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Are Human Taste Thresholds Similar on the Right and Left Sides of the Tongue?

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Abstract

The human tongue is a relatively symmetrical anatomical structure and is generally assumed functionally equivalent on both sides. Experimental evaluation of this assumption is complicated by the fact that psychophysical measurements tend to vary considerably across testing sessions. To address functional laterality, we determined the detection thresholds of six right-handed and six left-handed subjects for Na saccharin, NaCl, citric acid and quinine HCl. Five pairs of interwoven, left and right unilateral thresholds were obtained for each taste stimulus in 12 subjects (n = 480 separate thresholds). In most cases mean sensitivity based on multiple measurements was found to be laterally symmetrical, however, we observed a few cases of lateral asymmetry of both general and compound-specific sensitivity. Threshold values were found to vary considerably across sessions, consistent with the test–retest variability previously reported for whole mouth thresholds. We conclude that taste threshold sensitivity is equivalent on the left and right anterior tongue for most individuals. Given the occasional exceptions to this rule, however, it is advisable to employ a counterbalanced design for any experimental or clinical testing protocol in which treatments are applied asymmetrically to the tongue.

Introduction

Taste sensitivity is known to vary across different locations on the tongue and oropharyngeal cavity. The earliest report of this phenomenon dates back to Hanig's demonstration that regions of maximum sensitivity to sweet, sour, salty and bitter compounds are located in separate areas on the tongue (Hanig, 1901). The non-uniformity of taste sensitivity to different compounds on the anterior and posterior tongue, palate and pharynx has subsequently been confirmed using more rigorous psychophysical methods (Henkin and Christiansen, 1967; Collings, 1974). Relatively few studies, however, have compared the sensitivity on the left and right sides of the tongue. Because protocols are frequently employed in taste research which involve procedures that subject both sides of the tongue to different treatments [see, for example (Kroeze and Bartoshuk, 1985; Dessirier *et al.*, 1997, 1999; Shikata *et al.*, 2000)] but assume that the taste sensations elicited at both regions are equivalent, it is desirable to determine whether this assumption is indeed reasonable.

Several investigators have reported that electrogustometrically measured thresholds are laterally symmetrical (i.e. taste sensations elicited by punctate electrical stimulation of the tongue) (Tomita *et al.*, 1986; Murphy *et al.*, 1995). However, it is possible that such experiments reflect stimulation of additional sensory modalities to gustation. For example, the values for test–retest reliability reported by Murphy *et al.* (Murphy *et al.*, 1995) were higher than is usually observed for gustatory thresholds measured with solutions (Stevens *et al.*, 1995), suggesting that electric taste differs from taste sensations evoked by sapid solutions. Kroeze (1979) measured detection thresholds for NaCl and sucrose solutions on the left and right sides of the tongue using the method of constant stimuli (Kroeze, 1979). Based on threshold values obtained by fitting sigmoid functions to the raw data, he reported equivalent taste thresholds on the left and right sides of the tongue for both individuals and group averages. The method of constant stimuli, in which a fixed number of detection trials are presented to the subject at several concentration steps [see, for example (Shikata *et al.*, 2000)], has the advantage of sampling the observer's psychometric function across a broad range of peri-threshold sensitivities. In contrast, the modified staircase procedure (Levitt, 1970) does not sample the subject's threshold function across the full range of sensitivity, from near perfect

detection to chance. We suggest that the staircase method is preferable in cases where the experimenter wishes to make an ordinal comparison between the sensitivity of two subjects, but does not require further information about the psychophysical function (such as the Weber fraction). The rationale for this suggestion is as follows: the data collected with a staircase procedure can be used directly to make a single comparison between two means. In contrast, the data from the method of constant stimuli must either be used to fit a function so that an equivalent point from different data sets can be compared (typically the inflection point), or else multiple comparisons must be made between bins of data from each concentration step in the threshold. The former approach involves an extra processing step away from the raw data; the latter involves many comparisons based on small sample sizes, rather than a single comparison between two large samples.

