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Chemical stimulation of single human fungiform taste papillae.

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CHEMICAL STIMULATION OF SINGLE HUMAN FUNGIFORM TASTE PAPILLAE

A Dissertation Presented

By

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ABSTRACT

Chemical Stimulation of Single Human
Fungiform Taste Papillae

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Psychophysical responses to chemical stimulation of single human fungiform papillae were tested in 40 papillae from four Ss. Detection and recognition thresholds, as well as psychophysical functions, were determined for nine test compounds in each papilla. A comparison was made of the effectiveness of stimulating either the dorsal surface or the sides of these papillae, and the quality responses elicited by chemical stimulation were compared with the quality responses elicited by electrical stimulation of the same papillae.

Results of testing showed that single fungiform papillae mediate more than a single primary taste quality. The level of sensitivity in a papilla is reflected in the thresholds for all compounds, and those papillae which mediate less than the full number of taste qualities exhibit lower sensitivities. In addition, low correlations among thresholds for all pairs of compounds suggest that even simple chemical solutions may have a complex effect on receptor sites.

Psychophysical functions determined for single papillae, as well as for the whole mouth, were found to reach an asymptote at high concentrations, with the median exponents of the best-fitting power functions being lower for single papillae. The latter aspect of the data

calls into question the notion of exponent invariance and the physiological basis of the power law.

A "water taste" at the single-papilla level was observed in two subjects. A possible sex difference in the occurrence of the water taste was suggested by various aspects of the data. Also a consistent "sour-salty" confusion was found for small area dorsal tongue stimulation. The ubiquity of this confusion indicated that it is a robust phenomenon and deserves systematic evaluation at a future date.

Chemical stimulation of the dorsal surface of fungiform papillae resulted in more effective stimulation of the papilla than similar stimulation of its circumferential surfaces. This fact casts further doubt on the reported sensitivity of these circumferential surfaces (von Bekesy, 1966), but their ability to mediate some gustatory response suggests that taste buds may be present on these surfaces.

Finally, electrical stimulation of the same papillae which were tested chemically showed no correlation between the qualities mediated by each mode of stimulation. In addition, the use of a simple control procedure suggested that sweet and bitter responses to chemical stimulation are not the result of stimulation by the electric current, but may be the result of a verbal association between taste labels and non-gustatory sensations.

Table of Contents

List of Tables

List of Figures

Introduction

Much of the research in the field of gustation over the past quarter of a century has focused on the problems of neural coding. Specifically, the issue involves whether taste quality is neurally encoded by neo-Müllerian or a Neural Pattern Interpretation mechanism. As with many problems in sensory psychology, two separate approaches have been employed in an attempt to resolve the issue. The first approach has employed electrophysiological techniques, usually in subhuman species, to directly record the neuroelectric events occurring in the afferent neural elements. The second approach has employed psychophysical techniques, usually in humans, to obtain information directly related to these neural events. Both are valid approaches to the problem and have equal merit, especially in light of species limitations that make it difficult to employ both techniques within a single organism.

As is frequently the case when two separate and distinct research approaches are employed in solving a single problem, the available data on mammalian gustatory quality coding are conflicting. The electrophysiological data in animals generally support the Neural Pattern Interpretation view. The psychophysical data in man is unclear, with data available to support both views. If the discrepancies in the human data could be resolved, a major step toward the resolution of the overall problem of mammallian gustatory quality coding will have been made. The research described herein is an attempt to resolve the discrepancies in the human data.

In order to place into perspective the problems under consideration,

as well as to provide a complete historical background to the topics of discussion, a detailed review of the literature pertaining to mammalian gustatory quality coding, intensity coding, and intensity-quality interactions, follows.

Quality Coding

With regard to the problem of mammalian gustatory quality coding, current thought centers around two major theories: 1) the neo-Müllerian or Specificity Theory and 2) the Neural Pattern Interpretation Theory. Of the latter, two specific forms may be distinguished: the Across-Fiber Pattern Theory, and the Temporal Pattern Theory.

The neo-Müllerian position, based on an extension of Müller's Law of Specific Nerve Energies, assumes the existence of a small number of specific receptor types. Each receptor type is assumed to respond to a specific class of chemical stimuli, and to produce neural activity in a specific set of nerve fibers and corresponding cortical projection areas. Since it has been commonly held since the time of von Vintschgau (1880) that there are four primary gustatory qualities--sour, sweet, salty, and bitter, so it is that the neo-Müllerian theory of gustatory quality coding postulates the existence of four separate and distinct receptor types in man. Tastes other than the four "primary" taste are assumed to result from the simultaneous stimulation of two or more classes of receptors.

In contrast to the above schema is the neural pattern interpretation theory. This theory maintains that receptors are not specific to a single class of stimuli, but respond in varying amounts to all stimuli. In addition there is no specificity of response in afferent fibers or cortical locations, but rather, the quality of the stimulus is encoded by the spatial or temporal pattern of neural activity among fibers.

While the classical statements of both theories provide clear and

precise descriptions of tenable codes for taste quality, the empirical data suggest a more complex code than is specified by either theory alone. This apparent complexity is the result of species differences and differences in the nature of the experimental data. In general, these data fall into two discrete categories: 1) electrophysiological evidence obtained from infra-human species, and 2) psychophysical evidence obtained from man.

Lower mammalian species - peripheral units: Across-fiber patterning

Pfaffmann(1941) was the first to propose a neural pattern interpretation theory for the coding of gustatory quality. He based his proposal on studies of the electrical response characteristics of single fibers in the cat chorda tympani and glossopharyngeal nerves to chemical stimulation of the tongue. Single-fiber records in this species indicated three distinct types of gustatory fibers--one which responded only to acid (HCl or CH_3COOH), one which responded to both acid and quinine hydrochloride, and one which responded to both acid and salt (NaCl). Since the application of salt produced responses in the acid-salt fibers only, while the application of acid produced responses in these same fibers as well as in each of the other two types, Pfaffmann (1941) proposed that the difference in quality between the two compounds could only be encoded by taking into account the neural activity of all fibers.

Later studies by a number of investigators confirmed the multiple sensitivity of single taste fibers in the cat and in other mammalian

species. However, these studies provided evidence that the multiple sensitivity was much broader than Pfaffmann (1941) had first suggested. The first such evidence was reported by Pfaffmann (1955) himself. Recording both the total integrated response of the chorda tympani, and single-fiber activity from cat, rat, and rabbit, he found multiple sensitivities within fibers of a single species, as well as differences in total nerve activity to the same compound among species. In particular, with regard to the multiple sensitivity of fibers within a species, Pfaffmann drew from his data an example of two fibers in the rat--one of which gave a large response to NaCl and a small response to sucrose, and another which gave a large response to sucrose and a small response to NaCl. Since both fibers responded to both compounds, Pfaffmann (1955) argued that the discrimination of NaCl from sucrose depended upon a "quantitative difference between the activity in the two fibers." Expanding this example to a greater number of fibers he concluded that "the afferent nerve in taste is best described as a pattern of differences in the relative activity of different fibers, and such a pattern is the basis for gustatory discrimination." Pfaffmann specifically divorced this classical statement of the Across-Fiber Pattern Theory from any schema based on temporal patterns of response within single fibers.

In the same year that Pfaffmann reported the above data, Cohen, Hagiwara and Zotterman (1955) provided evidence that an even greater variation in fiber types existed in the cat chorda tympani nerve. This new evidence was obtained within the context of an investigation of the

response functions of "water fibers" in this species. Single unit responses revealed a number of different fiber types, including: 1) "water fibers" which responded to a flow of distilled water across the tongue, to QHCl, to mineral acids, and to various inorganic salts at concentrations below 0.03 M (salt solutions above 0.03 M depressed activity in these fibers); 2) "salt fibers," which responded to hypertonic salt solutions and to mineral acids; 3) "quinine fibers," which responded only to QHCl solutions; and 4) "acid fibers" which responded only to mineral acids. While the response characteristics of some of these fibers were similar to those found earlier in the cat by Pfaffmann (1941), the existence of those sensitive to water, and those specific to quinine indicated a greater multiplicity of fiber types than had previously been suggested. Furthermore, although all of these earlier studies, as well as later ones, identified some fiber types which were highly specific to a single class of compounds, this did not invalidate the Across-Fiber Pattern Theory, because these fiber types were in a distinct minority in all cases. The above facts led Cohen, et al. (1955) to agree with Pfaffmann (1941, 1955) concerning across-fiber patterning in the cat gustatory system. Furthermore, they extended this analysis to the taste system of the dog, after consideration of earlier data (Anderson, Landgren, Olsson and Zotterman, 1950) showing three fiber types with different multiple sensitivities in this species: 1) "sweet fibers," responsive only to sugars; 2) "acid fibers," responsive only to acids; and fibers responsive to both acids and salts.

