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Autonomic Nervous System Responses Associated with Primary Tastes

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Abstract

The hedonic dimension of the taste sensation plays a crucial role in the control of many taste-mediated responses related to food ingestion or rejection. The purpose of this study was to evaluate the emotional reactivity associated with each primary taste (sweet, salty, sour and bitter) through analysis of the variations of autonomic nervous system (ANS) parameters. Thirty-four healthy non-smoker volunteer subjects (17 males and 17 females, mean age = 28 years) participated in the experiment. Taste stimuli were solutions of 0.3 M sucrose (sweet), 0.15 M NaCl (salty), 0.02 M citric acid (sour) and 0.00015 M quinine sulfate (bitter). Evian mineral water was used as the diluent and control (neutral taste). Throughout the test, five ANS parameters (skin potential and skin resistance, skin blood flow and skin temperature, and instantaneous heart rate) were simultaneously and continuously recorded. Results of the ANOVA evidenced a significant effect of primary taste on skin resistance amplitude ($P < 0.001$) and duration ($P < 0.0001$), skin temperature amplitude ($P < 0.001$), skin blood flow amplitude (vasoconstriction) ($P < 0.0001$) and instantaneous heart rate increase ($P < 0.0001$). Skin resistance and cardiac responses were the most relevant ANS parameters to distinguish among the taste solutions. The four primary tastes could be associated with significantly different ANS responses in relation to their hedonic valence: the pleasantly connoted and innate-accepted sweet taste induced the weakest ANS responses whereas the unpleasant connoted tastes (salty, sour and bitter) induced stronger ANS responses, the innate-rejected bitter taste inducing the strongest ones. Such a neurovegetative characterization of each primary taste could provide references for the hedonic analysis of the more complex gustative sensation attached to foods.

Introduction

Gustative appreciation of foods is a crucial component of feeding behavior. In humans and other omnivorous animals, the major function of the sense of taste is to enable organisms to use chemical cues to select appropriate items for ingestion from among the multitude of nutritive, non-nutritive and toxic foods encountered in their natural habitat (Galef, 1981). Possession of such a sensory system would, however, be of little use without a concomitant behavioral capacity either to accept or reject foods on the basis of their chemical properties.

A gustatory stimulus evokes a two-dimensional response, discriminative at the cortical level and affective (emotional) at the hypothalamo-limbic level (Norgren, 1985). The discriminative dimension corresponds to the qualitative (chemical and physical properties of tastants) and quantitative (intensity) characteristics of the stimulus. It is generally assumed that the sense of taste can differentiate four primary sensory qualities (sweet, salty, sour and bitter)—or five, including the umami taste according to the Japanese. The affective or hedonic dimension, corresponding to the amount of pleasure or displeasure that a stimulus arouses in an organism, is critically important in the control of many taste-mediated responses related to food ingestion and rejection (Smith and Vogt, 1997). Pleasant stimuli elicit approach and acceptance, whereas unpleasant ones induce avoidance and rejection, thus determining taste preferences and aversions. Several subjective methods have been developed in attempts to estimate this affective dimension. Generally, subjects are instructed to judge each stimulus on a particular attribute by using different questionnaire or hedonic scales. However, these judgements imply a cognitive analysis which cannot faithfully translate the spontaneous affective-emotional response preceding cortical integration. This consideration, in addition to the lack of language to describe taste experiences, limits the validity of a large number of research methods which are based on asking subjects to describe their emotional experiences (Köster, 1990; Ledoux, 1994). Thus, if the use of such subjective

methods seems better adapted to the study of the gustatory sensory-discriminative component, more objective ones are needed for the evaluation of the emotional aspect of the gustative sensation. Aside from methods studying facial muscular expressions (Steiner, 1977, 1979; Perl *et al*., 1992), the analysis of autonomic responses recorded in real time could be of great interest, since the perception of a sensory stimulus may bring about physiological changes in the organism such as visceral, glandular and/or cardiovascular responses. Today, new concepts characterizing autonomic nervous system (ANS) functioning have been put forward (Ekman *et al*., 1983; Wallin and Fagius, 1986; Vernet-Maury *et al*., 1990), so that ANS may be considered a highly and rapidly activated system capable of differentiating emotions (Ekman *et al*., 1983; Collet *et al*., 1997). New sensors and indices for ANS activity measurement have been developed (Dittmar, 1989; Dittmar *et al*., 1992, 1995; Vernet-Maury *et al*., 1991, 1995), permitting non-invasive and simultaneous recording of different autonomic parameters (electrodermal, thermovascular and cardiorespiratory) in real time.