In this study we hypothesized that any differences that might exist in taste sensitivity were likely to be small in healthy subjects. Moreover, the fact that test–retest reliability for taste thresholds are known to be notoriously low (Stevens, 1995) indicates that basing sensitivity estimates on a small number of measurements is likely to produce a Type II error (i.e. incorrect acceptance of the null hypothesis). Therefore, we designed the following experiment to maximize statistical power by obtaining five separate threshold values for each of four different taste stimuli on the left and right sides of the anterior tongue. We further increased the resolution of our methodology by employing an up–down modified staircase rule (three down, one up) designed to converge on a relatively stable cross-section of the psychophysical function, and utilized staircase increments of 1/4 log steps (as explained below). Obtaining multiple threshold measurements within individual subjects provided us with the opportunity to: (i) compare the left–right sides of the tongue; (ii) evaluate trends within compound classes (e.g. tastes mediated by ionotropic or metabotropic transduction mechanisms); (iii) evaluate reliability across experimental sessions. Therefore, secondary objectives of this study were to examine the correlation of general to compound-specific taste sensitivity as well as test–retest reliability.

Materials and methods

Subjects

Twelve subjects with no history of known taste disorders completed this study (five male, seven female; one Asian, four African-American, seven Caucasian), all either employees or students at the Monell Chemical Senses Center, the University of Pennsylvania, or Temple University. All subjects were non-smokers. One prospective subject was excused from the experiment because she was found to be completely aguesic on one side of her anterior tongue, and it was not the purpose of this study to examine gustatory pathology. There were six left-handed and six right-handed subjects, as evaluated by a questionnaire based on well-documented lateral preference trends (Porac and Coren, 1981). Left-handed subjects were numbers 2, 6 and 9–12. Each subject was tested in five sessions with each of four taste solutions, for a total of 20 sessions per subject. All subjects signed informed consent forms and were paid for their participation. The Human Subjects Institutional Review Board of the University of Pennsylvania approved the protocol followed in this study.

Procedure

The compounds used were solutions of Na saccharin (SAC), NaCl, citric acid (CA) and quinine hydrochloride (QHCl), all dissolved in deionized water. We used a forced choice staircase procedure to measure the detection thresholds of all four taste stimuli on laterally symmetrical regions of the anterior tongue (Levitt, 1970). A three-down, one-up rule was employed (i.e. the stimulus concentration was lowered after three correct trials in a row and raised after a single incorrect trial). Stimulus concentration was adjusted in 1/4 log steps. Both the taste solution and a blank (deionized water) were delivered to the targeted tongue region with cotton swabs, which were held on the tongue for ~5 s. All stimuli were presented at room temperature. The cotton swabs were applied to laterally symmetrical regions ~8 mm posterior to the leading edge of the tongue and 3 cm apart from each other [cf. figure 2 in (Shikata *et al.*, 2000)]. The experimenter made use of distinct features on the tongue, such as lines or papillae, to place the swab on the same area in all trials. We assessed the area affected by our procedure by applying swabs dipped in methylene blue to the tongue and observing the extent to which the dye spread. In every such case the stain did not spread beyond the area covered by the cotton swab, indicating that the stimulation elicited by our taste stimuli was restricted to a small area of ~50 mm^2. A single trial consisted of both a blank and a taste stimulus presented to the same side of the tongue. After both presentations the subjects raised one or two fingers to indicate which swab they believed contained the taste stimulus (first or second). The experimenter rinsed the tongue with a water bottle before each swab was applied and the subject had to provide an answer before the tongue was withdrawn into the mouth. The subjects were given feedback on every trial after indicating their choice. Trials alternated between the left and right sides of the tongue, always beginning on the right, and continued until seven reversals were obtained on each side. The stimulus presentation and inter-stimulus intervals were ~5 s and the inter-trial interval was ~15 s. (A reversal in a staircase procedure is defined as a change in the direction of stimulus intensity adjustment; either an increase in stimulus level immediately following a decrease or vice versa.) For each testing session two threshold values were calculated, one for each side of the tongue, by taking the geometric mean of the concentrations at which the last six reversals occurred.

Sessions were discarded in which the highest and lowest reversals in a given sequence differed by more than five steps (or 1.25 log units).

Analysis

To assess test–retest reliability across testing sessions we constructed eight matrices of correlation coefficients (a separate matrix for each side and compound; see Table 1A). The elements in each matrix are the correlation coefficients for all possible pairwise combinations of the five sessions of a single compound, based on the log of threshold values. We also repeated the same correlation analysis after the following transformation was applied to remove the contribution of inter-subject variability from the correlation coefficient (see Table 1B):

$$z_i = x_i \times (\mu_{group}/\mu_{subject})$$

where z_i is the transformed datum, x_i is the observed datum, μ_{group} is the mean threshold value of the population for a given taste compound and side of the tongue ($n = 60$) and $\mu_{subject}$ is an individual subject's mean threshold for a single compound and side of the tongue ($n = 5$).