While Cohen, et al. (1955) confirmed Pfaffmann's results with the

cat, Fishman (1957), and Gordon, Kitchell, Strom and Zotterman (1959) provided confirming evidence of multiple sensitivities in the chorda tympani fibers of rat, hamster, and monkey. Fishman's work with the rat and hamster, besides establishing the existence of a large multiplicity of afferent fiber types, also established that differences existed among fibers as to their responsiveness to different compounds which normally elicit the same "primary" quality. Thus, he found that a series of chloride salt solutions would differentially affect the response of single fibers, depending on the cation of the salt. These data are problematic in the sense that compounds eliciting the same taste quality should produce similar patterns of neural activity if such patterns are, in fact, coding quality. However, these results may be explained by reference to human psychophysical data which show that different chloride salts have different taste qualities depending on their concentration. If such a quality-intensity interaction also occurs in lower species, then the neural effects found by Fishman might merely reflect this fact.

In the chorda tympani fibers of monkey, Gordon, et al. (1959) found a similar multiple sensitivity to solutions of NaCl, sucrose, quinine, HCl, saccharine, and water. However, these investigators also reported highly specific fibers which responded only to sugars or saccharine. Recently, Frank (1974), and Pfaffmann (1974) have reported a similar specificity in the chorda tympani fibers of the squirrel monkey, and the latter author has used these data as a point of focus for the development of a compromise position on gustatory quality coding,

similar to that proposed earlier by Dzendolet (1969a). A discussion of this compromise position appears in a later section.

Taken in their entirety, the complexity of single fiber responses found in the above studies would appear to argue favorably for a neural pattern theory of quality coding in these species. Yet, one important aspect of these data cannot be overlooked; namely, that the neural activity in first-order neurons does not necessarily reflect the response characteristics of receptors or of more central units. In particular, the multiple innervation of taste buds by first-order neurons, established by the early histological work of Foley (1945), and subsequently verified by Graziadei (1969a,b) and by Murray (1971) leave open the possibility of highly specific receptors, in keeping with the neo-Müllerian position.

In an attempt to provide evidence on the response characteristics of single taste receptors, Kimura and Beidler (1961) succeeded in recording intra-cellularly from taste cells in fungiform papillae of rats and hamsters. Using solutions of 0.5 M sucrose, 0.01 M HCl, 0.10 M NaCl, and 0.02 M QHCl and recording with micropipette electrodes, they found individual receptors to be responsive to a number of compounds characteristic of different taste qualities. These results, later confirmed by Tateda and Beidler (1964), and by Sato and Ozeki (1972), seemed to eliminate the possibility of a neo-Müllerian mechanism for the coding of taste quality in these species. Therefore, efforts were turned toward providing a more detailed analysis of the Across-Fiber Pattern Theory, as well as providing other lines of evidence in support

of it.

Erickson (1963) provided the first truly significant analysis in this regard by correlating neural activity in groups of afferent neurons with overt discriminatory behavior in the rat. His technique was to record the neural impulses of a number of single chorda tympani fibers in response to the application of various chemical solutions. By plotting the number of impulses in the first second of activity to a given compound, as a function of the particular fiber from which the recording was made, he was able to determine "across-fiber patterns" for each of a number of inorganic salt solutions. Correlations among these patterns showed that some salts (NH_4Cl, KCl, $CaCl_2$) elicited a similar pattern of firing across the neurons tested while other salts (NaCl, LiCl) elicited patterns which, although similar to each other, differed from the former group. In order to assess the importance of these pattern differences for quality coding, he undertook a behavioral generalization test on these same compounds. Establishing a shock-induced avoidance to one of the three salts, NH_4Cl, KCl, NaCl, and testing for generalization of avoidance to all three, he found that conditioned avoidance to KCl generalized to NH_4Cl but not to NaCl. Similarly, conditioned avoidance to NH_4Cl generalized to KCl but not to NaCl, while avoidance to NaCl generalized somewhat to both KCl and NH_4Cl, but not differentially to either. Erickson concluded from these data that KCl and NH_4Cl taste more nearly alike to rats than do either to NaCl. Furthermore, this qualitative difference in the taste of these compounds is reflected in the across-fiber pattern of afferent neural

activity.

While the number of fibers sampled by Erickson was exceedingly small (7-10) to have expected any significant degree of correlation between the pattern of neural activity and the behavior of the organism, Marshall (1968) was able to establish a similar correlation between neural response patterns and discriminatory behavior in the opposum. Using a procedure similar to that of Erickson, he established an inverse relationship between the similarity of across-fiber patterns and behavioral discriminability for KCl, NaCl, and NH_4Cl. In addition, he confirmed earlier data (Erickson, Doetsch, and Marshall, 1965; Erickson, 1967, 1968) related to the problem of primary sensations and receptor-fiber types. These earlier data were based on a data analysis technique developed by Erickson (see Erickson, 1967). This technique involves the determination of scatterplots of response activity in a series of single fibers to two discriminable stimuli. By the grouping or non-grouping of the data points in these graphs it is possible to assess the number of distinct fiber types present in the whole nerve, even though the underlying stimulus continuum for taste quality is not known and cannot be varied systematically. From these data, it was concluded that there exists a large number of different fiber types (and receptor types) in the species tested, and that no stimulus primaries exist for gustation, as they do for vision. These conclusions have been subsequently supported by the data of Schiffman and Falkenberg (1968), and Schiffman and Erickson (1971) who have also concluded that "the present model does not require, or support, the idea of taste primaries." As such, one may

conclude that Frings' (1946) postulate, that the four basic tastes are merely "points of familiarity along a continuous taste spectrum," is supported by the above studies, although Frings' designation of "solution mobility" as the underlying stimulus dimension is, most probably, incorrect.

Even while the above correlations between physiological and behavioral responses were being made, a number of Japanese investigators began to provide evidence that multimodal information was carried in the chorda tympani fibers of cat, rat, and hamster (Nagaki, Yamashita and Sato, 1964; Yamashita, Ogawa, and Sato, 1967a,b; Ogawa, Sato, and Yamashita, 1968; Sato, Yamashita, and Ogawa, 1969). Although a certain proportion of these fibers (19% in rat, 18% in hamster) were found to respond to only one type of stimulus, the vast majority responded to both chemical and thermal stimulation of the tongue. In particular, in the rat, it was found that 17% of the units were sensitive to only NaCl; 17% were sensitive to two compounds (NaCl + sucrose, NaCl + HCl, or NaCl + quinine); 17% to NaCl + sucrose + HCl; 23% to NaCl + HCl + quinine; and 25% to all four compounds. Most of these units also responded to cooling of the tongue. In the hamster, on the other hand, 14% of the units were sensitive only to sucrose, 14% to sucrose + HCl, and all of these were more sensitive to warming than to cooling of the tongue. In addition, 14% of the units were found to be sensitive to NaCl + HCl + quinine and 14% to NaCl + HCl + sucrose. Of the latter fiber types, most were responsive to both warming and cooling. Lastly, of the total number of hamster units tested, 25% responded to compounds characteristic

of all of the four gustatory qualities. Each of these latter type was also found to respond to cooling of the tongue.

It should be pointed out that in each of the above studies a fiber was classified as being sensitive to a given stimulus if the impulse frequency during the first five seconds after stimulation was equal to or greater than the mean plus the standard deviation of the spontaneous impulse frequency during a similar five-second period (Sato, et al., 1969). By determining the overall proportion of fibers responding to each stimulus, it was possible to determine the probabilities of occurrence of fibers with any combination of sensitivities, assuming a totally random distribution of sensitivities among fibers. A comparison of these predicted values with the actual proportions of each fiber type found, indicated that the distribution of sensitivities among fibers was not random, but that correlations existed among the sensitivities present within individual fibers (Ogawa, et al., 1969). These correlations included a positive correlation between responses to HCl, quinine, and cooling in rat and hamster fibers, a positive correlation between sucrose and warming in hamster fibers, and a concomitant negative correlation between sucrose and NaCl in hamster fibers.