Previous results obtained in the olfactory field have shown that odors induce different amplitudes and durations of ANS responses according to the hedonic valence or emotional load of odorants (Alaoui-Ismaïli *et al*., 1997a,b; Robin *et al*., 1998, 1999). These findings clearly indicate the validity of the use of ANS recording procedures to estimate the emotional response associated with odors. Considering the close interconnection between smell and taste, this method would provide original data on the emotional reactivity induced by each of the four primary tastes (sweet, salty, sour and bitter). A similar approach was recently applied to study the effect of beverage ingestion on physiological responses and mood (Quinlan *et al*., 1997).

The purpose of this study was therefore to extend previous studies by including autonomic measures in addition to subjectives responses. From our previous olfactory results and from a study by Perl *et al.* (Perl *et al*., 1992), who showed that the duration of facial expressive behavioral responses induced by aversive tastes is longer than that triggered by pleasant or indifferent ones, we make the hypothesis that pleasant gustative stimulation (sweet) would induce weaker ANS activation than unpleasant ones (in particular, bitter).

Materials and methods

Subjects

Thirty-four healthy, non-smoker volunteer subjects (17 males and 17 females) were recruited to take part in the study. Their mean age was 28 years, ranging from 20 to 40. All subjects were free from medications and did not report any olfactory or gustatory disorders. Each subject reviewed and signed an informed consent in the protocol and was paid for his (her) participation.

Taste stimuli

Taste stimuli were solutions of 0.3 M sucrose (Merck, Darmstadt, Germany) for sweet taste, 0.15 M NaCl (Carlo Erba) for salty taste, 0.02 M citric acid (Prolabo) for sour taste and 0.00015 M quinine sulfate (Cooper, Cooperative Pharmaceutique Française) for bitter taste. The concentration of these solutions was determined from preliminary tests to allow the subjects to clearly recognize each primary taste. Evian mineral water (pH 7.2) was used as diluent and served as the control (neutral taste) (Prescott *et al*., 1992; Laing *et al*., 1993). All solutions were dispensed in a 10 ml volume and presented at room temperature (20–22°C). They were placed on a table in front of the subject in identical and opaque beakers numbered from 0 to 5. Beaker no. 0 (Evian water) was always presented first in order to suppress the surprise effect induced by the first stimulus (not taken into account in the data analysis). Beaker no. 5 always contained the bitter solution because of its long aftertaste duration (Leach and Noble, 1986) and its masking effect (Dallenbach and Dallenbach, 1943). The other four beakers (nos 1–4) contained sweet, salty, sour or control solutions presented in a randomized order. For complete impregnation of the oral cavity, subjects were instructed to keep the liquid sample in the mouth for 5 s and then to swallow it. Subjects were instructed to rinse their mouth with Evian water *ad libitum* after each solution.

Procedure

Subjects were individually involved in a test session lasting ~1 h. They were requested to abstain from eating or drinking for 1 h prior to testing. They had to be present 15 min before the beginning of the test in order to adapt to the experimental conditions. They were seated in a comfortable chair in a room where the temperature was maintained constant (22°C) and were verbally informed about the procedure. The test started with an adaptation phase to the light signal used to give subjects the order to taste the solutions, and to the associated movement of the hand. Thus, 10 rehearsals were carried out with an empty beaker. After this adaptation phase, subject were informed that the test was to begin. At the next light signal, they were to taste the first solution (beaker no. 0). When ANS parameters recovered their prestimulus basal level (time interval ~2 min), a second light signal was delivered indicating that subjects were to fill out a questionnaire. In the first part of this questionnaire, subjects had to identify the taste of each solution by choosing one label from the five following labels: sweet, salty, sour, bitter and neutral. If none of the given labels corresponded to the perceived sensation, the subjects could indicate a label of their own choice. In the second part of the procedure, subjects had to situate each solution on an 11-point hedonic scale with a score varying from 0 to 10. Three labels were indicated on this scale: 0 = highly pleasant, 5 = neutral and 10 = highly

unpleasant. Subjects then rinsed their mouth *ad libitum* with Evian mineral water and waited for the next light signal to taste the following solution. This experimental procedure was repeated identically for the six solutions.

Autonomic nervous system parameters

Throughout the test, five ANS parameters were simultaneously and continuously recorded with no interference: skin potential (SP) and skin resistance (SR) (electrodermal parameters), skin blood flow (SBF) and skin temperature (ST) (thermovascular parameters), and instantaneous heart rate (IHR).