We tested for differences between left- and right-side thresholds within individual subjects using paired *t*-tests, with the Bonferroni correction for multiple comparisons. Multiple *t*-tests were used to test the following hypotheses regarding individual differences: (i) individual subjects are asymmetrically sensitive to specific taste compounds (48 comparisons of five paired observations); (ii) individual subjects are asymmetrically sensitive to taste compounds sharing a general category of transduction mechanism [e.g. ionotropic (NaCl, CA) or metabotropic (SAC, QHCl); 24 comparisons of 10 paired observations]; (iii) individual subjects are asymmetrically sensitive to all taste stimuli (12 comparisons of 20 paired observations).

In order to evaluate the extent to which sensitivities to compounds within the ionotropically or metabotropically mediated classes co-vary, we constructed a scatter plot of the subjects' ranked sensitivity to both compounds within a class (SAC and QHCl in one scatter plot and NaCl and CA in another) and fitted a linear regression line to the plots. The ranking was determined on the basis of pooled left- and right-side thresholds ($n = 10$) for both compounds. The correlation coefficient was used to determine the degree to which sensitivity to compounds mediated by similar transduction mechanisms is correlated.

Finally, we tested the hypothesis that left- and right-handed subjects have different lateral advantages in taste sensitivity. We pooled the data obtained from left- and right-handed subjects separately and performed a single *t*-test comparison between the two groups of 120 paired observations. In this case the *t*-test compared the laterality values (left threshold – right threshold) obtained for each session, rather than the threshold values themselves.

Results

Threshold values for both individual subjects and the population are displayed in Figure 1A–D. Each data point in the histograms represents a single testing session. For comparison purposes each set of graphs is centered on the population mean and the abscissa spans an equal order of magnitude (3 log steps) to allow comparison of the variability of each compound. The group means for each compound irrespective of side were: 0.0791 mM SAC, 0.00737 M NaCl, 1.75 mM CA and 0.120 mM QHCl.

To evaluate the variability of our threshold measurements across testing sessions we calculated a set of correlation matrices for each possible pair of sessions (Table 1A). The average correlation coefficients for each compound irrespective of side were: SAC 0.418, NaCl 0.451, CA 0.290 and QHCl 0.720. After transforming the data set to remove the effect of inter-subject variability from the correlation coefficients (Table 1B) the averages were: SAC –0.127, NaCl –0.218, CA –0.196 and QHCl –0.109.

Table 2 displays the differences in taste sensitivity for all subjects and each compound, expressed in log values as the mean of all five left thresholds minus the mean of all five right thresholds. Thus, a difference value of 0 indicates symmetrical sensitivity; a negative value indicates a lower threshold on the left; a positive value indicates a lower threshold on the right. With regard to lateral asymmetries in taste sensitivity, several possibilities are of interest. We first used a paired Student's *t*-test, with a correction for multiple comparisons, to determine whether any of our subjects had a lateral advantage in taste sensitivity across all compounds. Twelve such tests were performed (a separate test for each subject) on 20 paired observations of left versus right sensitivity (i.e. five paired threshold measurements for four compounds). Out of all subjects, one (no. 6, a left-handed subject) had a very small but significant difference in lateral taste sensitivity, on the right side (L – R = 0.22 log units, $P < 0.002$; see Table 2). We also tested for lateral asymmetries in sensitivity to only a single taste compound. No significant differences in thresholds for a single compound were detectable for any subject [$P > 0.001$ for all 48 cases tested; this significance threshold comes from the corrected *P* value of 0.05/(4 compounds × 12 subjects)]. However, any such putative differences would have to be relatively large; greater than an order of magnitude to be detected (see Discussion). In order to increase our statistical power for detecting potential compound-specific asymmetries we pooled threshold values for classes of related compounds. This analysis involved 24 separate comparisons of 10 paired left versus right threshold measurements. [Bonferroni corrected significance level = 0.0021, calculated from 0.05/(2 compound classes × 12 subjects).] Because NaCl and CA taste perception is believed to be mediated by the direct passage of Na^+ and H^+ ions through cation channels into taste receptor cells, whereas SAC and QHCl primarily bind as ligands