Although the above studies have extended the range of sensitivities of single mammalian chorda tympani fibers to thermal stimuli, the observed correlations among these sensitivities argue for the existence of a "weak" form of fiber specificity in these taste systems. While this form of specificity is not the same as that originally proposed by neo-Müllerian theory, its possible implications for quality coding in

gustation are important. In this regard, Frank and Pfaffmann (1969) have refuted the existence of this type of specificity in rat chorda tympani and glossopharyngeal fibers. Using similar procedures as the Japanese investigators, they concluded that the taste nerves of rat showed a random distribution of sensitivities to the four classical taste qualities. However, they did conclude from their data that specificity at the receptor level was possible.

Since Frank and Pfaffmann (1969) used similar procedures and techniques of data analysis as the Japanese investigators (Sato, et al., 1969) it appears that the discrepancy in results can only be attributed to differences in the concentrations of test solutions used by these investigators. Frank and Pfaffmann (1969) used test solutions of 0.3 M NaCl, 0.01 N HCl, 0.001 M QHCl, and 0.3 M sucrose, while the Japanese investigators used solutions of 0.1 M NaCl, 0.01 N HCl, 0.02 M QHCl and 0.5 M sucrose. The differences in the concentrations of NaCl, QHCl and sucrose would obviously affect the frequency of responses in fibers and, in turn, the decision as to whether or not the fiber was sensitive to that compound. This fact has great significance for the entire literature on quality coding, since many differences in the response characteristics of fibers of different species might be attributed to inherent species differences, whereas, the true cause of these differences may lie in the use of different solution concentrations.

That the confusion between concentration effects and species differences is a real one is demonstrated by the fact that Frank (1972, 1973, 1974) has more recently examined the response characteristics of

chorda tympani fibers in hamster and squirrel monkey and found that the quality sensitivities in these species are distributed non-randomly among fibers. However, since the solution concentrations used in these studies were different from each other, as well as from those used by Frank and Pfaffmann (1969), it is not clear whether the differences in fiber sensitivities are completely due to species differences or also related to concentration differences. Such a possibility warrants the more frequent use of parametric variation of concentration in all studies of gustatory quality coding. This topic, central to the present research, will be returned to in a later section.

Temporal Patterning

While much of the above data was inspired by an attempt to distinguish between the neo-Müllerian mechanism of quality coding and the Across-Fiber Pattern mechanism, other data suggest that temporal changes in the pattern of neural activity may play a role in quality coding. The first such data was presented by Halpern (1963). Drawing upon data of multi-unit summated responses in rat chorda tympani, he showed that the temporal pattern of these neural responses varied as a function of both the stimulating compound and the concentration. Thus, the response to 1.5 M glycine and 1.2 M DL-alanine is characterized by long latency, slow build-up of response to peak magnitude, no high-frequency large-spike burst, and little adaptation. In contrast to this, the response to 0.1 M NaCl has temporal characteristics opposite in each of these four respects (Halpern, Bernard, and Kare, 1962; Halpern, 1963). Halpern

(1963) also pointed out that similar temporal differences in neural responses had been found by Pfaffmann (1955) between NaCl and amino acids, and by Beidler (1953) between NaCl, $CaCl_2$, and $MgCl_2$; however, neither of these investigators attached particular significance to this fact with regard to a mechanism for quality coding.

Later work on the summated response of the chorda tympani in the rat has reinforced the notion that temporal aspects of neural activity are important for quality coding. When a stimulus is applied to the tongue of this species, the summated response shows a phasic portion which rises and declines rapidly, and a tonic portion which declines very slowly and is maintained for many minutes (Pfaffmann and Powers, 1964). Furthermore, it has been demonstrated that adaptation of the tongue to a solution will reduce or eliminate the phasic response, but have no effect on the tonic response (Pfaffmann and Powers, 1964; Smith and Frank, 1972; Smith, 1974). This fact implies that the phasic or transient portion of the whole nerve response encodes important environmental information in this species. Halpern and Tapper (1971), and Halpern and Marowitz (1973) have recently provided behavioral evidence that such is the case, by showing that rats conditioned to avoid solutions of NaCl can recognize and reject these solutions within 100-600 msec of the onset of the stimulus--a period of time during which only the phasic portion of the neural response is occurring.

The above results in the rat, along with similar findings in the cat (Wang and Bernard, 1970) provide a strong indication that the phasic and tonic portions of the neural response encode different aspects of

the stimulus. Furthermore, since it has long been thought that the phasic response is, in some ways, capricious, many investigators have omitted this datum from their analyses, or only concerned themselves with aspects of the steady-state response. Such is the case with much of Beidler's work on chemoreception (Beidler, 1953, 1962, 1963, 1967), and as a result, this work has come under renewed scrutiny (Faull and Halpern, 1972; Heck and Erickson, 1973).

All of the above work provides strong evidence that different temporal aspects of the neural response serve a role in the coding of quality. Yet more direct evidence on the role of temporal neural patterns has been provided in single units by Mistretta (1970, 1972). It is common procedure in most electrophysiological studies of single nerve fibers to use the average frequency of impulses recorded during some post-stimulus time period as the dependent measure of the response. However, the procedure of calculating an average frequency from a long impulse train necessarily results in the loss of information--specifically, information about temporal changes in the response frequency during that time period. Mistretta (1970, 1972) recorded responses from single fibers in the rat chorda tympani to chemical stimulation of the tongue. Her records showed a multiplicity of temporal response characteristics among fibers. In particular, she found fibers that showed either 1) a high-frequency phasic component followed by a lower frequency tonic phase, 2) a gradual increase in response frequency to a maximum, or 3) periodic high-frequency bursts of impulses. Some fibers exhibited one type of temporal response regardless of the stimulus,

while other fibers showed different temporal responses to different stimuli. With regard to the latter type, Mistretta was able to quantify the differences in the temporal aspects of the response by computing interspike intervals, and then performing an auto-correlation on the data. Her results showed that a large number of fibers produced different temporal patterns of response to 0.1 M NaCl and 0.01 N HCl. The interspike interval data for NaCl approximated a Poisson distribution, indicating a random discharge pattern, whereas the distribution for HCl stimulation was found to be bimodal, indicating the existence of periodic bursts of discharges. In addition, the modal interspike interval in response to the two chemicals differed, being 24 msec for NaCl, and 10 msec for HCl.

These findings are of great importance in the consideration of quality coding, since the non-random temporal discharge patterns exhibited in these data must have some biological significance in order to have been phylogenetically selected. More recently, Hayashi (1976) has shown differences in the temporal impulse trains of rat chorda tympani fibers during the first 250-300 msec of stimulation with compounds characteristic of the four primary taste qualities. His data showed the impulse trains for salty compounds to differ from those of each of the other three qualities. In addition, the impulse trains for sweet and sour compounds differed from each other, although no difference was observed between impulse trains for bitter and sour solutions or for bitter and sweet solutions.

In summary, it appears that the available data on quality coding

in the afferent nerves supports a neural pattern interpretation view of quality coding. Yet, whether this pattern is an across-fiber pattern of neural activity or a temporal pattern of discharges within single fibers has not been resolved.

Lower mammalian species - central units

Whereas it is clear that any pattern or code present in the neural activity of the receptors or first-order afferent neurons may be altered as the information is sent more centrally, the relative paucity of data concerning the response characteristics of thalamic or cortical gustatory cells makes any in-depth analysis of this "ultimate code" difficult. The first breakthrough in this area was made by Cohen, Landgren, Strom and Zotterman (1957) who recorded single fiber responses from the cortical taste projection area of the cat. Recording from an area anterior to the ectosylvian gyrus, they found cells which were multisensitive to tactile, chemical, and thermal stimulation of the tongue. Out of a total of 80 such cells, five responded to chemical stimulation, and each of these was found to be sensitive to solutions of 0.5 M NaCl, 0.1 M acetic acid, and 0.02 M quinine in Ringer's solution. Consistent with the data on chorda tympani responses in the cat, no cells responded to sucrose solution. In a similar manner, Landgren (1957) recorded from 101 cortical cells in the cat, and found seven cells to have multiple chemical sensitivity to 0.5 M NaCl, 0.3 M acetic acid in Ringer's solution, and 0.01 M OHCl in Ringer's solution. Although Landgren found the same proportion of multi-modal cells as did Cohen, et al. (1957), a

later study (Landgren, 1961) of 106 cortical cells showed a much larger proportion of mo[illegible]ity-specific fibers. This modality specificity was found to be still greater in the nucleus ventralis postomedialis of the thalamus, yet, in both these cells, and the cortical cells, all chemically sensitive units responded to compounds characteristic of more than a single quality.

