a target taste sipped from a 100-ml drinking glass containing 80 ml of liquid (10 mM analytical reagent grade citric acid [citric] or 2 mM United States Pharmacopoeia sodium saccharin [NaSac] or a mixture containing both [mixture], prepared in distilled water (H_2O) (refractive index = 1.3330; conductivity < 1.5 μS), and instructing subjects to then take a sip from 100-ml drinking glasses containing 80 ml of test liquids. The sipped test liquids were to be spit out if they corresponded to the target taste, but were otherwise to be swallowed. Subjects used each of the three target tastes once in individual sessions separated by 10 min. Sessions began with a vigorous whole mouth rinse with H_2O, a practice series of sips and spits or swallows, and then another whole mouth rinse with H_2O. 10 min after the completion of the practice sips, the 8 data sips of each session were begun. No information whatsoever was given on the taste of the target or test tastes, or the accuracy or speed of spits or swallows. Two of the 8 test drinking glasses contained the sour target liquid citric, the equally intense[19,20] sweet target liquid NaSac[21], the sweet/sour[19] mixture, or H_2O, in random order. Start of contact between



Bar diagrams giving mean spit (A) or swallow (B) reaction times (RT), in seconds (bars and left hand ordinates), with vertical lines extending from the tops of bars indicating SEM, combined with scatter-plots (symbols and right hand ordinates) of percent (%) spitting (A) or swallowing (B), of 4 test stimuli. Absence of an RT bar denotes 0 mean, SEM. The target taste was either the same as (=) the test taste (left-most triad of each diagram) or was citric or NaSac or mixture (three right hand triads of each diagram). Horizontal striped bars denote RT for spits (A) or swallows (B) to citric test stimuli; black-dotted bars, to NaSac; gray bars, to mixture; clear bars, to water test stimuli. Filled ellipses are percent spits (A) or swallows (B) for citric test stimuli; squares, for NaSac; circles, for mixture, and triangles, for water test stimuli. For the spit diagram and scatter-plot (A), the correct response was to spit the test taste liquid when it corresponded to the target taste (left-most triad), but to otherwise *not* spit. For the swallow diagram and scatter-plot (B), the correct response was to swallow the test liquid *except when* it corresponded to the target taste (left-most triad).

the subject and the liquid in each glass was detected by a drinkometer, onset of spitting was indicated by EMG recording from the lips, and swallows were registered by a laryngophone[22]. Reaction times were derived from these measures.

We found that the frequencies of spitting versus swallowing the test liquids when the latter corresponded to a target liquid (*correct* spitting & *incorrect* swallowing) were significantly different from the frequencies when the test liquids were not the same as the specified target liquid (*correct* swallowing & *incorrect* spitting) (fig.), $p = 4.16 \times 18^{-18}$ (Pearson chi-square $[\chi^2] = 75.242$, $df = 1$, $\phi = 0.471$). Swallow reaction times also differed significantly between correct (test liquid $\neq$ target liquid) and incorrect swallows (analysis of variance [ANOVA] derived contrast, $F[1, 223] = 15.326$, $p < 0.0001$) although spitting reaction times did not ($F[1, 93] = 1.865$, $p = 0.175$). However, between the three target liquids and their corresponding test liquids (target = test; *correct* spitting & *incorrect* swallowing) there were no differences in either frequencies of spitting versus swallowing ($\chi^2 = 4.335$, df = 2, p = 0.144, $\phi = 0.226$) or in reaction times for spitting (ANOVA, F[8, 95] = 11.25, p = 0.353) or swallowing (ANOVA, F[2, 24] = 0.438, p = 0.650). This absence of differences indicates that oral rejection of a sour tasting liquid (citric) is neither faster nor more reliable than rejection of a sweet liquid (NaSac) when rejection is dependent upon recognition of the taste. In similar fashion, the amount of sourness did not affect frequencies of spitting versus swallowing (comparison between all conditions for which the test solution was more sour than the target liquid [citric or mixture = test & NaSac = target; citric = test & mixture = target] versus all conditions for which the test solution was less sour than the target liquid ([e.g., NaSac = test & citric = target], $\chi^2 = 0.371$, df = 1, p = 0.542, $\phi = 0.046$). The amount of sourness also failed to affect reaction times for swallowing (ANOVA derived contrast, F[1, 223] = 0.049, p = 0.826) or spitting (ANOVA, F[8, 95] = 11.25, p = 0.353).

The mean *incorrect* swallowing reaction time was 1.4 times as long for citric = target & test (citric-citric) as for mixture-mixture, with NaSac-NaSac in an intermediate position. Thus, reaction time for swallowing when target = test (*incorrect* swallowing reaction time) tended to be slowest for the sour stimulus (1.1–1.6 s longer); this difference approached statistical significance (ANOVA derived contrast, F[1, 223] = 3.686, p = 0.056). This trend does not appear to be due to the taste of citric per se, since *correct* citric swallowing reaction times when NaSac or mixture was the target liquid did not differ from *correct* NaSac or mixture swallowing reaction times when citric was the target liquid (ANOVA derived contrast, F[1, 223] = 0.153, p = 0.696). In addition, *correct* citric swallowing reaction times were much faster (1.1–3 s) than, and significantly different from, the *incorrect* citric swallowing reaction times (ANOVA derived contrast, F[1, 223] = 10.713, p = 0.001).