Table 1 Test–retest reliability for each compound by side of the tongue

Compound	Left					Right				
	1	2	3	4	5	1	2	3	4	5
(A) Saccharin										
1		0.212	0.483	0.422	0.335		0.110	0.080	0.544	0.393
2			0.260	0.353	0.482			0.627	0.707	0.227
3				0.179	0.688				0.512	0.604
4					0.650					0.494
5										
	Mean = 0.406					Mean = 0.430				
NaCl										
1		0.618	0.542	0.458	0.522		0.800	0.061	0.365	0.598
2			0.732	0.429	0.433			–0.017	0.323	0.420
3				0.720	0.372				0.589	0.269
4					0.346					0.428
5										
	Mean = 0.517					Mean = 0.384				
Citric acid										
1		0.886	0.133	0.168	0.439		0.759	–0.230	0.597	0.601
2			0.342	0.083	0.388			–0.281	0.154	0.298
3				0.077	–0.117				0.145	0.073
4					0.640					0.646
5										
	Mean = 0.304					Mean = 0.276				
Quinine HCl										
1		0.858	0.892	0.682	0.856		0.594	0.787	0.654	0.822
2			0.932	0.273	0.513			0.913	0.943	0.660
3				0.321	0.645				0.888	0.698
4					0.802					0.665
5										
	Mean = 0.677					Mean = 0.762				
(B) Saccharin										
1		–0.626	–0.148	–0.115	–0.602		–0.352	–0.566	0.215	–0.213
2			–0.154	–0.068	0.151			0.350	0.461	–0.720
3				–0.384	0.459				–0.076	–0.044
4					0.331					–0.433
5										
	Mean = –0.116					Mean = –0.138				
NaCl										
1		–0.276	–0.495	–0.346	–0.259		0.573	–0.563	–0.513	–0.152
2			0.168	–0.326	–0.376			–0.405	–0.327	–0.342
3				0.366	–0.343				+0.309	–0.429
4					–0.263					–0.370
5										
	Mean = –0.215					Mean = –0.222				
Citric acid										
1		0.572	–0.589	–0.483	–0.071		0.119	–0.618	–0.289	–0.209
2			–0.140	–0.627	–0.214			–0.303	–0.653	–0.556
3				–0.110	–0.521				–0.044	–0.204
4					0.503					0.507
5										
	Mean = –0.168					Mean = –0.225				
Quinine HCl										
1		–0.540	–0.255	–0.021	0.522		0.278	0.003	–0.142	–0.567
2			0.477	–0.198	–0.542			0.129	0.450	–0.497
3				–0.444	–0.606				0.054	–0.392
4					0.387					–0.283
5										
	Mean = –0.122					Mean = –0.097				

Each term in the correlation matrices is the correlation coefficient calculated by simple linear regression for each pair of testing sessions. Results in part A are from calculations based on the raw log values of the threshold movements. Part B contains the results of similarly constructed correlation matrices, computed after transforming the data to remove inter-subject variability (see Materials and methods).