Skin resistance

SR was recorded by a 15 μA DC current using 25 mm^2 Ag/AgCl round electrodes (E 243, Clark Electromedical Instruments, Reading, UK), fixed by adhesive tape on the second phalanx of the index finger and the third digit of the non-dominant hand. Electrode positioning was in compliance with traditional recommendations (Fowles *et al*., 1981). SR responses were measured (i) with the traditional amplitude index, defined as the difference between the pre-stimulus SR level and the lowest SR level within 10 s post-stimulus onset; and (ii) with the more recently defined temporal ohmic perturbation duration (OPD) index, corresponding to the time during which the subject responds to the stimulus (Vernet-Maury *et al*., 1995). When a stimulus is delivered, SR decreases and remains at a lower level as long as the subject is submitted to the stimulus influence; SR then increases towards its initial level without fluctuating any more. This index is measured from the onset of the sudden fall in SR to the offset point indicating the SR increase recovering its initial slope. The OPD index was shown to reflect the emotional load of the stimulus (Vernet-Maury *et al*., 1995).

Skin potential

SP was recorded using Beckman 78 mm^2 electrodes, fixed by double-face adhesive tape. Electrode positioning and electrode cream were in compliance with traditional recommendations (Fowles *et al*., 1981). The active electrode was placed on the hypothenar eminence of the subject's non-dominant hand (after alcohol–ether cleansing of the skin). The reference electrode was placed 10 cm higher on the wrist (on the equidistant line of the median plane and the outer extremity of the forearm). While positive SP waves are the most frequent, negative SP waves were shown to possibly reflect a high emotionally loaded stimulus (Vernet-Maury *et al*., 1996).

Skin blood flow

SBF was assessed using the original Hematron patented sensor (Dittmar, 1989). The non-invasive sensor was placed on the skin with adhesive tape (thenar eminence of the non-dominant hand). The transducer consisted of a disk 25 mm in diameter and 4 mm thick. The measuring surface in contact with the skin was made up of two parts: the reference area at the periphery of the disk and the measurement area at the center of the disk. The temperature difference between these two areas was measured using 16 thermocouple junctions. A very low thermal inertia flat heater was located in the central part of the disk. A proportional, integrative and derivative device controlled the heating power in order to maintain a constant temperature difference of 2°C between the central area and the periphery. The size and shape of the heater were designed in such a manner that a thermal field was induced in the capillary network. The power necessary to maintain the temperature difference constant depends on the SBF: heat is transferred through the skin and washed out by the blood flow. At all times, electric power is proportional to the heat evacuated by the tissue blood flow (Dittmar, 1989). Blood flow in capillaries is submitted to microchanges reflecting variations in emotional load (Vernet-Maury *et al*., 1991). The response amplitude (positive or negative) was measured by the difference between the pre-stimulus tonic level and the maximum variation induced by the stimulus. The onset of the SBF response is characterized by a break of the pre-stimulus tonic level slope, so that the lack of slope disruption was considered as a non-response.

Skin temperature

ST was measured by a slow inertia thermistor [10 K3 MCD2 Betatherm]. A 4 mm^2 sensor was placed in the middle of the palm of the non-dominant hand with non-caustic glue. A variation of about one-thousandth of a degree can be detected under such conditions. As for the SBF, the ST response amplitude (positive or negative) was measured by the difference between the pre-stimulus tonic level and the maximum variation induced by the stimulus. The onset of the ST response is also characterized by a break of the pre-stimulus tonic level slope, so that the lack of slope disruption was considered as a non-response.

Instantaneous heart rate

The IHR was recorded from three silver electrodes in a precordial position. The D2 derivation signal (interval between two consecutive R waves) was processed and delivered in the form of instantaneous heart frequency. The smallest appreciable variation was 0.5 of a beat per min and the calibrated scale ranged from 0 to 200 beats per min. The IHR response was measured by the difference between the pre-stimulus level value and the maximum increase induced by the stimulus.

Recording system and signal analysis

The five measured signals were recorded by a 80286 microcomputer (Toshiba T3200). Signal sampling was carried out by a 16-bit data acquisition card (ADAC 5508HR) at a frequency of 8 HZ. Signals were recorded in parallel by a

Table 1 Recognition rates[a] (%) of the taste of the five tested solutions

Perceived gustative sensation	Tested solutions				
	Sucrose (0.3 M)	Sodium chloride (0.15 M)	Citric acid (0.02 M)	Quinine sulfate (0.00015 M)	Mineral water
Sweet	94				3
Salty		91			6
Sour			68		3
Bitter			12	91	20
Neutral					62
Sweet/sour	3		3		
Sweet/bitter	3				
Salty/sour		3	6		
Salty/bitter		6		6	3
Sour/bitter			9		
None			2	3	3

[a]This rate is close to 100% for sweet (94%), salty (91%) and bitter (91%) and lower for sour (68%) and control (as neutral taste) (62%).

six-channel potentiometric DC recorder (YTSE 460 type BBC) to allow rapid visual inspection of the recordings and quality control of experimentation.

