Adaptation and cross-adaptation of the four gustatory qualities[1]

HERBERT L. MEISELMAN[2]
UNIVERSITY OF MASSACHUSETTS

On the basis of magnitude estimations of solutions of NaCl, quinine sulfate, sucrose, and HCl, a seven-step series of each compound was chosen. The concentration of each compound in the same ordinal position of the series was of approximately the same sensory magnitude. The middle concentration of each series was presented as an adapting stimulus, and the entire series was used to test the effects of 2 min of adaptation on magnitude estimations and quality reports. Both NaCl and sucrose adaptation markedly lowered magnitude estimations of test stimuli of the same compounds for concentrations lower than that of the adapting stimulus, but had little effect on higher concentrations. Cross-adaptation generally enhanced the magnitude estimations over those obtained in initial estimations. Neither adaptation nor cross-adaptation procedures produced quality changes.

Receptor mechanisms in gustation have been investigated with the technique of cross-adaptation, with which one seeks to determine whether or not prolonged stimulation with one compound, and the resulting sensory decrement, depresses responsiveness to other test compounds. If decreased responsiveness to another compound is observed, then it is assumed that the adapting stimulus and the test stimulus share common loci of stimulation on the gustatory receptors.

Currently, two opposing views suggest models for gustatory quality coding. The spectrum theory, or neural pattern theory, postulates that it is the pattern of firing rather than which fibers are firing that is important (Pfaffman, 1964; Erickson, 1967). In many cases, some of the same fibers respond to stimuli which are often considered to be perceptually quite different. The classic view of gustatory specificity postulates that separate receptors and fiber tracts mediate activities that covary with the four taste qualities (Bekésy, 1964, 1966). These two models of gustatory quality coding would predict different results from an attempt to demonstrate cross-adaptation between stimuli supposed to represent the four gustatory qualities. The specificity model would be supported by finding no cross-adaptation, i.e., receptors and nerves for each quality are separate and, hence, adaptation of any one should not affect the responsiveness of the others. On the other hand, the neural patterning view would predict some sensory decrement because of the common fibers involved. Prolonged stimulation with some compounds would be expected to adapt receptors and fibers that normally signal other compounds.

Cross-adaptation procedures with stimuli representing the four taste qualities have generally resulted in a reduction of thresholds from those determined without an adaptation procedure (Mayer, 1927; Dallenbach & Dallenbach, 1943). However, threshold data and suprathreshold sensory magnitude data are apparently not equally affected by adaptation for salts (McBurney & Lucas, 1966). Furthermore, equating sensory magnitude appears to be a necessary condition for obtaining cross-adaptation at least for salts, both in human psychophysical experiments (McBurney & Lucas, 1966), and in electrophysiological recording of summated neural activity in the nucleus of the fasciculus solitarius of the rat (Halpern, 1967).

A series of experiments on NaCl adaptation have investigated changes in quality and sensory magnitude. McBurney (1966) obtained magnitude estimation functions of NaCl solutions following adaptation to NaCl, and found a minimum magnitude estimation at the adaptation concentration, and an increase at both higher and lower concentrations of the NaCl test solutions. The lower concentrations were reported to have a sour-bitter quality, confirming the earlier report of Bartoshuk, McBurney, and Pfaffmann (1964). Bartoshuk (1968) obtained similar magnitude estimation functions and changes in quality reports for adaptation of NaCl, quinine hydrochloride (QHCl), HCl, and sucrose. The low concentrations of NaCl were reported to taste bitter, QHCl sweet, HCl mixed, and sucrose bitter. The present experiment was designed to extend the findings with NaCl adaptation to suprathreshold concentrations, and to compare these findings with adaptation to other stimuli and cross-adaptation among the stimuli.

METHOD

Subjects

Ss were four nonsmoking female students at the University of Massachusetts. Their ages ranged from 17 to 22. These four were chosen from a larger group on the basis of their performance in a gustatory screening task previously described by Meiselman and Dzendolet (1967). None of the Ss had previous experience with gustatory adaptation or with magnitude estimation, although two of the Ss had participated in an experiment on quality changes with concentration (Dzendolet & Meiselman, 1967). Ss were paid for their participation in the experiment.