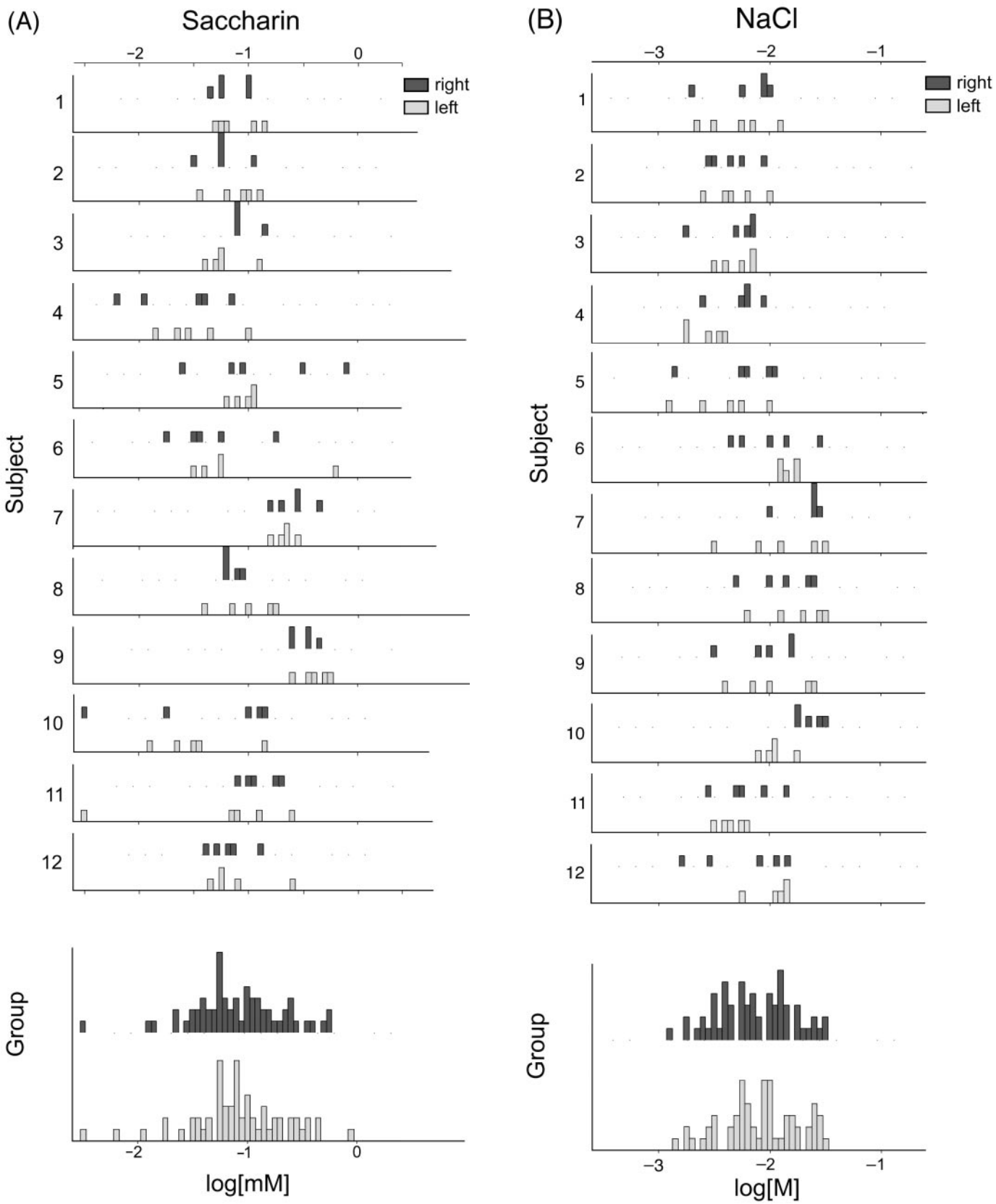

Figure 1 (**A**–**D**) Histograms displaying thresholds in log units for both individual subjects and the total population (bin size 0.05 log steps). Dark bars are threshold values for the right side of the tongue, light bars for the left. In each figure the abscissa spans 3 log steps and is centered around the population mean. Population means: SAC 0.0791 mM; NaCl 0.00737 M; CA 1.75 mM; QHCl 0.120 mM.