A special software package was designed and developed for rapid analysis and processing of the recorded data. The interactive software permits calculation of all indices (including waveform pattern recognition of skin potential responses). The software features have other uses, such as amplification and attenuation of signals and zooming. A digital signal processing library of functions was designed and added to the software to allow processing of all types of artefacts and to filter random noise whenever present in the recorded signals (Rada *et al.*, 1995).

Extracted autonomic indices

Phasic responses appeared within 1 or 2 s following the intake of the solution. These were measured for each ANS parameter (SP, SR, ST, SBF and IHR) through the six following indices: (i) the sign (+ or –) of the SP response; (ii) the amplitude of the SR response (KΩ); (iii) the duration of the SR response with the OPD index (s); (iv) the amplitude (+ or –) of the SBF response (mW/cm·°C); (v) the amplitude (+ or –) of the ST response (°C); and (vi) the amplitude (+ or –) of the IHR response expressed in beats per min (bpm). As a response, the maximal change for SBF, ST and IHR from pre-stimulus level was measured within the electrodermal response (OPD), since this temporal index was shown to correspond to the autonomic subject response duration (Vernet-Maury *et al.*, 1995).

Statistical analysis

The effect of taste solutions (sweet, salty, sour, bitter and control) on hedonic scores and ANS responses was tested by one-factorial ANOVA. The post-hoc Tukey test permitted two-by-two comparisons. The chi-square test was used to compare recognition rates, the sign of the SP response and the percentage of non-electrodermal response between each taste solution. The Pearson rank correlation coefficient was used to analyze the relation between hedonic scores and ANS responses. All differences were considered significant at a level of $P < 0.05$.

Results

Subjective evaluation

Recognition rates (Table 1)

Recognition rates were significantly different among the five solutions ($\chi^2 = 20.63$; $P < 0.0001$). It was very close to 100% for sucrose (94%), sodium chloride and quinine sulfate (91%) and less high for citric acid (68%), either confused with bitter (12%) or analyzed as a mixture of sour/bitter (9%), sour/salty (6%) or sour/sweet (3%). The taste of the control solution (mineral water) was perceived as neutral in 62% of cases and also as bitter in 20% of cases.

Hedonic scores (Figure 1)

Mean hedonic scores were significantly different among the five solutions [$F(4,141) = 53.47$; $P < 0.0001$). Sucrose was rated as the most pleasant (2.9 ± 2.2). Citric acid (6.3 ± 2.7), sodium chloride (8 ± 1.9) and quinine sulfate (9.8 ± 0.6) were rated as increasingly unpleasant, with the greatest standard deviation for citric acid. Mineral water (4.6 ± 1.9) was rated neither pleasant nor unpleasant.

Autonomic responses

An example of a simultaneous recording of the variations of the five ANS parameters in response to sucrose and quinine sulfate is presented in Figure 2. It can be observed that ANS responses are stronger for quinine sulfate, especially through the electrodermal parameters (duration of the response = 14 s for sucrose and 79 s for quinine

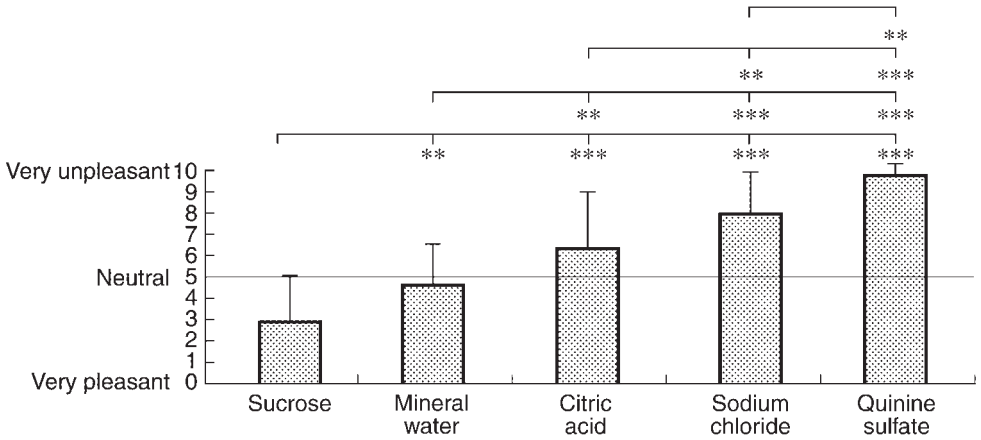

Figure 1 Mean hedonic scores (± SD) associated with each solution from highly pleasant (0) to highly unpleasant (10). Two-by-two comparisons (post-hoc Tukey test): $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

sulfate) and the thermovascular parameters (no response for sucrose whereas quinine sulfate induced an ST increase of +0.09°C and an SBF decrease of –0.24 mW/cm·°C). Both solutions induced an increase in heart rate of +10 bpm for sucrose and +15 bpm for quinine sulfate.