Responses when target = mixture may have been more difficult than for the other target solutions. The frequency of *incorrect* spits when target = mixture was ≥ twice the frequency when target = citric or NaSac, and the *incorrect* spit reaction times when target = mixture were ≥0.8 s longer then when target ≠ mixture (fig., A). Furthermore, correct swallow reaction times for citric and mixture as target or test liquid were higher than, (fig., B) and significantly different from all correct swallow reaction times with other liquids (ANOVA derived contrast, F[1, 223] = 11.963, p = 0.001). However, a significant difference was not present when correct swallow reaction times for citric and NaSac as target or test liquid were compared with correct swallow reaction times for mixture = target (ANOVA derived contrast, F[1, 223] = 2.149, p = 0.144). Thus, swallowing decisions involving citric and mixture, but not NaSac and mixture, were especially problematic, although mixture is composed of both NaSac and citric.

H_2O was a test liquid but *not* a target liquid so that there would be one test liquid for which no possible confusion could exist due to some instances in which the liquid should be spit and others when it was to be swallowed. The correct response was always to swallow H_2O. Approximately 100% swallowing of the H_2O test liquid would be expected if subjects understood and followed the instructions. We found that the frequency of H_2O swallowing, which ranged from 97% to 100% (fig., B), was > all other test liquids ($\chi^2 = 19.188$, df = 1, $p = 1.19 \times 10^{-5}$, $\phi = -0.275$). Reaction time for H_2O swallowing also could not be lengthened by possible confusion from prior contrary instructions. However, before choosing to swallow, subjects must always decide that the taste of a test liquid is not the same as the target taste. Therefore, swallowing reaction times for H_2O and the other test liquids should be similar unless particular target and test liquid combinations were especially difficult. We found that H_2O's mean swallow reaction times were within 0.6 s of the correct swallow reaction times for all other test liquids except for citric and mixture as target or test liquid (fig., B). As noted above, citric and mixture reaction times were significantly different from all correct swallow reaction times with other liquids (p = 0.001).

Overall, the total variance of swallow reaction times (ANOVA sum of squares [SS] = 150.966, error SS = 829.833, df = 223) was accounted for by two significant components: incorrect versus correct swallow reaction times (SS = 57.030), with the incorrect longer, and correct swallow reaction times for citric-mixture or mixture-citric versus all other correct swallow reaction times (SS = 44.519), with citric & mixture longer. When these two components were subtracted from the total SS, the remaining SS was no longer significant (SS = 49.417, F[9, 223] = 1.4395, p = 0.172).

Our observations failed to support the hypothesis that 'natural' human behavior is to rapidly reject sour tasting substances and accept sweet items. For adults, at least, learned rules (e.g., reject taste X but consume tastes Y and Z) appeared to be a major factor in taste-dependent acceptance. This is perhaps not surprising since the adults who were tested probably had been exposed to, and had learned to consume, a wide variety of cuisines. Changes in the rules were easily learned (e.g., now reject taste Y but consume tastes X and Z). Such gustatory plasticity may be related to prior knowledge or experience that particular substances are not to be consumed on certain days, or in specified contexts or locations. One positive observation was the difficulty of citric versus mixture responses, resulting in a high frequency of incorrect spits and longer correct swallow reaction times for these pairings. The difficulty may reflect the increased complexity of certain taste mixtures[23, 24], or may indicate that discriminations between citric and mixture are especially troublesome.