Stimuli

All solutions were made with distilled water and reagent grade chemicals except for commerical grade sucrose. The adapting stimuli were the solutions of middle concentration in a seven-step series of each of the compounds HCl, NaCl, quinine sulfate (QSO_4), and sucrose. That is, the adapting concentration was the fourth member of a series of seven solutions placed at equal intervals along the dimension of log molar concentration.

In order to equate the solutions at each position in the series in terms of sensation magnitude, each solution was judged in relation to a standard solution of 0.36 M NaCl which was called Magnitude 10. Solutions of NaCl, QSO_4, sucrose, and HCl (Table 1) were presented on separate days for magnitude estimation using the NaCl standard. All stimulus concentrations lie above the recognition thresholds of salt, bitter, sweet, and sour, respectively, for these compounds (Pfaffmann, 1959). Solutions were maintained in a water bath at 35 deg C.

Procedure

To obtain initial magnitude estimation functions, each of the seven test solutions was presented on each of two days for

Table 1
Stimuli for Initial Magnitude Estimations

	Compound			
Concentration	NaCl	QSO_4	Sucrose	HCl
1	180 nM	0.032 nM	25 nM	2.00 nM
2	225	0.052	50	2.85
3	285	0.082	100	4.00
4	360	0.130	200	5.70
5	455	0.210	400	8.10
6	570	0.330	800	11.50
7	720	0.530	1600	16.50

estimation using the NaCl standard. The order of the 21 presentations was randomized, with the restriction that the same solution was not presented more than three times consecutively. The standard was presented three times during each 50-min session, at the beginning, after the first seven solutions, and after the first 14 solutions. Testing followed this procedure: S was asked to pour into her mouth 10 ml of solution from a beaker, hold the solution in her mouth for 3 sec, expectorate it into the sink in front of her, and then report the magnitude of that solution in relation to the standard. No rinses were used. Two minutes elapsed between successive presentations, and 3 min followed presentation of the standard. The order of testing the compounds was the same for all Ss: sucrose, QSO_4, HCl, NaCl, sucrose, QSO_4, HCl, NaCl.

The magnitude estimation functions which resulted from this procedure were used to construct four series of solutions in which the solutions at each ordinal position in each series were of the same sensation magnitude. The original concentrations of NaCl and HCl were maintained as above, but the concentrations of the sucrose and QSO_4 series were changed so that the lowest position was called Magnitude 3, the middle 10, and the highest 20. The new concentrations for the sucrose series were 88, 140, 220, 350, 560, 880, and 1400 mM. For QSO_4 they were 0.037, 0.059, 0.094, 0.155, 0.237, 0.375, and 0.600 mM.

During the main body of the experiment each compound was used for the adapting solution and test compound series. S was given a beaker containing 50 ml of adapting solution and asked to pour into her mouth an amount which comfortably filled it. Generally, about 20 ml was taken. She was instructed to move her tongue during the adaptation procedure to insure that the solution penetrated into all the tongue folds. After 1 min, she expectorated and immediately took more of the adapting solution. Replacement of the adapting solution was used to avoid excessive salivary dilution of the stimulus. At the end of the second minute, S expectorated the adapting solution and immediately poured 10 ml of test solution into her mouth. After 5 sec, she expectorated the test solution, and then first gave a quality report, followed by the magnitude estimation. Forty-five seconds after expectorating the test solution, the next 2-min adaptation began. In this way, each test stimulus of a particular compound was tested twice during each of two sessions. Within each session, the order of the 14 test stimuli was randomized. All combinations of adaptation and test compound were completed before the entire series of sessions was replicated. The order of the combinations of adapting and test stimuli was approximately the same for all Ss.

RESULTS

The mean initial magnitude estimations are presented in Fig. 1 on log-log coordinates in order to estimate their closeness to power functions. Although the concentration values differ for each function, the four functions have been superimposed on the same abscissa in Fig. 1 for easier comparison. Calculation of the exponents of the best-fitting straight lines with the method of least squares (Edwards, 1962) yielded 1.43 for NaCl, 0.98 for QSO_4, 0.70 for sucrose, and 0.87 for HCl.