Results of the ANOVA evidenced a significant effect of the five solutions on ANS responses for all recorded parameters except the sign of the SP response which was always positive (only one subject responded with a negative SP to sodium chloride): SR amplitude [$F(4,139) = 5.31$; $P < 0.001$], OPD [$F(4,139) = 14.56$; $P < 0.0001$], ST [$F(4,134) = 4.94$; $P = 0.001$), SBF [$F(4,127) = 5.98$; $P < 0.0001$] and IHR [$F(4,139) = 15.24$; $P < 0.0001$).

The results of post-hoc comparison for each ANS parameter are specified below (P values are given in Table 2):

SR: the amplitude index distinguished three solution pairs from 10 (30%). Two-by-two comparisons showed that the mean response induced by the control (0.62 ± 1.17 KΩ) was significantly lower than those induced by citric acid (3.14 ± 4.6 KΩ), sodium chloride (3.34 ± 3.37 KΩ) and quinine sulfate (3.60 ± 4.49 KΩ). Other comparisons indicated no significant difference between any pair of mean values. The OPD index distinguished seven taste solution pairs from 10 (70%). Two-by-two comparisons showed that mean SR responses induced by the control (1.9 ± 3.4 s) and sucrose (4.3 ± 6 s) were significantly shorter than those induced by citric acid (12.9 ± 14.5 s) or quinine sulfate (18.6 ± 10.8 s), with no significant difference between the control and sucrose on the one hand and citric acid and quinine sulfate on the other. The mean value of the OPD index in response to sodium chloride was intermediate (11 ± 9.3 s) and significantly different from the control, sucrose and quinine sulfate. Moreover, we observed that taste stimuli did not induce electrodermal responses (SP and SR) in 28.5% of cases. This percentage of non-response was significantly different among the 5 solutions ($\chi^2 = 20.26$; $P < 0.0001$): it was higher for the control (73%) and sucrose (45%) than for citric acid (12%), sodium chloride (10%) and quinine sulfate (0%). Subjects with no electrodermal response rated sucrose (2.92 ± 2.33) as significantly more pleasant than the control (4.62 ± 1.88) [$F(1,32) = 5.44$; $P = 0.03$].

ST: ST distinguished between two taste solution pairs from 10 (20%). Two-by-two comparisons of ST amplitude (absolute value) showed that the mean ST response for the control (0.01 ± 0.02°C) was significantly lower than for citric acid (0.07 ± 0.08°C) and quinine sulfate (0.06 ± 0.07°C). Other comparisons indicated no significant difference between any pair of mean values.

SBF: All responses showed a decrease in SBF (vasoconstriction), which distinguished among four taste solution pairs from 10 (40%). Two-by-two comparisons showed that the amplitude of the vasoconstriction was significantly higher for quinine sulfate (–0.40 ± 0.36 mW/cm·°C), citric acid (–0.33 ± 0.31 mW/cm·°C) and sodium chloride (–0.33 ± 0.33 mW/cm·°C) than for the control (–0.07 ± 0.18 mW/cm·°C), and was significantly lower for sucrose (–0.17 ± 0.23 mW/cm·°C) than for quinine sulfate. Other comparisons indicated no significant difference between any pair of mean values.

IHR: Cardiac responses always showed a heart rate increase. IHR distinguished among six taste solution pairs from 10 (60%). Two-by-two comparisons showed that IHR increases induced by the control (1.3 ± 3.3 bpm) and sucrose (3.4 ± 4.8 bpm) were significantly lower than those induced by citric acid (8.3 ± 7.3 b.p.m) and quinine sulfate (11 ± 5.4 bpm), with no significant difference between the control and sucrose on the one hand, and citric acid and quinine sulfate on the other. The mean value of IHR in response to sodium chloride was intermediate (6.7 ± 7.3 bpm), and significantly different from the control and quinine sulfate.