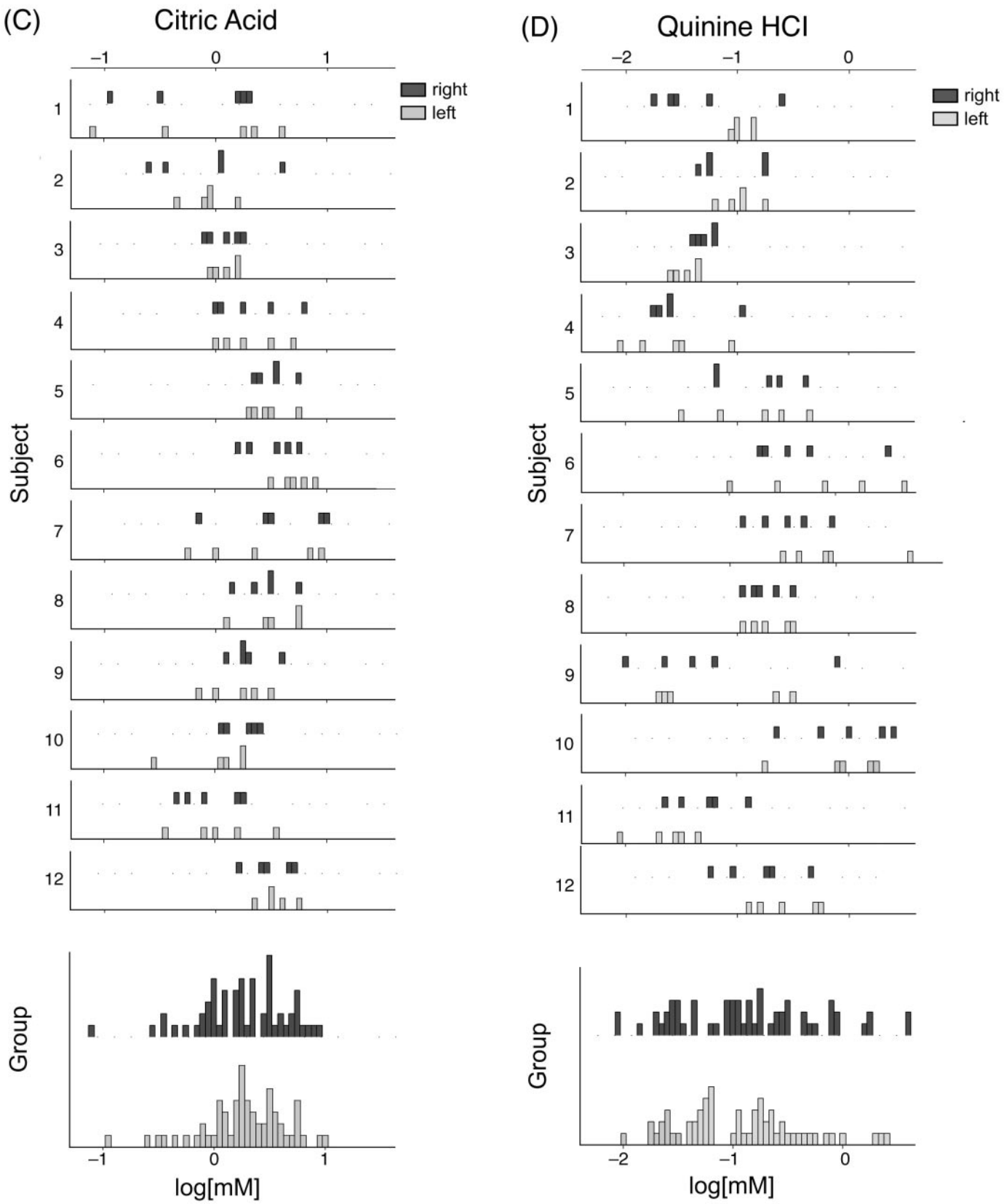

Figure 1 (continued)

Table 2 Mean left–right threshold differences for individual subjects by compound, expressed as log values ± SEM

Subject	Saccharin	NaCl	Citric acid	Quinine HCl
1	0.052 ± 0.112	–0.092 ± 0.136	0.080 ± 0.192	0.384 ± 0.166
2	0.116 ± 0.092	0.022 ± 0.111	–0.010 ± 0.133	0.100 ± 0.194
3	**–0.162 ± 0.042**[a]	0.016 ± 0.065	0.010 ± 0.060	**–0.176 ± 0.058**[a]
4	0.142 ± 0.083	–0.308 ± 0.132	–0.008 ± 0.029	–0.088 ± 0.127
5	–0.150 ± 0.244	–0.160 ± 0.072	–0.058 ± 0.111	0.046 ± 0.281
6	**0.200 ± 0.101**[b]	**0.166 ± 0.118**[b]	**0.218 ± 0.048**[b]	**0.292 ± 0.208**[b]
7	–0.078 ± 0.062	–0.250 ± 0.171	–0.168 ± 0.142	0.500 ± 0.214
8	0.126 ± 0.097	0.106 ± 0.166	0.042 ± 0.085	0.026 ± 0.140
9	0.086 ± 0.072	0.088 ± 0.104	–0.106 ± 0.120	0.050 ± 0.213
10	–0.076 ± 0.252	**–0.310 ± 0.072**[c]	**–0.232 ± 0.105**[c]	–0.050 ± 0.147
11	–0.360 ± 0.308	–0.136 ± 0.080	0.108 ± 0.127	–0.340 ± 0.093
12	0.034 ± 0.150	0.230 ± 0.170	–0.002 ± 0.058	0.190 ± 0.222

A difference value of 0 indicates symmetrical sensitivity, a negative value indicates a lower threshold on the left and a positive value indicates a lower threshold on the right. Bold laterality values are significantly different from 0, as determined by one of three *t*-test comparisons: [a]pooled SAC and QHCl sensitivity; [b]pooled sensitivity to all four compounds; [c]pooled NaCl and CA sensitivity.

to metabotropic receptors (Lindemann, 1996), we reasoned that sensitivity to these two classes of compounds might be expected to co-vary. This expectation is further supported by the fact that sensitivity to SAC is correlated with sensitivity to several bitter tasting compounds (Bartoshuk, 1979).