Two occurrences prevented the gathering of all the data for the main part of the experiment. HCl adaptation was discontinued as an adapting condition because three Ss reported that repeated 2-min adaptations with 57 mM HCl resulted in a painful irritation of the mouth, especially the upper palate, which lasted for periods up to one week. Secondly, S D.M. completed two replications of each combination of adapting and test stimulus, instead of the four replications completed by the other three Ss.

In four instances Ss labeled a solution with a quality name usually associated with another of the compounds. These all occurred at the lowest concentration of the test compound, and in cases in which the adapting and test compounds were the same. A sweet report was elicited when 0.36 M NaCl was the adaptation stimulus and when 0.18 M NaCl was the test stimulus, and when 0.1550 mM QSO_4 was the adaptation stimulus and 0.0375 mM QSO_4 the test stimulus. With 350 mM sucrose as the adaptation stimulus and 88 mM sucrose as the test stimulus there were reports

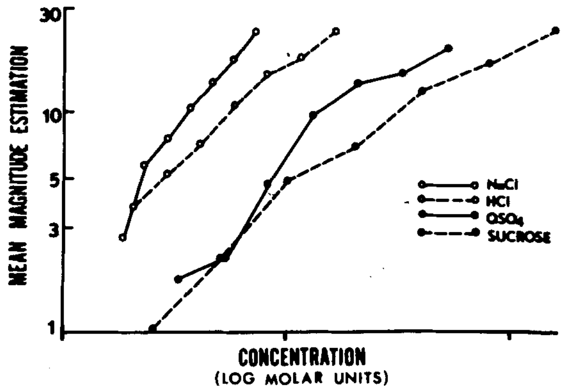

Fig. 1. Log mean initial magnitude estimation as a function of log concentration. Each point represents the mean of six presentations to each of four Ss. The four functions are superimposed on one abscissa for ease of comparison; the abscissa for each stimulus compound is different.

of bitter twice for one S. The magnitude estimations of the four quality changes were not included in the data submitted to statistical tests. Hence, all figures present both magnitude estimation data and quality data, since the quality is always that usually associated with the compound.

Two analyses of variance were performed on the magnitude estimations resulting from the adaptation and cross-adaptation procedures. First, a five-factor repeated measurements analysis of variance excluded the data of S D.M. so that the effects of procedural variables could be investigated. Because of the small size of the effects of the procedural variables and because the mechanisms underlying them are unclear, they will not be treated in this paper. The interested reader is referred to a previous report (Meiselman, 1968a). Second, a three-factor analysis was run on the means of each combination of adapting and test stimulus for each S. With one exception, all sources of variance that were significant in the five-factor analysis of variance, and were present in the three-factor analysis, were found to be significant there also. No additional significant cources of variance were found in the three-factor analysis. In the five-factor analysis, the sensory magnitudes of sucrose and HCl increased more rapidly over the range of concentrations of test stimuli than did NaCl and QSO_4. In other words, the plots of sensory magnitude as a function of concentration were of steeper slope for sucrose and HCl than they were for QSO_4 and sucrose. The K by C interaction was not found to be significant in the three-factor analysis and will be ignored in the discussion of results.

A three-factor repeated measurements analysis of variance (Myers, 1966) assessed the effects of the following variables on the mean magnitude estimations given by each of the four Ss: test compound (K), adapting compound (A), and concentration of test compound (C). Ss tended to assign higher numbers to test solutions of HCl (16.51) than to test solutions of NaCl (13.17), QSO_4 (12.42), or sucrose (12.05). The tendency for increasing

Table 2
Three-Factor Analysis of Variance

Source	df/df	F	p
Test compound (K)	3/9	4.780	.05
HCl vs QSO_4, NaCl, sucrose	1/9	13.596	.01
Test compound concentration (C)	6/18	36.036	.001
C_3 vs C_4	1/18	4.441	.05
C_4 vs C_5	1/18	5.703	.05
C_6 vs C_7	1/18	6.048	.05
Adapting compound (A)	2/6	15.288	.005
NaCl vs QSO_4, sucrose	1/6	35.438	.005
K x A	6/18	8.435	.001
K x C x A	36/108	2.090	.005

magnitude estimations with increasing concentration of the test stimulus was demonstrated by the highly significant effect of C. Arithmetic means of the levels of C were as follows, beginning with C_1: 5.01, 6.73, 9.16, 12.72, 16.75, 20.12, 24.28. Adaptation with NaCl produced significantly smaller mean magnitude estimations (10.76) than adaptation with either QSO_4 (14.47) or sucrose (15.38).