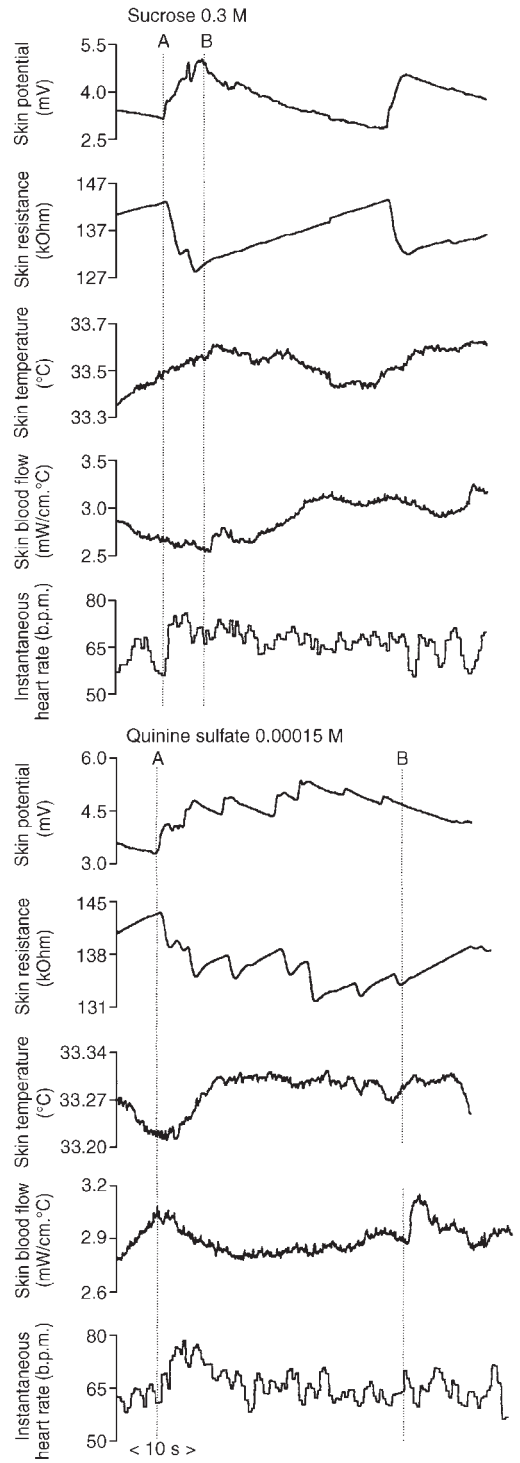

Figure 2 Example of a simultaneous recording of the variations of the five ANS parameters in response to sucrose and quinine sulfate solutions (A = beginning of the response 1 or 2 s after the intake of the solution, B = end of the response). ANS responses are stronger for quinine sulfate than for sucrose. Sucrose only induced a short electrodermal response (OPD = 14 s) and a heart rate increase (+10 bpm), with no response through the thermovascular parameters (ST and SBF). By contrast, quinine sulfate induced a long SR response (OPD = 79 s), an ST increase (+0.09°C), an SBF decrease (–0.24mW/cm·°C) and a higher heart rate increase (+15 bpm).

Correlation between hedonic scores and autonomic indices (Figure 3)

Hedonic scores were significantly and positively correlated to all ANS parameter variations, except for SP (SR amplitude: $r = 0.33$, $P < 0.001$; OPD: $r = 0.46$, $P < 0.001$; ST: $r = 0.21$, $P < 0.01$; SBF: $r = 0.31$, $P < 0.001$; IHR: $r = 0.39$, $P < 0.001$). The low hedonic score, corresponding to the pleasant-connoted solution (sucrose), was associated with weak amplitude and short duration of ANS responses. Conversely, high hedonic scores, corresponding to the unpleasant-connoted solutions (sodium chloride, citric acid and quinine sulfate), were associated with stronger ANS responses (higher amplitude and longer duration).

Discussion

The purpose of this study was to characterize each primary taste by ANS responses which objectively reflect the subject's emotional reactivity (Öhman *et al.*, 1993; Collet *et al.*, 1997). The concentrations chosen for the four taste solutions allowed a high recognition rate, so that they can be considered as representative of the four primary tastes. The confusion between sour and bitter in 12% of cases is in accordance with results from O'Mahony *et al.* (O'Mahony *et al.*, 1979). Moreover, the bitter taste reported by some subjects for mineral water has already been described by several authors and could be linked to the 'water taste' phenomenon (Bartoshuk, 1968). As expected, primary tastes could be associated with significantly different ANS responses related to their hedonic score. The pleasant-connoted sweet taste induced the weakest electrodermal, thermovascular and cardiac responses whereas the unpleasant-connoted tastes (salty, sour and mainly bitter) induced the strongest ANS responses. The response magnitude was three or four times higher for quinine sulfate than for sucrose according to ANS parameters. The affective neutrality of the control solution (Evian mineral water) was evidenced by both its medium hedonic score and a high percentage (75%) of non-electrodermal responses or their very weak amplitude.