Pfaffmann, Erickson, Frommer and Halpern (1961) provided further information about the chemical specificity of central units in the mammalian gustatory system by recording single cell activity in the rostral portion of the nucleus of the solitary tract in the rat medulla. Using various concentrations of NaCl, HCl, QHCl, and sucrose, they found a number of fibers which responded to more than a single solution, and in addition, the distribution of sensitivities among fibers was found to be the same as reported earlier for the chorda tympani (Pfaffmann, 1941, 1955; Cohen, et al., 1955; Fishman, 1957). Although Pfaffmann, et al. (1961) admitted some possibility that their electrodes were actually recording from presynaptic chorda tympani fibers, their general conclusion was that they had found fibers with multiple sensitivity in the rat medulla.

More recently, in an attempt to directly compare the response characteristics of cells in the chorda tympani and medulla, Doetsch, Ganchrow, Nelson and Erickson (1969), and Doetsch and Erickson (1970) recorded from both areas in the rat. Using test stimuli of 1.0 M sucrose; 0.3 M KCl and $CaCl_2$; 0.1 M NaCl, $NaNO_3$, Na_2SO_4, LiCl, Li_2SO_4,

NH_4Cl, $MgCl_2$, and NaOH; 0.03 M HCl and HNO_3; and 0.01 M QHCl; they reported the following results: 1) cells in both the chorda tympani (CT) and in the nucleus of the solitary tract (NTS) responded to a broad range of chemical compounds, 2) the neural response functions (see Erickson, 1967), of CT and NTS neurons were similar, and 3) compounds which elicited similar across-fiber patterns in the CT also elicited similar patterns in the NTS. In addition to the above similarities in response at the two levels, the following disparities were found: 1) the average frequency of responses in the NTS was magnified by a factor of 4.3 over the same responses in the CT, 2) the phasic portion of the response was diminished in the NTS, and 3) the across-fiber patterns in the NTS showed less temporal variability than in the CT. Scott and Erickson (1971) have extended this comparison to the thalamus by recording from single cells in the thalamic taste nuclei of rats. Using the same stimulus solutions as in the earlier studies, they found that these third-order cells, 1) responded to a wide range of stimuli, and 2) gave diminished response frequencies over those in the NTS, thereby reducing the response rate to that found in the CT. Furthermore, correlations among across-fiber patterns for similar compounds were lower in the thalamus than in the NTS or CT, while the temporal variability in these patterns was greater. The major conclusions reached by all of these investigators was that as one ascends the central pathway for taste, gross discriminations appear to be made at the level of the medulla, while finer discriminations appear to be made at the thalamus. In addition while the across-fiber pattern encodes

quality at all levels, temporal changes in this pattern at the thalamus may sharpen the code and enhance discrimination.

It is clear that the above data provide direct support for an across-fiber pattern theory of taste-quality coding. However, the temporal variability in this pattern at the thalamus suggests that a temporal code may also exist. This notion is supported by recordings from the thalamus of the cat. Emmers (1969), recording from thalamic nuclei in the cat, has shown that neurons carrying information about different lingual sensory modalities show characteristic temporal patterns of responding. He first determined whether a neuron in the thalamus carried touch, pressure, thermal, or gustatory information by stimulating with normal physiological stimuli. Then each neuron was driven by electrical stimulation of the peripheral receptor field with square wave pulses of 0.5 msec duration at a frequency of 1 Hz. The amplitude of the stimulation was adjusted to give the maximum spike frequency in each neuron. The response records of these neurons to this type of stimulation showed marked differences in their temporal pattern of response, depending on whether it was a touch, pressure, thermal, or gustatory neuron. In particular, an interspike interval analysis showed that each of these neuron types produced bursts, but that the pattern of bursts differed for each. Emmers (1969) concluded from this that the modality of a stimulus is encoded in the thalamus by the temporal pattern of impulse bursts in specific neurons. Furthermore, he suggested that a finer analysis of the temporal patterns existing among spikes within a single burst may serve to code the qualities within any one

modality.

While Emmers' data are suggestive of the possible role that temporal neural patterns may play in central gustatory quality coding, his failure to actually demonstrate differences in the temporal patterns elicited to different chemical stimuli, severely limits the conclusions that can be made. Furthermore, recent data on the chemical responsiveness of single neurons in the cat geniculate ganglion (Boudreau, Bradley, Bierer, Kruger, and Tsuchitani, 1971); Kruger and Boudreau, 1972; Boudreau and Alev, 1973; Boudreau, 1974) having further complicated the quality coding picture by producing evidence of a relative specificity in the responsiveness of these fibers. These investigators, while demonstrating that cat geniculate fibers respond to a broad range of chemical compounds, were also able to classify the responsiveness of these fibers into three types, similar to those found by Cohen, et al. (1955) for the chorda tympani. The presence of a weak specificity of this nature in both first-order and second- or third-order gustatory neurons hints at a possible neo-Müllerian mechanism of quality coding, although the nature of this mechanism must necessarily differ from the classical statement of Müllerianism.

In further support of the notion that quality coding may be achieved by a mechanism similar to that proposed by specificity theory, Halpern (1965, 1967) has presented evidence for a chemotopic organization in the nucleus fasciculus solitarius of the rat. Multi-unit recordings have shown that stimulation with either sucrose or QHCl will produce maximum summated responses in two separate and discrete areas

within this nucleus (Halpern, 1965, 1967). Such a chemotopic organization of taste qualities is in keeping with one aspect of neo-Müllerianism--namely, that the quality of the stimulus is encoded by the location in the brain to which the information is sent.

Funakoshi, Kasahara, Yamamoto and Kawamura (1972) have recently provided evidence that a similar chemotopic organization exists in the cortical projection areas of both dogs and rats. Using test solutions of 0.1 M sucrose, 0.1 M NaCl, 0.01 M tartaric acid, and 0.01 M QHCl and recording from single units in the cortex of rats and dogs, they found the chemical sensitivity of cortical cells in the anterior ectosylvian gyrus of dogs to be distributed, from anterior to posterior, in the order of acid, salt, sucrose, and quinine. Likewise, they found the chemical sensitivity of cortical cells in a region posterior to the middle cerebral artery of rats to be distributed, from dorsal to ventral, in the order of quinine, acid, salt, and sucrose. Although these data are based on only 23 units in dog, and 16 units in rat, they are suggestive of a maintained chemotopic organization throughout the central pathways. Their data is also noteworthy in another aspect. While finding multiple chemical sensitivity in some of the fibers tested, they found a much greater proportion of highly specific fiber types than did either Cohen, et al. (1957), or Landgren (1957). Furthermore, they were able to distinguish a spectrum of fiber types ranging from "specific" to "relatively specific" to "non-specific." Each of these types could further be categorized as being either "ON," "ON-OFF," or "inhibitory." "ON" cells gave the commonly observed neural response to

stimulation. "ON-OFF" cells responded normally to presentation of one type of taste stimulus, but other stimuli produced both an "ON" and "OFF" response. "Inhibitory" cells responded normally to the presentation of one type of stimulus, but their spontaneous firing rate was inhibited by presentation of other stimuli. These "inhibitory" cells have also been observed by Norgren (1970) in hypothalamic nuclei of rats, but their existence at this level of the taste system is in sharp distinction to what has been found more peripherally.

The presence of chemotopic organization, as well as a weak specificity in central neurons for taste, leaves the status of central quality coding in much the same position as that for quality coding in the periphery. In summary, the data on quality coding in lower mammalian taste systems may be characterized as showing: 1) that units at all levels respond to more than a single class of compounds, 2) that while this broad-tuning supports an across-fibers pattern theory, the relative specificity of fiber types and central chemotopic organizations argue in favor of some form of specificity coding, and 3) ample evidence exists to show that temporal patterns in neural activity also have some role in the overall coding mechanism.

Quality coding in man

While a plethora of data is available on taste quality coding in lower mammalian species, no large body of literature exists for the human taste system. This is a result of the relative inability, based on ethical grounds, to record electrophysiological events in humans. As

such, data bearing on questions of quality coding in man are primarily psychophysical in nature. Yet, even these data are contradictory in many respects and pose further problems for the analysis of mammalian quality coding.