The K by A interaction and the K by C by A interaction were both significant. Adapting solutions of NaCl and sucrose depressed the sensory magnitudes of the test stimuli of the same compounds below the level of the adapting stimulus. QSO_4 test stimuli were equally affected by both NaCl and QSO_4 adaptation. Since HCl was never used as an adapting solution, its effects could not be assessed. The K by C by A interaction is presented in Fig. 2 as four groups of functions, with each group representing the effects of adaptation and cross-adaptation on a particular compound. Since the seven-step series of concentrations for each compound is represented along the abscissa, the abscissae of the four groups of functions are different.

The exponents of the best-fitting straight lines of Fig. 2 were calculated with the method of least squares (Table 3). In all cases, exponents calculated for the concentrations below the adapting concentration (C_1, C_2, C_3) were higher than those calculated for the higher concentrations (C_5, C_6, C_7). There was a reduction in the size of the exponents from the initial magnitude estimations to those obtained with the cross-adaptation and adaptation procedures, except for the whole-function exponents representing NaCl adaptation and sucrose adaptation, both of which were markedly increased.

DISCUSSION

The adaptation and cross-adaptation procedures failed to produce any systematic changes in the quality of test stimuli. Bartoshuk et al (1964), McBurney (1966), and Bartoshuk (1968) all reported that test stimuli below the level of the adapting concentration were of a quality other than that usually associated with the compound, and that this subadapting quality increased in intensity as one moved to lower test stimulus concentrations.

Several points of difference between the studies deserve comment. The adaptation procedure used in the present study has been demonstrated by Meiselman (1968b) to produce only partial adaptation. The initial sensory magnitudes of NaCl and of sucrose dropped by about 60% during 2-min adaptations and by about 40% for QSO_4 in that study. McBurney (1966) noted that his dorsal tongue flow system did not produce complete adaptation, i.e., disappearance of the sensation, and Bartoshuk (1968) found that some Ss did not completely adapt to HCl and QHCl in the 40 sec allotted, but that complete adaptation was not a necessary condition for elicitation of subadapting qualities. It is doubtful, therefore, that the different results of the prior studies and those of the present experiment are due primarily to different degrees of adaptation.

The earlier studies did not report any attempt to screen their Ss for gustatory quality responsiveness. Meiselman and Dzendolet (1967) found that many college students performed poorly in a quality-naming task even when given the correct answers through a correction procedure. Bartoshuk (1968) has suggested that some of her Ss were confusing sour and bitter, a phenomenon mentioned by Meiselman and Dzendolet (1967) as being especially