We tested whether SAC and QHCl thresholds co-vary in the present data set by ranking the subjects' sensitivity to both compounds. The ranking was determined on the basis of pooled left- and right-side thresholds ($n = 10$) for both compounds. A linear regression line fitted non-parametrically to the subjects' threshold ranks revealed a significant correlation between SAC and QHCl sensitivity ($r = 0.58$, $P < 0.05$), thus confirming Bartoshuk's observation (Bartoshuk, 1979). The same trend was not evident between NaCl and CA sensitivity ($r = 0$, $P = 1$), however, in contrast to what might be expected if lateral asymmetry of both NaCl and CA thresholds co-occur (as the data of subject no. 10 in the present study suggests).

Comparisons using the *t*-test of left and right thresholds revealed one subject (no. 3, right-handed) with a lower left threshold for SAC and QHCl (L – R = –0.17, $P < 0.001$), but no difference for NaCl and CA (see Figure 1). A second subject (no. 10, left-handed) had a left-side advantage for only the NaCl and CA class (L – R = –0.27, $P < 0.002$) (see Figure 1). As a control comparison, we repeated the same tests for 'nonsensical' groupings of compounds (i.e. SAC and NaCl, QHCl and CA, SAC and CA, QHCl and NaCl.). None of these groupings revealed any significant differences.

Finally, we tested whether handedness influences lateral taste sensitivity. We calculated a laterality value for all 240 pairs of sensitivity. (Laterality = left threshold – right threshold. A negative laterality value indicates a lower left-side threshold.) Laterality values from the six left-handed and six right-handed subjects were pooled separately into two groups of 120 laterality values. A comparison of left and right thresholds, pooled across compounds and all subjects with the same manual preference, revealed no significant difference (paired *t*-test, $P = 0.68$).

Discussion

Our principal finding is that taste sensitivity for most subjects is equivalent on the left and right sides of the tongue for four compounds that represent different taste qualities. Although left–right lateral taste detection thresholds obtained in a single session could differ by more than an order of magnitude, analysis based on repeated measurements reveals that symmetry is the general rule in taste sensitivity. A recent study reporting equivalent sensitivity in the left and right nostrils based on repeated threshold measurements (Shimomura and Motokizawa, 1995) suggests that taste and olfaction are similar in this respect. Thus, lateral symmetry in the chemical senses appears to be in contrast to the somatosensory system, in which small but persistent lateral advantages have been observed (Weinstein, 1968). Similarly, we did not observe lateral asymmetry as a function of handedness, which has been reported for touch. In addition to the general finding of lateral equivalence, we observed noteworthy exceptions to this rule. Using multiple threshold measurements for four different compounds, we found that three of our 12 subjects (nos 3, 6 and 10) had asymmetrical taste sensitivities on the anterior tongue which were statistically significant after Bonferroni correction for multiple comparisons. In one case the asymmetry was obtained across all compounds (no. 6), while in the other two cases the lateral differences were specific to a transductive category (no. 3 metabotropic, no. 10 ionotropic). We did not find any asymmetries that were specific to only a single compound. However, an analysis of statistical power revealed that, after accounting for multiple comparisons

(48 tests in all), we could only expect to detect a difference as large as an order of magnitude ($\beta = 0.1$). Analysis of compounds classified as a function of transductive category allowed us to detect lateral asymmetries of the order of 0.2 log steps. Our results suggest that cases of asymmetrical taste sensitivity on the tongue, although in the minority, are not particularly uncommon. This finding is consistent with a previous study, which reported one subject (out of 10) with a strong lateral advantage for sucrose but equivalent sensitivity for NaCl (Kroeze, 1979).

The threshold measurements reported in this study are comparable to values we recently reported using a similar stimulation protocol (Shikata *et al.*, 2000). The fact that they are higher than previously reported whole mouth thresholds (Pfaffmann *et al.*, 1971; Bartoshuk *et al.*, 1986; Stevens, 1995) presumably reflects the extent to which spatial summation can render a taste stimulus more detectable (McBurney, 1969; personal observation).