Since a major assumption of the neo-Müllerian hypothesis of quality coding is that there exist highly stimulus-specific receptors, the human psychophysical work on quality coding has focussed on attempts to stimulate single taste papillae, so as to determine whether one or more taste qualities are elicited. The choice of the papilla as the unit for examination appears to have been determined by anatomical and practical considerations. Although numerous early attempts to stimulate single papillae were undertaken with both chemical and electrical stimulation, technical problems involved in this work were sufficiently pronounced so as to cast doubt on the conclusions of these early studies, and it was not until the ingenious experiments of von Bekesy (1964a, 1966) that suitable techniques of stimulation were developed.

That taste sensations can be elicited by electrical stimulation of the tongue has been known since the early studies of Sulzer (1767), and of Volta (1792). However, these and most later studies of "electric taste" (see Bujas (1971) for a review) were concerned with taste qualities elicited by stimulation of large areas of the tongue surface. The first noteworthy study that attempted to restrict stimulation to a single papilla was that of Oehrwall (1891), who used d-c stimulation and a brush electrode. He found stimulation of a single papilla to result in the perception of more than a single taste quality. While

these data could be interpreted as reflecting either stimulation of multi-sensitive taste buds, or stimulation of a number of different but highly specific taste buds, von Bekesy (1964a) has argued that Oehrwall's data do not reflect direct stimulation of taste buds at all. Von Bekesy (1964a) noted that the d-c stimulation employed by Oehrwall (1891) would produce significant hydrolysis of saliva, a situation which would result in long-lasting chemical stimulation, in addition to direct electrical stimulation. That this was probably the case can be inferred from Oehrwall's statement (Oehrwall, 1891, p. 63, translated by Dr. E. Dzendolet) that "the perceptions lasted not only when the current was on, but remained yet for a while after the brush was removed."

Dzendolet (1962) has reviewed the problem of the nature of the electrode used in early studies of "electric taste" and has concluded that all of these early studies employed non-reversible electrodes, and therefore, the reported data probably reflect the effects of hydrolysis. Dzendolet (1962), himself, attempted to directly stimulate single human fungiform papillae using Ag-AgCl-Cl^- fluid electrodes while varying both the duration of the pulse and the type of electrode-salt solution. The use of NaCl as the electrode fluid and low current pulses resulted only in reports of "detection." At higher current values the reported quality for both NaCl and KCl electrodes was "prickly." For negative pulses the reported sensation was "prickly," regardless of the electrode fluid or current value. A consideration of both the data and the physical properties of the electrodes led Dzendolet (1962) to conclude

that the data did not reflect the direct stimulation of either the receptor or the first-order neuron, but were the result of changes in the quantity of ionic species present at the receptor.

In 1964, von Bekesy published an ingenious set of experiments in which he electrically stimulated single human fungiform papillae with small diameter (0.3 mm) gold-tipped electrodes and positive square-wave pulses of 0.5 msec duration. Under these stimulating conditions hydrolysis is not likely to occur. Von Bekesy (1964a) found that stimulation of the dorsal surface of individual papillae elicited only one of the four primary taste qualities, or no taste at all. At no time did he find a single papilla that mediated more than a single taste quality, although he did report the existence of "fused" papillae which usually elicited both a salty and a sour taste quality. In addition to finding a high degree of specificity among papillae, von Bekesy (1964a) found that the sensations produced by electrical stimulation sometimes differed from the sensations produced by chemical stimulation. Thus, the sweetness produced by electrical stimulation of "sweet papillae" was described by some subjects as being "angelically sweet." Von Bekesy interpreted this to mean that chemical stimuli do not produce "pure" sensations, but that they stimulate other receptor types to some extent, thereby producing taste "overtones." Electrical stimulation, on the other hand, elicits only the pure quality associated with a single receptor type.

In addition to the above findings of specificity in single papillae, von Bekesy (1964a) also found that the distribution of papillae types

across the surface of the tongue was random. This fact is contrary to the classical description of taste sensitivities being localized on various portions of the tongue surface (Shore, 1892; Hanig, 1901). Although there is no apparent reason for the discrepancy between single-papilla and large-area stimulation, the results are important for calling into question the textbook notion of localized tastes on the tongue and suggesting a re-evaluation of this problem.

While it is true that von Bekesy did not attempt to stimulate individual taste buds, one experiment he reports bears directly on the role of individual taste buds in quality coding. Using an electrode with a tip diameter of 0.1 mm, he was able to slowly "roll" the electrode around the entire circumference of the papilla without stimulating adjoining papillae or tissue. This procedure necessarily results in the stimulation of a different subset of taste buds on the papilla at each instant in time. Yet, during these experiments each subject reported only a single quality, regardless of electrode location. If the pattern of firing in receptors or afferent neurons is important for taste quality coding, then changing the pattern of stimulated taste buds should have altered the reported taste quality. These results, in combination with those discussed earlier, led von Bekesy (1964a) to reject the across-fiber pattern theory for quality coding in man.

Although von Bekesy's experiments pose distinct problems for neural pattern interpretation theories, no attempt was made to replicate von Bekesy's experiments until 1972 when Plattig attempted to do so. Plattig (1972) aspired to use a similar procedure to that of von Bekesy (1964a),

but instead, used silver electrodes and a 2msec pulse duration. Both of these procedural changes would serve to produce a greater degree of hydrolysis than in von Bekesy's experiments. Plattig's results were ambiguous, but suggested that hydrolysis was a problem. Specifically, he found that some subjects gave 50% "no taste" responses, and 50% "sour" responses, while other subjects gave totally random quality reports. At the very least these data suggest that Plattig (1972) could not replicate von Bekesy, but the high proportion of "sour" responses in some subjects is also indicative of an hydrolysis reaction having occurred.

In a more recent study, Plattig and Innitzer (1976) again used silver electrodes but with a 0.5 msec pulse duration. Again their data showed a predominance of sour responses (90% of all tested papillae which gave a taste response produced either a pure sour or "mixed" sour taste), and the authors themselves state that "For the responses 'sour,' 'bitter,' and 'salty' in our experiments, one cannot exclude that they might be caused by electrolyte processes." As such, their conclusion that the results indicate only a relative specificity for single human taste papillae must be viewed with reserve.

Although the above investigators failed in their attempt to replicate von Bekesy's results, Dzendolet and Murphy (1974) repeated von Bekesy's experiments with great detail, using gold electrodes, and confirmed both the specificity of single fungiform papillae and the relatively random distribution of papillae types across the front and sides of the tongue.

Besides the work on electrical stimulation, a number of studies have been reported on chemical stimulation of single papillae. The first

such experiments were those of Oehrwall (1891) and of Kiesow (1898), who chemically stimulated single human papillae with brush applicators. Using solutions representative of the four taste qualities they found that about one-half of all papillae were highly specific, while the other half responded to some combination of the four taste stimuli. While these results support a general non-specificity of papillae, von Bekesy (1966), as well as a number of more recent investigators (Harper, Jay and Erickson, 1966; Bealer and Smith, 1974), have pointed out that the use of brushes to apply the stimuli in these early studies was crude and probably resulted in the stimulation of surrounding papillae also.

The first study which appears to have actually succeeded in chemically stimulating single papillae was that of von Bekesy (1966). His procedure was to use a pencil-like syringe stimulator with a 30-gauge needle, ground smooth at the tip. By touching the tip of the needle to the surface of a fungiform papilla, a constant-volume droplet of solution was deposited on its surface. While such a droplet would tend to spread if the tongue were wet, von Bekesy avoided this problem by allowing the tongue to remain in an atmosphere of 30% relative humidity until the saliva evaporated. Furthermore, since pilot work showed that stimulation of the dorsal surface of these papillae resulted in ambiguous sensations, von Bekesy (1966) restricted his stimulation to the sides of the papillae. The solutions used in these studies were HCl, in concentrations between 0.0002 M and 0.001 M, NaCl between 0.005 M and 0.02 M, QSO_4 between 0.0003 M and 0.0001 M, and sucrose between

0.0023 M and 0.0086 M. For any one papilla each solution was presented in increasing concentration until a quality report was evoked for one of the compounds. Following this, each of the other three solutions were presented in higher concentrations to determine if the papilla would mediate another quality. A ten-minute inter-stimulus interval was employed to minimize any adaptation effects.

The results of this procedure were clear in indicating that a single papilla would mediate only a single taste quality. Furthermore, changes in the concentration of the stimulating solution produced no apparent change in the reported quality for any papillae, and stimulation of single papillae with mixtures of sucrose and quinine resulted in only a sweet quality in sucrose-sensitive papillae and only a bitter quality in quinine-sensitive papillae.