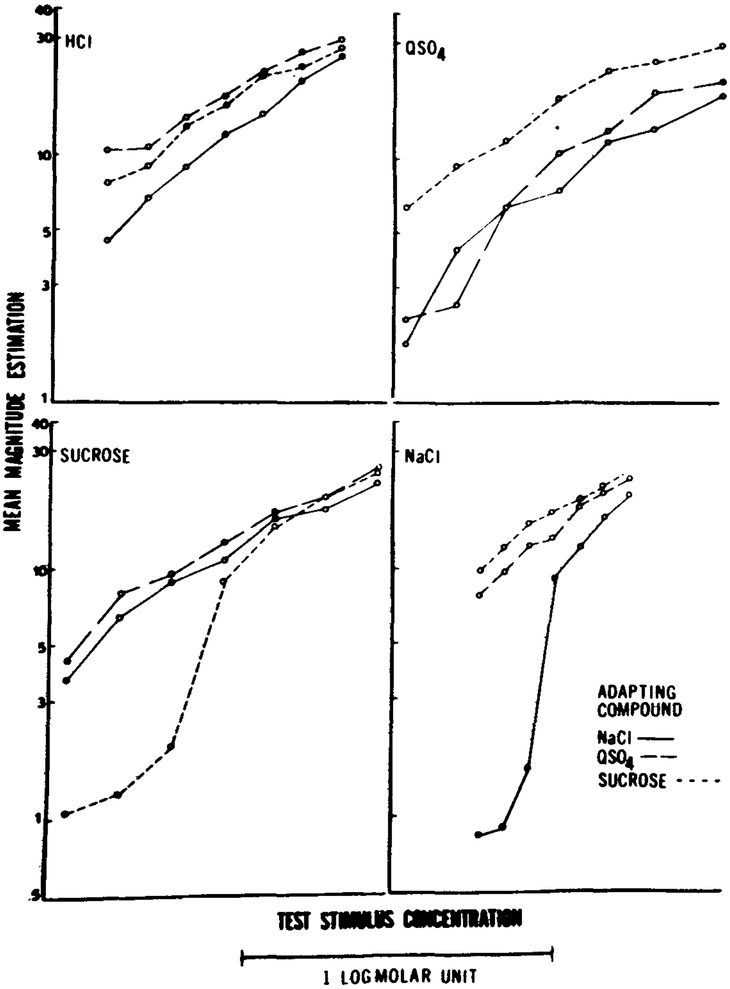

Fig. 2. Log mean magnitude estimation as a function of log concentration of test stimuli after adaptation with NaCl, QSO_4, or sucrose. Note that the abscissa for each compound, i.e., for each grouping of these functions, is different.

Table 3
Exponents of the Best-Fitting Straight Lines of the K x C x A Interaction

Test Compound	Concentration Range	Adapting Compound			Initial Estimations
		NaCl	QSO⁴	Sucrose	
NaCl	low	1.35	0.97	1.07	2.26
	high	1.10	0.57	0.68	1.22
	total	2.87	0.84	0.67	1.43
QSO_4	low	1.53	1.16	0.68	1.91
	high	0.48	0.50	0.25	0.43
	total	0.80	0.89	0.56	0.98
Sucrose	low	0.97	0.86	0.66	1.10
	high	0.36	0.44	0.55	0.48
	total	0.62	0.59	1.31	0.70
HCl	low	1.00	0.46	0.78	0.97
	high	0.67	0.38	0.33	0.65
	total	0.77	0.52	0.60	0.87

Note: Separate exponents were calculated for each function of the K x C x A interaction (Fig. 2) at low concentration (C_1, C_2, C_3), at high concentration (C_5, C_6, C_7), and for all concentrations (C_1, . . . , C_7). The analogous exponents for the initial magnitude estimation functions (Fig. 1) are presented for comparison.

common. A screening test would probably have eliminated those Ss. The sour-bitter confusion might also be responsible for the tendency of Ss in earlier studies to report the quality of subadapted NaCl as sour-bitter rather than sour or bitter.

Last, and perhaps most important, in comparing the present results with the prior studies is the range of concentrations involved. The highest concentration of NaCl which showed a sour and/or bitter taste after adaptation was 0.03 M in the earlier studies. This is considered to be the recognition threshold for saltiness in NaCl, and the concentration at which solutions of NaCl change in quality from salty to sweet as one decreases concentration (Pfaffmann, 1959). It is assumed that salty and sweet responses to NaCl would show frequency distributions of the form described by Dzendolet and Meiselman (1967) for other simple salts. Thus, the presence of a quality change at about 0.03 M NaCl is not necessarily related to the adaptation procedure. The interesting point is that the quality change reported for NaCl by Bartoshuk et al and by McBurney was from salty to sour-bitter. Perhaps the sour-bitterness reported in earlier studies is dependent on the quality change from salty to sweet already existing in responses to NaCl solutions. This suggestion is supported by Bartoshuk's findings of predominantly bitter subadapting tastes for both NaCl and sucrose. Similar mechanisms might account for other subadapting tastes.

The assignment of higher average magnitude estimations to HCl was due to the fact that HCl adaptation was not used, thus elevating the average estimation given to HCl test stimuli. Sucrose adaptation appears to have affected only sucrose test stimuli, while NaCl adaptation produced lower estimations than adaptation with either sucrose or QSO_4 for test stimuli of QSO_4, HCl, and NaCl itself. It is unclear whether this finding is related to the fact that NaCl was used as the standard, or whether NaCl adaptation masked the other solutions. Clearly, however, the comparison should be made between NaCl and sucrose adaptation, both of which had strong effects.