The higher correlation values on the untransformed data sets (Table 1A) associated with the QHCl thresholds are probably due to the broader distribution of quinine sensitivities compared with the other taste compounds. This interpretation is borne out by the fact that, after transforming the data set to remove all inter-subject variability, the correlation coefficients were lower for every matrix and the correlation values for QHCl were no longer higher than for the other compounds (Table 1B).

These results are comparable to test–retest reliability values reported in previous studies, in which repeated measurements were made for whole mouth taste thresholds [e.g. (Stevens *et al.*, 1995)]. This analysis does not indicate whether the high variability across sessions is due to changes in the subject's taste sensitivity from one day to the next or whether this variability simply reflects the limits of our ability to measure thresholds accurately in a single session. However, the relatively low test–retest reliability does clearly reaffirm that multiple measurements are necessary for drawing inferences about individual subjects (Stevens *et al.*, 1995).

Our decision to pool SAC and QHCl and NaCl and CA thresholds into separate groups was based on both physiological and psychophysical evidence that these two groups primarily utilize distinct types of transduction mechanisms. At the molecular level, both SAC and QHCl are believed to elicit taste sensations predominantly by binding to G protein-coupled receptors (Bernhardt *et al.*, 1996; Wong *et al.*, 1996; Adler *et al.*, 2000; Chandeshekar *et al.*, 2000), whereas NaCl and CA are thought to depolarize taste receptor cells by acting directly on ion channels (Kinnamon and Margolskee, 1996). At the behavioral level, these relationships among transduction mechanisms may account for the tendency for SAC and bitter compound sensitivities to co-vary (Bartoshuk, 1979). We confirmed the correlation between SAC and QHCl sensitivity in the present data set. However, NaCl and CA thresholds were not found to co-vary across subjects, as might be expected if similar transduction mechanisms implies similar psychophysical profiles. One possible explanation for this discrepancy is that the variance in both SAC and QHCl sensitivity is much greater across subjects than sensitivity to NaCl and CA, thus making the correlation between SAC and QHCl easier to detect. Alternatively, the statistically significant difference that we observed in the sensitivity of subject no. 10 to ionotropically mediated tastes might be a Type I error, in spite of the unlikelihood of such an error at the corrected significance level ($\alpha = 0.0021$ in this case).

A critical issue in the chemoreceptive field is how sensory input from multiple modalities (including taste, touch, thermal and olfactory sensations) is integrated to produce a subjectively coherent percept. SA, NaCl, CA and QHCl at the concentrations used in this paper evoke taste qualia in most subjects and detection of these compounds is usually believed to be mediated exclusively by the taste system. Moreover, these compounds are not lateralizable on oral surfaces that are bare of taste buds but rich in somatosensory receptors, even at very high concentrations (Shikata *et al.*, 2000). However, these observations do not exclude the possibility that the somatosensory system might contribute to detection of these presumed taste stimuli. Electrophysiological recordings from both nerve fibers and cultured ganglion cells indicate that some receptors in the trigeminal system are sensitive to non-irritating chemical stimuli, including QHCl and CA at relatively low concentrations (Liu and Simon, 1998; Pittman and Contreras, 1998). Assuming that the trigeminal nerve does not mediate taste perception directly, these results raise the question of whether the somatosensory system also participates in the coding of sensations that are customarily attributed to the taste system. A promising approach to this question would be to evaluate taste thresholds in subjects in whom taste perception has been eliminated, either by anesthesia or infection entirely restricted to the chorda tympani nerve (cf. Yanagisawa *et al.*, 1998).

The overall trend of our findings bears out the clinical expectation that taste sensitivity is comparable on both sides of the tongue. Our findings are also pertinent to methodological issues in taste research that employs spatially separated stimuli. Several experimental procedures subject the tongue to asymmetrical treatments to study the effect of taste perception under conditions of spatial separation [see, for example (Kroeze and Bartoshuk, 1985; Dessirier *et al.*, 1997, 1999; Shikata *et al.*, 2000)]. It is also common to subject the two sides of the tongue to separate experimental and control conditions [see, for example (Dessirier *et al.*, 1997)]. Our findings support the viability of this methodology in principle. However, it is apparently relatively common to observe differences in lateral sensitivity of the order of 0.15–0.25 log steps. Given this possibility, it seems advisable to counterbalance asymmetrical treatments

of the tongue with an equal number of opposite lingual observations.

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