In order to compare these results with electrical stimulation, von Bekesy stimulated these same papillae using the procedure outlined earlier for his electrical stimulation (von Bekesy, 1964a). He found "complete agreement" of the taste quality within a single papilla, regardless of whether the papilla was stimulated electrically or chemically.

The above finding of quality-specific papillae in humans, using chemical stimulation, poses difficult problems for the neural pattern interpretation theory of quality coding. However, more recent work on the chemical sensitivities of single papillae has cast doubt on von Bekesy's results. In particular, Harper, Jay and Erickson (1966) pointed out that, while von Bekesy reported to have stimulated the sides of fungiform papillae in his studies, histology of these papillae (von

Skramlik, 1926; Kolmer, 1927) indicates that taste buds only exist on their dorsal surface. In addition, these investigators have suggested that the threshold concentrations of solutions that von Bekesy used were not sufficient to elicit all of the "available" qualities from a papilla, but only that which had the lowest threshold. In order to test this possibility, Harper et al. chemically stimulated single human fungiform papillae with extremely concentrated solutions (2.6 M and 3.6 M NaCl, 1.2 M sucrose, 0.005 M dulcin, 0.041 M and 0.06 M QHCl, and 0.47 M and 0.6M citric acid). They employed a water rinse between stimuli and a 15-sec inter-stimulus interval. While many of the quality responses they obtained were "inappropriate" for the stimulus compound tested, and many sensations were reported as being ambiguous, these authors still concluded from their data that the results were "unequivocal with respect to the question of whether a single taste papilla may mediate more than one of the so-called primary taste sensations." In particular, out of 23 papillae tested, 10 were found to produce qualitatively "accurate" sensations, but only four of these mediated a single quality.

Whereas the above results could be interpreted as lending support to a neural pattern interpretation theory of quality coding, they are not inconsistent with either von Bekesy's results or a neo-Müllerian mechanism. To begin, von Bekesy (1966) stimulated the sides of papillae, whereas Harper et al. (1966) stimulated the dorsal surface of these papillae. While a hypothesis to explain the difference in the degree of specificity between taste buds on the top and sides of papillae is

lacking, this difference in locus of stimulation may account for the discrepant results. Secondly, Harper et al. used a small flow-chamber arrangement which fit over a single papilla in order to present their stimuli. This apparatus was held in place by a vacuum. Such an arrangement is quite different from the pencil-type stimulator used by von Bekesy (1966), and it is likely that the diminished sensitivity found in their subjects was the result of a decreased blood supply to the papillae, produced by the vacuum. Lastly, these investigators used very high concentrations of test solutions to ensure that all existing sensitivities in a papilla were evoked, regardless of threshold. However, it may be argued that these concentrations were effectively "overdriving" the receptors and eliciting sensations independently of the stimulus. Such a situation is analgous to stimulating visual receptors by sufficient pressure on the eyeball. This phenomenon reflects a corrollary of the Law of Specific Nerve Energies, which states that any stimulus, if sufficiently intense, will excite any nerve and elicit a sensation characteristic for that nerve. That such stimulation could have occurred in Harper, et al.'s study is suggested by the large proportion of "inappropriate" responses found in their data.

In an attempt to improve upon these efforts, McCutcheon and Saunders (1972) attempted to replicate von Bekesy's (1966) more delicate technique. Using 30-gauge syringe needles, a water rinse between stimuli, and a 60-second inter-stimulus interval, they presented solutions of 0.4 M NaCl, 0.1 M citric acid, 0.0003 M QSO_4 and 0.4 M sucrose to the dorsal surface of fungiform papillae. These investigators obtained results which were

not as ambiguous as those of Harper, et al. (1966). Although their data were characterized by a number of inappropriate responses, an absence of quality responses to QSO_4, and a peculiar absence of any quality reports other than "sour" in response to NaCl stimulation, the stability of appropriate quality responses to sucrose and citric acid led McCutcheon and Saunders (1972) to conclude that single human papillae were multi-sensitive to compounds characteristic of the four taste qualities. An interesting additional aspect of their data was that responses were stable in a single papilla over testing periods as long as a month. This long-term response stability led them to conclude that an explanation of these data in terms of either specificity or pattern theory was impossible, since it has been shown that individual rat taste cells are replaced every five to seven days (Beidler and Smallman, 1965), and that the innervation of these receptor cells by the afferent neurons is random (Frank and Pfaffmann, 1969). They argued that such an unstable system should produce a greater temporal variability in the qualities elicited by single-papilla stimulation than was observed in their data.

While the long-term stability of McCutcheon and Saunders' (1972) quality reports is an interesting aspect of their data and gives an indication of the reliability of single papilla stimulation, these results are not inconsistent with either Beidler and Smallman's (1965) or Frank and Pfaffman's (1969) data. The reason for this is that these latter data were obtained with rats, while McCutcheon and Saunders' data were obtained from humans. A species difference in taste bud renewal is not an implausible hypothesis, and it has already been shown that evidence

exists for nonrandom innervation of receptor cells in some species (Sato, et al., 1969; Frank, 1972, 1974; Pfaffmann, 1974). Similarly these data are not incongruous with von Bekesy's (1966) results, since both the locus of stimulation and the concentration of test stimuli differed.

The most recent attempt to chemically stimulate single papillae is that of Bealer and Smith (1975). These investigators have also taken the position that the concentrations used by von Bekesy were too weak to elicit all of the 'available' qualities; but they were dissatisfied with the large number of ambiguous and inappropriate quality reports found by Harper, et al. (1966) and by McCutcheon and Saunders (1972). Using small platinum loops (0.5 mm diameter) to present droplets of 5.0 M NaCl, 0.5 N citric acid, 0.1 M QHCl and 1.0 M sucrose to single fungiform papillae, Bealer and Smith (1975) confirmed the multiple sensitivity of these earlier investigators, but with less ambiguous data. Their results showed that 13% of all tested papillae were insensitive to the four test compounds. Twenty percent of the papillae responded to only a single compound, while 33% responded to three compounds, and 33% to all four compounds. A conspicuous absence of papillae responsive to a combination of two compounds was also reported.

While Bealer and Smith's study used a water rinse after each stimulus and an inter-trial interval of 60 seconds, rather than 10 minutes, as used by von Bekesy (1966), it is difficult to attach significance to these variables in accounting for the difference in results between the two studies. Rather, it appears that, as with the studies of Harper, et al. (1966), and McCutcheon and Saunders (1972), the data of Bealer and Smith

(1975) differ from those of von Bekesy (1966) because of a difference in the locus of stimulation (dorsal surface of papilla vs. sides) or the concentration of stimuli employed.

So, as with the electrophysiological data in lower mammalian species, the psychophysical data on quality coding in man is inconclusive. Yet in spite of this, the discrepant results in both bodies of data are characterized by one common factor--namely that the concentrations of the test stimuli vary dramatically from one study to the next. Such a situation can seriously confound the interpretation of quality coding data, particularly since it has already been noted that changes in the concentration of various solutions can result in perceived quality changes. The obvious solution to this problem would be to include concentration as a variable in these studies. However, such parametric investigations are rarely undertaken in studies of quality coding, in spite of the obvious fact that the intensity of a stimulus must be encoded within the same neuro-electric events that encode quality. Thus, to the extent that the neural code for taste intensity overlaps with the code for quality, a basis exists for the interaction of quality and intensity.

Intensity Coding

Since the early work of Adrian's laboratory (Adrian, 1926; Adrian and Matthews, 1927; Matthews, 1931) on the optic nerve of the eel, and muscle splindle of the frog, it has become a basic principle of neurophysiology that the intensity of a stimulus is encoded by the frequency

of firing in the afferent nerves. Subsequent work on the graded potentials found in receptor and nerve cells has established that these generator potentials are the neural events that give rise to action potentials and that their amplitude is linearly related to the frequency of the generated action potentials. But while both the amplitude of the generator potential and the frequency of nerve impulses are known to increase monotonically with increasing stimulus intensity, the function relating these neural response magnitudes to stimulus intensity is decidedly non-linear. In particular, for most sensory modalities, there is a compression of the response functions, so that at low stimulus intensities the neural response increases rapidly with increasing concentration, but then diminishes its rate of increase and reaches an asymptote at some relatively high stimulus intensity. While this general aspect of the stimulus-response function is well known, the exact form of this function is much less agreed upon. In this regard, the controversy in neurophysiology has paralleled the controversy in psychology over the correct form of the psychophysical function.