Adapting solutions of NaCl and sucrose depressed the sensory magnitudes of test stimuli of the same compounds below the level of the adapting stimulus. Magnitude estimations of the lower concentrations of QSO_4 were not reduced in sensory magnitude by the QSO_4 adaptation procedure, although it should be noted that the QSO_4 test series used in the adaptation procedure was not the same one used in the initial testing. The exponent of the power function fitted to the initial estimations is 0.98, whereas the exponent fitted to the QSO_4-adapted test stimuli is 0.89.

Magnitude estimations of QSO_4 adaptation obtained from the same Ss and reported earlier by Meiselman (1968b) indicated that with 45-sec intervals between adaptations, less adaptation was shown to QSO_4 than to either NaCl or sucrose. Apparently, QSO_4 adaptation did not take place to the degree that it exerted a noticeable affect on the test stimulus. Both Mayer (1927), and Dallenbach and Dallenbach (1937) found changes in thresholds of other compounds after QHCl adaptation. However, the recent demonstration of cross-adaptation of salts by McBurney and Lucas (1966) led them to conclude that thresholds and magnitude estimations were not equally affected by adaptation. It is suggested that the present experiment be repeated with other bitter compounds and with another method of stimulus presentation to attempt to produce more complete bitter adaptation.

Thus, the cross-adaptation procedure did not produce decreases in the sensory magnitude of the test stimuli. This is interpreted as providing support for the classic view of gustatory quality coding through specific, separate receptors. However, such a conclusion is sharply limited by the lack of evidence for HCl adaptation and QSO_4 adaptation in the present experiment. It is suggested that cross-adaptation experimentation be attempted with other stimuli for sour and bitter.

The exponents of straight lines fitted to each end of the adaptation functions were reasonably close to the exponents obtained from the initial magnitude estimations of the entire functions, and to exponents of cases of attempted cross-adaptation. Exponents fitted to the entire adaptation function for NaCl and sucrose were markedly increased. For example, the exponent of the initial magnitude estimation function of sucrose was 0.70. The exponents of the high and low concentrations of the adaptation functions were 0.66 and 0.55, respectively, while the exponent for the overall adaptation function was 1.31. Adaptation with NaCl (0.62), or with QSO_4 (0.59) produced little change in the overall exponent for the sucrose function. Thus, each end of the adaptation function approximates the form of the entire psychophysical function for a compound. The adaptation procedure apparently shifts the function of the lower concentrations (C_1, C_2, C_3) down the scale of sensory magnitude without changing the form of the function. Thus, the effect of adaptation was apparently greatest near the adapting concentration as suggested by McBurney (1966).

The cross-adaptation procedure appears to have produced a rather marked enhancement effect. This is observed in Figs. 1 and 2. The test stimuli were chosen so that each solution of lowest concentration would have a magnitude estimation of approximately 3, each adapting concentration approximately 10, and each highest concentration approximately 20. It is clear in Fig. 2 that, with the exception of the adaptation functions, the functions generally begin at a level much higher than an estimation of 3, are higher than 10 at the middle concentration, and rise to as much as 30. Furthermore, the exponents of the best-fitting straight lines of these functions show that generally the exponents are slightly smaller than those found for the same compounds in the initial magnitude estimations. In other words, the sensory magnitude has not only been elevated by the cross-adaptation procedure, but the increase in sensory magnitude with concentration has been altered. The general enhancement in sensory magnitude observed in the present study is in agreement with the decreased thresholds observed by Mayer (1927) for most cases of cross-adaptation among stimuli representing the four taste qualities. Either of two different mechanisms could account for this enhancement effect: (1) Possibly the cross-adaptation procedure actually affects receptors other than those specifically activated by the adapting compound, but rather than decreasing their responsiveness, the effect is one of increased sensitivity. (2) The enhancement could result from an attentional variable. The estimated strength of a solution might have been raised; by its contrast to a different adapting compound. When viewed by itself, as in the initial estimations, it did not seem as intense as when contrasted with a different compound.

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NOTES

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2. Present address: Department of Psychology, and Section on Neurobiology and Behavior, Cornell University, Liddell Laboratory, Ithaca, New York.

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