The ability of the ANS parameters to distinguish among the five taste solutions varied for each of them. The two most discriminant were SR and IHR, as previously shown in the olfactive field (Alaoui-Ismaïli *et al.*, 1997a; Robin *et al.*, 1998), whereas ST and SBF were less relevant. Concerning SR, the duration of the response (OPD index) was more discriminant than the amplitude in differentiating the four primary tastes. Phasic electrodermal responses can be obtained in response to a wide variety of stimuli, this ANS parameter being sensitive to stimulus novelty, intensity, emotional content and significance (Dawson *et al.*, 1990). The electrodermal responses induced by the unpleasant bitter taste indicate a strong sympathetic activation, as confirmed by the strong cardiac and thermovascular responses. This high ANS activation makes it possible to

Table II Mean value ± SD (first column) and two-by-two comparisons (post-hoc Tukey test) of each ANS parameter for the five taste solutions

	Mean ± SD	Sucrose	Sodium chloride	Citric acid	Quinine sulfate	Mineral water
Sucrose	SR (Amp.) (1.08 ± 2.17) SR (OPD) (4.3 ± 6) ST (0.03 ± 0.04) SBF (–0.17 ± 0.18) IHR (3.4 ± 4.8)					
Sodium chloride	SR (Amp.) (3.34 ± 3.37) SR (OPD) (11 ± 9.3) ST (0.04 ± 0.04) SBF (–0.33 ± 0.33) IHR (6.7 ± 7.3)	SR (OPD)[a]				
Citric acid	SR (Amp.) (3.14 ± 4.06) SR (OPD) (12.9 ± 14.5) ST (0.07 ± 0.08) SBF (–0.33 ± 0.31) IHR (8.3 ± 7.3)	SR (OPD)[b] IHR[b]				
Quinine sulfate	SR (Amp.) (4.60 ± 4.49) SR (OPD) (18.6 ± 10.8) ST (0.06 ± 0.07) SBF (–0.4 ± 0.36) IHR (11 ± 5.4)	SR (OPD)[c] SBF[a] IHR[c]	SR (OPD)[a] IHR[a]			
Mineral water	SR (Amp.) (0.62 ± 1.17) SR (OPD) (1.9 ± 10.8) ST (0.01 ± 0.02) SBF (–0.07 ± 0.18) IHR (1.3 ± 3.3)		SR (Amp.)[a] SR (OPD)[b] SBF[b] IHR[b]	SR (Amp.)[a] SR (OPD)[c] ST[b] SBF[b] IHR[c]	SR (Amp.)[b] SR (OPD)[c] ST[b] SBF[c] IHR[c]*	

SR (Amp.) = skin resistance response amplitude, SR (OPD) = skin resistance response duration, ST = skin temperature (amplitude), SBF = skin blood flow (amplitude) and IHR = instantaneous heart rate. Only ANS parameters which significantly differentiated taste solutions are plotted: [a]$P \leq 0.05$, [b]$P \leq 0.01$, [c]$P \leq 0.001$.

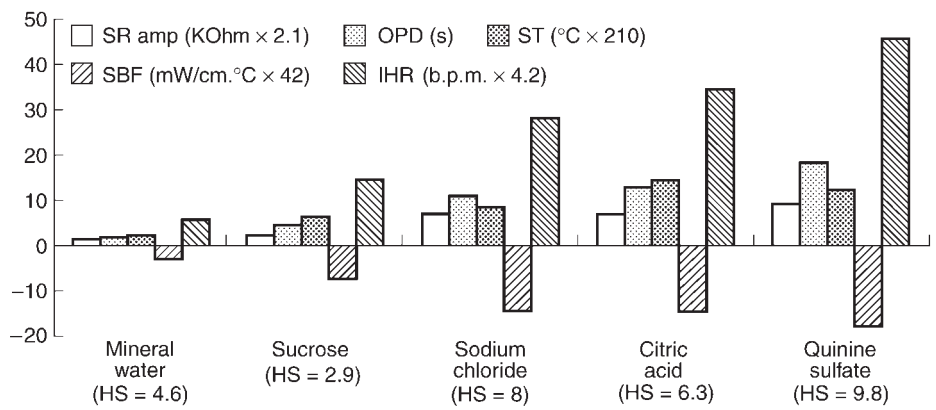

Figure 3 Pattern of ANS responses associated to each taste solution. HS = mean hedonic score, SR amp = skin resistance amplitude, OPD = ohmic perturbation duration, ST = skin temperature, SBF = skin blood flow and IHR = instantaneous heart rate. In order to present the mean value of each parameter on the same scale (ordinate axis), arbitrary units have been used for SR amplitude (×2.1), ST amplitude (×210), SBF amplitude (×42) and IHR amplitude (×4.2).

face up to an emergency situation due to the perception of bitter taste which generally characterizes noxious foods and traduces the innate feature of the aversion to bitter taste in humans (Steiner, 1977, 1979; Chiva, 1985; Köster, 1990; Mennella and Beauchamp, 1997). The bitter solution, at the concentration used in this study, can therefore be considered as a very disordering substance.