In 1850, Gustav Fechner proposed that sensation magnitude increased as a logarithmic function of the physical intensity of the stimulus:

$$\Psi = c \log \frac{\phi}{\phi_o}$$

where Ψ = sensation magnitude,

ϕ = the physical intensity of the stimulus,

ϕ_o = the physical intensity of the stimulus at threshold, and

c = a constant of proportionality.

This formulation, based upon a mathematical derivation of a more fundamental psychophysical relationship--that of Weber's Law, was at first greeted with general approval. However, as time passed and evidence was amassed to show that Weber's Law, relating the difference threshold to the stimulus intensity at which it is measured, was only correct throughout a limited range of stimulus intensities; Fechner's Law also came under scrutiny. This scrutiny led to attacks on Fechner because of his assumption of psychological equality among j.n.d.'s, as well as his methodology, which required the indirect measurement of sensations through procedures such as "summing j.n.d.'s" or "category scaling" (see Savage, 1970).

The discontent with Fechner's Law culminated with a proposal for a new methodology of psychophysical scaling and a new psychophysical law. S. S. Stevens was the proponent of this "new" psychophysics, and through the use of scaling methods which produced ratio data, he was able to show that sensation magnitude increases in proportion to a power of the physical intensity of the stimulus:

$$\Psi = k\,(\emptyset - \emptyset_o)^n$$

where Ψ = sensation magnitude,

$\emptyset$ = the physical intensity of the stimulus,

$\emptyset_o$ = the physical intensity at threshold,

n = an exponent, and

k = a constant of proportionality.

According to this formulation, the psychophysical function for any stimulus continuum can be described by a power function of the form noted

above, and each continuum is characterized by its own exponent. (A similar psychophysical law had been proposed much earlier by Plateau (1872), but the lack of empirical data to support it, and the earlier success of Fechner's law, caused it to be neglected.) Using the direct ratio methods of fractionation, magnitude estimation, and magnitude production, the exponents for a number of sensory continua have been empirically determined. Some common values for these exponents are: 0.33 for brightness, 0.66 for loudness, 1.0 for visual length, 1.4 for lifted weights, and 3.5 for electric shock (Stevens, 1971). In addition, the exponents for the four gustatory qualities have been determined to be 1.0 for bitterness, 1.1 for sourness, 1.3 for sweetness, and 1.4 for saltiness, although each of these values varies somewhat depending on the chemical compound and the procedure used in testing (Ekman and Akesson, 1965; Stevens, 1969; Moskowitz, 1970a, 1971; Meiselman, 1971).

One further aspect of the power law which has relevance for the consideration of neural response functions is that the value of the exponent reflects the overall shape of the psychophysical function. Exponents with a value less than 1.0 reflect a negatively accelerated function, exponents equal to 1.0 reflect a linearity between sensation and stimulus magnitude, while exponents greater than 1.0 reflect a positively accelerated function. Furthermore, a power function with an exponent less than 1.0 is almost indistinguishable from a logarithmic function, making discrimination between Fechner's Law and Stevens' Law extremely difficult for many stimulus continua.

When the first neural correlates of stimulus intensity were

identified by Adrian's laboratory, plots of impulse frequencies as a function of stimulus intensity revealed a logarithmic relationship. Since Fechner's Law had been proposed some 75 years earlier to describe the increase in psychological magnitude as a function of stimulus intensity, the finding of a logarithmic relationship in the neural data was looked upon as confirmation of Fechner's Law. In the years that followed, research in the electrophysiology of the senses continually revealed a logarithmic relationship between the frequency of firing in a neuron, or the amplitude of the generator potential, and stimulus intensity. However, with the first suggestion of a power law for subjective magnitude (Stevens, 1957), a shift in the trend of findings in neurophysiology began to manifest itself. This trend was characterized by an increasing frequency of reports that the neural correlates of sensory intensity were power functions of stimulus intensity (see Stevens, 1970 for a review of these findings). That such a change in the interpretation of the neural data would appear so shortly after the proposal of a new psychophysical law reflects two basic facts: 1) that analyses of data are often influenced by the expectations of the researchers gathering the data and 2) that power functions with exponents less than 1.0 closely resemble logarithmic functions and, unless proper indices of goodness-of-fit are employed, such data can be interpreted as showing support for either psychophysical law (see Cardello (1974) for a review of these problems).

Returning to the literature in gustation, a similar shift in

findings can be observed. Pfaffmann (1941), in his early study of afferent gustatory neurons, proposed that the intensity of a stimulus was encoded by both the frequency of firing in the stimulated neurons, as well as the total number of neurons stimulated. The latter aspect of the code was necessitated by the wide range of psychologically discriminable intensities of taste, compared to the limited range of impulse frequencies available to a single neuron. Later, Pfaffmann (1955) provided evidence that the relationship between single fiber response frequency and stimulus concentration was a sigmoid function of the logarithm of the stimulus concentration (i.e., a logarithmic function in the mid-range). Because it had been proposed that the intensity of the stimulus was, in part, coded by the number of responding fibers, it appeared possible that the total activity in the afferent nerve reflects the algebaraic sum of the individual response frequencies and, thereby, gives an accurate measure of total neural response magnitude. Fishman (1957) showed that the total integrated response of the chorda tympani was, in fact, the sum of the individual fiber responses, and later work by Pfaffmann, Erickson, Frommer and Halpern (1961) in the medulla of rats, and by Yamada (1965) in the glossopharyngeal nerve of rats, rabbits, and cats has shown that the integrated response is a logarithmic function of solution concentration for a wide range of chemical stimuli. Although a large number of other studies have employed the integrated response measure (i.e., Beidler's group), few of these studies have directly addressed themselves to the log-power controversy.

While these earlier studies agreed in their support of a logarithmic relationship between neural response magnitude and stimulating concentration, more recent analyses have provided support for a power function. In their study of single taste cells in rat, Kimura and Beidler (1961) reported data concerning the total integrated response of the chorda tympani, and the amplitude of receptor potentials, as a function of the concentration of NaCl stimulation. Uttal (1973) has replotted these data and found that both sets of data conform to a power law with an exponent of 0.31. Similarly Uttal (1973) has replotted the data of Pfaffmann, Fisher, and Frank (1967) on the integrated response of rat glossopharyngeal and chorda tympani nerves and found that these data may also be described by a power function, with an exponent of 0.53.

An obvious discrepancy between the above electrophysiological findings and the psychophysical data in man is that the exponents of the power functions differ greatly. Such discrepancies are common throughout the literature on this problem and probably indicate the difference in the operating characteristics of taste cells in man and other species. However, a series of studies (Borg, Diamant, Oakley, Strom and Zotterman, 1967; Borg, Diamant, Strom and Zotterman, 1967; Zotterman, 1971) comparing both electrophysiological and psychophysical measures of sensation magnitude in man bear on this problem. These experiments, conducted with patients undergoing middle ear surgery, involved the recording of the integrated response of the chorda tympani to a concentration series of a number of chemical solutions. The concentration-response functions

obtained in this manner were then compared to similar functions obtained by the psychophysical method of magnitude estimation in these same patients. The results of these unique studies showed that subjective and electrophysiological response measures were linear with one another, and that each could be described by a power function, although the neural data could also be described by a logarithmic function. The exponents obtained for the various test compounds were 0.85 for citric acid, 1.1 for sucrose and dextrose, 1.1 for NaCl and 1.0 for QSO_4.

Although the above studies differ with regard to whether neural measures of response magnitude support a logarithmic or a power law, they all agree in their use of either spike frequency, total integrated nerve response, or amplitude of the generator potential as the neural measure of sensory magnitude. Such parameters of the neural response have long been considered to be the code for stimulus intensity. However, recent data suggest that temporal patterns within these responses may also play a role in the coding of intensity.