1 Acknowledgments. K. M. Dorries, R. E. Johnston, and C. L. Krumhansl provided critical comments; R. B. Darlington, statistical consultation; the anonymous referees, encouragement for a better analysis. Study supported by grant BNS-8518865 from NSF and the Pew Undergraduate Program in Science Education.
2 Arnott, M. L., Gastronomy. The Anthropology of Food and Food Habits. Mouton, The Hague 1975.
3 Woolfe, J. A., in: The Potato in the Human Diet, pp. 191–221. Cambridge University Press, Cambridge 1987.
4 Pangborn, R. M., in: The Chemical Senses and Nutrition, pp. 45–60. Eds M. R. Kare and O. Maller. The Johns Hopkins Press, Baltimore 1967.
5 Beauchamp, G. K., and Maller, O., in: The Chemical Senses and Nutrition, pp. 291–311. Eds M. R. Kare and O. Maller. Academic Press, New York 1977.
6 Bernstein, I. L., and Webster, M. W., Physiol. Behav. *25* (1980) 363.
7 Cain, W. S., in: Food Acceptance and Nutrition, pp. 63–77. Eds J. Solms, D. A. Booth, R. M. Pangborn and O. Raunhardt. Academic Press, London 1987.
8 Jerome, N. W., in: Taste and Development: The Genesis of Sweet Preference, pp. 235–248. Ed. J. M. Weiffenbach. U. S. Department of Health, Education, and Welfare, Bethesda, MD 1977.
9 Rozin, P., and Schull, J., in: Stevens' Handbook of Experimental Psychology, 2nd ed., vol. 1, pp. 503–546. Eds R. C. Atkinson, R. J. Herrnstein, G. Lindzey and D. Luce. John Wiley & Sons, New York 1988.
10 Hill, D. L., and Mistretta, C. M., Trends Neurosci. *13* (1990) 188.
11 Steiner, J. E., in: Taste and Development: The Genesis of Sweet Preference, pp. 173–189. Ed. J. M. Weiffenbach. U.S. Department of Health, Education, and Welfare, Bethesda, MD 1977.
12 Ganchrow, J. R., Steiner, J. E., and Daher, M., Infant Behavior and Development *6* (1983) 189.
13 Beauchamp, G. K., and Moran, M., in: Clinical Measurement of Taste and Smell, pp. 305–315. Eds H. L. Meiselman and R. S. Rivlin. Macmillan Publishing Company, New York 1986.
14 Nowlis, G. H., in: Taste and Development: The Genesis of Sweet Preference, pp. 190–204. Ed. J. M. Weiffenbach. U.S. Department of Health, Education, and Welfare, Bethesda, MD 1977.
15 Pfaffmann, C., in: Handbook of Perception, vol. VIA, pp. 51–121. Eds E. C. Carterette and M. P. Friedman. Academic Press, New York 1978.
16 Halpern, B. P., Neurosci. Biobehav. Rev. *10* (1986) 135.
17 Kelling, S. T., and Halpern, B. P., Chem. Senses *12* (1987) 543.
18 Halpern, B. P., in: Umami: A Basic Taste, pp. 327–354. Eds Y. Kawamura and M. R. Kare. Marcel Dekker, New York 1986.
19 Kelling, S. T., and Halpern, B. P., Chem. Senses *13* (1988) 559.
20 McBurney, D. H., and Shick, T. R., Percept. Psychophys. *10* (1971) 249.
21 Settle, R. G., Meehan, K., Williams, G. R., Doty, R. L., and Sisley, A. C., Physiol. Behav. *36* (1986) 619.
22 Halpern, B. P., in: Taste, Olfaction, and the Central Nervous System, pp. 181–209. Ed. D. W. Pfaff. The Rockefeller University Press, New York 1985.
23 Erickson, R. P., and Covey, E., Physiol. Behav. *25* (1980) 527.
24 Kuznick, J. T., and Turner, L. S., Chem. Senses *11* (1986) 183.

0014-4754/92/11-12/1106-04$1.50 + 0.20/0

Behavioural and electrophysiological evaluation of oviposition attractants for *Culex quinquefasciatus* Say (Diptera: Culicidae)[1]

A. J. Mordue (Luntz), A. Blackwell, B. S. Hansson[2], L. J. Wadhams[3] and J. A. Pickett[3]

Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen (United Kingdom), Department of Ecology, University of Lund, S-223 62 Lund (Sweden), and Department of Insecticides and Fungicides, AFRC/IACR Rothamsted Experimental Station, Harpenden, Herts (United Kingdom)
Received 23 June 1992; accepted 18 August 1992

Abstract. The attraction of gravid *Culex quinquefasciatus* by the oviposition pheromone, *erythro*-6-acetoxy-5-hexadecanolide, and by polluted water is described. Both materials increase oviposition and when combined the effect is additive. The oviposition behaviour is reflected by the antennal sensitivity to these compounds.
Key words. Oviposition pheromone; polluted water volatiles; oviposition behaviour; electroantennogram.

Culex quinquefasciatus is the principal urban vector of Bancroftian filariasis in the tropics[4] and is the vector for St. Louis encephalitis (SLE) virus and other arboviruses in the USA[5]. An efficient surveillance programme for arbovirus vectors such as this species would greatly benefit affected areas. Existing trapping techniques are expensive, inconvenient and inefficient; using light, CO_2 and vertebrate baits, they catch mainly unfed individuals. Recently introduced oviposition traps, baited with fermented organic infusions of materials such as hay and cattle manure[6–8], are more promising. They mainly catch blood-engorged and gravid females preferentially, resulting in higher arbovirus isolation. Clearly a synthetic attractant for these ovi-traps would greatly facilitate their servicing but the attractive components of such infusions are only now being identified[9]. In the field, gravid females use a combination of physical and chemical cues such as visual, tactile, contact chemoreceptory and olfactory stimuli[10–12] to locate and select oviposition sites. Some chemical stimulants arise from the environment, e.g. microbial decomposition products[13], and communicate the presence of larval food in the prospective oviposition site. In addition, *C. quinquefasciatus* oviposits egg rafts on the surface of water which, on maturing, release a pheromone from apical droplets formed on the eggs[14] that attracts females of this species and others of the genus[15]. The pheromone comprises (−)-(5*R*,6*S*)-6-acetoxy-5-hexadecanolide[14,16] and in the field, the synthetic racemic pheromone effectively concentrates oviposition[17,18]. We report on behavioural and electrophysiological studies on the attraction of *C. quinquefasciatus* to the oviposition pheromone alone and