Likewise, salty and sour solutions also induced strong neurovegetative responses, but these were weaker than those induced by the bitter solution. The sympathetic responses

induced by the sodium chloride solution, in addition to its unpleasant hedonic evaluation, could be considered inconsistent with the physiological need for this mineral substance and its innate appeal to humans (Mattes, 1997). However, this result could be explained by the high intensity of the salty sensation compared with the very low molar values required from daily meals. Within a usual food context, salt is never eaten as a pure tastant but is added to food in small amounts to enhance flavor. The results of several studies (Cardello and Murphy, 1977; Bartoshuk *et al*., 1978; Smith and Van der Klaauw, 1995) have shown that for many salts, taste quality changes with concentration. For example, NaCl is somewhat sweet at low concentrations and sour at mid-range intensities. Van der Klaauw and Smith (Van der Klaauw and Smith, 1995) showed that the profile for 0.1 M NaCl (very close to the concentration used in our study) corresponds to a relatively strong sour side taste.

Autonomic responses to citric acid were of the same order as those obtained for NaCl and slightly lower than those obtained for quinine sulfate. Thus, the strong ANS responses induced by the pure solution of citric acid used in this study tend to indicate rejection behavior toward sour taste. In usual alimentation, the sourness of food is frequently attenuated by sweet compounds, such as in lemons, oranges, apples or yogurts. Frank and Archambo (Frank and Archambo, 1986) have shown that sucrose tends to eliminate the unpleasantness associated with increasing concentrations of citric acid. Moreover, the hedonic score attributed to citric acid showed the greatest variability, probably reflecting the more or less prominent degree of familiarity with the food's sourness. Individual differences in salivary characteristics (composition, pH, flow rate, buffering capacity) are also known to be an important source of individual variation in the perception of sour taste (Christensen *et al*., 1987). It is, then, possible that the perceived intensity of the sourness of the citric acid solution varied among subjects, resulting in more variable hedonic judgements.

Sucrose was the only solution to induce a weak sympathetic activation; this could be explained by the innate organic acceptance of sweet (Steiner, 1977; Mennella and Beauchamp, 1997). Regarding species evolution and adaptation, natural selection resulted in the production of physiological systems that caused a sensation of pleasure in response to gustatory stimuli predicting the presence of needed nutrients (such as sucrose) or molecules that serve as energy carriers and a sensation of displeasure in response to gustatory stimuli predicting the presence of toxins frequently characterized by bitter taste. An interesting finding concerning sweet taste is that the sucrose solution did not induce an electrodermal response in almost half of the subjects. Two hypotheses may be proposed to explain this phenomenon. First, sweet is a familiar and usual taste appreciated early in newborns. Its frequent consumption could explain the lack of sympathetic activation, particularly revealed by the electrodermal response, which is known to decrease and even disappear with repetition of the same stimulus (Dawson *et al*., 1990). This hypothesis is supported by the fact that Evian water induced a large amount of non-electrodermal response (75%), in contrast to unpleasant tastes, which induced electrodermal responses in 90% of cases for salty and sour and in 100% of cases for bitter, the less usual taste. Also, Fisher and Fisher (Fisher and Fisher, 1969) observed that the galvanic skin response component of the orienting reflex was slower to habituate to quinine than to sucrose. The second hypothesis may be related to sensory pleasure, and in this case the lack of SR responses could be interpreted as 'extremely weak' responses. This could be supported by the fact that subjects with non-electrodermal response rated the sucrose solution as more pleasant than the control and by the results of a previous study in which the lack of electrodermal responses to pleasantly flavored yogurts was correlated to hedonic preference for sweetness (Rousmans *et al*., 1998). Further studies are needed to elucidate the exact signification of the lack of electrodermal response to sweet stimuli.

In conclusion, the ingestion of a solution representative of each primary taste induced, at the concentration used, significantly different ANS responses related to hedonic valence. In addition to stimulus quality, the influence of stimulus intensity of ANS responses cannot be excluded and could be further evaluated using different concentrations of each tastant. Such neurovegetative characterization of each primary taste could constitute references for the hedonic analysis of the more complex gustative sensation of foods with industrial implications for the development and marketing of foods and clinical implications (e.g. in studying the affective-emotional impact of sweet foods in patients suffering from appetite control disorders).

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