Werner and Mountcastle (1963) have observed that the variability in interspike intervals of thalamic somatosensory neurons changes as a function of the degree of rotation of the peripheral joint. Similarly, Goldberg, Adrian and Smith (1964) in the auditory system of the cat, and Buller, Nicholls and Strom (1953) in the muscle spindle of the frog, have noted monotonic increases in interspike interval regularity with increasing stimulus intensity. Segundo, Moore, Stensaas, and Bullock (1963) have supported the validity of these reports by artificially varying the temporal pattern of impulses in giant nerve cells of the visceral

ganglion of the sea hare and observing the amplitude of the postsynaptic potential (PSP) that is produced. The particular procedure used in these studies was to present a series of three electrical pulses to a presynaptic neuron within a given time period. By varying the delay time of the second pulse it was possible to change the temporal pattern of the impulses without changing the frequency. Observations of the PSP's indicated that the temporal pattern of the impulses was important in determining their amplitude, but that certain conditions, such as high pulse amplitude or long latencies between the second and third pulses, could minimize the effect of the temporal pattern. Uttal (1960), and Uttal and Smith (1967), using a similar procedure to that described above, established that such temporal patterns actually affect perceived magnitude. By stimulating the ulnar and median nerves in the arms of humans with different temporal patterns, they found that psychophysical estimates of stimulus intensity covaried systematically within certain limited frequency ranges. In particular, when the interpulse interval was between 10 and 20 msec (100-200 pulses/second) the temporal pattern of pulse intervals carried additional information concerning stimulus intensity. Outside of this frequency range no effect was observed. From these data it was concluded that the temporal pattern of nerve impulses does serve to encode information about stimulus intensity through limited ranges of the stimulus.

Although none of the evidence suggesting a temporal pattern code for intensity has been obtained within the gustatory system, the existence of such a code in other sensory modalities is important. These data

clearly suggest that a neural basis for quality-intensity interactions exists, since both dimensions appear to be encoded by similar parameters of the neural events.

Intensity-Quality Interactions

Observed changes in taste quality as a function of solution concentration have been reported by Hober and Kiesow (1898), by Renqvist (1919), by Dzendolet and Mieselman (1967a), and by Cardello and Murphy (1976). Each of these investigations has shown that as the concentration of various inorganic salts is changed, the taste quality of the solution changes. Most such salts taste sweet at low concentrations, bitter and/or sour at higher concentrations, and salty only at concentrations well above threshold.

Doetsch, et al. (1969) have proposed one explanation of these data, based on the above-mentioned overlap in quality and intensity codes. These investigators compared the across-fiber patterns elicited in rat chorda tympani, and in solitary tract nucleus fibers to KCl, NaCl, and QHCl stimulation. They found that the across-fiber pattern to 0.03 M KCl, which is reported to be bitter by humans, closely resembles the pattern elicited by 0.01 M QHCl. Likewise, the pattern for 0.3 M KCl, which is reported to be salty by humans, was found to more closely resemble the pattern elicited by 0.07 M NaCl. Doetsch, et al. (1969) concluded from this that changes in the concentration of salt solutions produce changes in the firing rates among fibers, and that this produces changes in the across-fiber pattern, and thereby, the quality of the

stimulus.

While Doetsch, et al.'s explanation of these intensity-quality interactions is plausible, it does not satisfactorily account for the fact that not all chemical compounds change their quality with changes in concentration. Any explanation of these quality changes based on an interaction of intensity and quality codes must also explain why they occur primarily in inorganic salt solutions.

Dzendolet (1968) has proposed one mechanism by which these concentration-dependent quality changes can occur without resort to an explanation based on interaction of neural codes. This theory is also in keeping with a neo-Müllerian mechanism of quality coding. Dzendolet (1968) proposed that the localized hydrolysis which is known to occur at low concentrations of ionic solutions, produces a chemical structure in which the cation of the salt is surrounded by a shield of hydroxyl ions. The hydrogen ion product of this hydrolysis is assumed to be neutralized by constituents of the saliva. Assuming a proton-acceptor theory of sweet stimulation (Dzendolet, 1968), the presence of an hydroxyl ion structure would account for the sweet taste of these solutions. As the concentration of the salt solution is increased, other physico-chemical changes in the solution would account for the sour and/or bitter qualities experienced. Thus, for the lithium salts, which have a strong sour component, Dzendolet proposes that the increased rate of hydrolysis produces hydrogen ions in sufficient quantity that the salivary constituents cannot neutralize them. Such a situation results in stimulation of "sour receptors," that then inhibit the previously

activated "sweet receptors." (Evidence for such peripheral inhibition in the rat taste system has been provided by Wang and Bernard (1969), Bernard (1972), and Wang (1973). At still higher concentrations the anion of the salt reaches sufficient concentration to stimulate "salty receptors," and an inhibition of the previously activated "sour receptors" occurs.

While the above quality changes in inorganic salts might also be explained by a "water taste" phenomenon (Bartoshuk, McBurney and Pfaffmann, 1964; Bartoshuk, 1968; McBurney and Shick, 1971) this possibility has been ruled out as a general explanation, although under certain testing conditions a "water taste" can influence the data (Cardello and Murphy, 1976). In sum, it appears that quality-intensity interactions in taste may be explained either by overlapping of patterned quality codes, or by physico-chemical changes in the solutions, which result in a series of excitatory and inhibitory effects on highly specific receptors.

Analysis of Coding Data

The early electrophysiological work on taste quality coding in the afferent nerve fibers of lower mammalian species established the fact that these single units have a multiple sensitivity to chemical compounds characteristic of the four primary taste qualities (Pfaffmann, 1941, 1955; Cohen, et al., 1955; Fishman, 1957). The results of these and later studies led to the formulation of the across-fiber pattern theory of quality coding (Pfaffmann, 1955; Erickson, 1963). However, the knowledge

of response characteristics in first-order neurons, as provided by these studies, did not eliminate the possibility of highly specific receptors, nor did it answer the question of the ultimate code of taste quality to be found more centrally in the nervous system. The former possibility seems to have been eliminated by the work of Kimura and Beidler (1961), Tateda and Beidler (1964), and Sato and Ozecki (1972), although the latter study found the receptor cells in rat to be more specific than fibers in the chorda tympani. As concerns the central code of taste quality, the work of Erickson's laboratory on the response characteristics of taste cells in the medulla and the thalamus indicates that the across-fiber pattern found in the afferent nerves is maintained more centrally (Erickson, 1963; Doetsch, et al., 1969; Scott and Erickson, 1971).

While Erickson's work is important for its contribution of much-needed correlations between electrophysiology and behavior, the procedure of examining "across-fiber patterns" among as few as 7-10 units seems less than convincing. It is unlikely that such a small number of units out of the total number responding, could account for quality discrimination in any species. In this regard, the correlations obtained by Erickson between these patterns and behavioral discriminability are remarkable. Von Bekesy (1964) has found similar fault with the across-fiber theory, noting that the variability in single fiber impulse frequency can vary by a factor 10, even over short periods of time. Such a variability among individually responding fibers would certainly be expected to affect the pattern of firing across them.

In addition to providing an adverse criticism of the across-fiber pattern theory, the temporal variability of neural responses has also suggested a new parameter for quality coding. This temporal pattern theory of quality coding has found support in the behavioral work of Halpern and Tapper (1971), as well as in the electrophysiological work of Halpern (1963), Pfaffmann and Powers (1964), Smith and Frank (1972), Smith (1974), and Mistretta (1972). The work of Mistretta (1970, 1972) and Hayashi (1976) on the interspike interval distribution of single fiber responses is particularly convincing, because a similar analysis of behavioral responding in operant conditioning procedures has proved successful in uncovering important, yet previously obscured, aspects of the data (Weiss, 1972; Collins, 1973). An interesting test of the importance of these temporal factors would be to determine the auto-correlograms for separate taste compounds, and then present a mixed solution of the two compounds to determine whether the new inter-spike interval distribution is a composite of the two individual distributions. Such an analysis might provide valuable evidence on the way in which taste mixtures are encoded in the nervous system. Regardless of the results, Mistretta's approach can only lead to a more detailed analysis of neural responses than is provided by a simple frequency averaging technique.

In addition to the support given to some form of neural pattern interpretation theory by the above electrophysiological results, some aspects of the data provide support for a neo-Müllerian, or "labelled line" mechanism of quality coding. In particular, the data which support

this view are those which give evidence that single units are maximally sensitive to one class of compounds, but only weakly sensitive to other chemical classes (Ogawa, et al., 1968; Sato, et al., 1969; Frank, 1973, 1974; Pfaffmann, 1974). Pfaffmann (1974), in a major shift of position has suggested that these findings support the view that there exist both labelled line coding and across-fiber patterning within the mammalian taste system. Basing his proposal on data obtained primarily from the squirrel monkey (Frank, 1974; Pfaffmann, 1974) he states that

> ...empirically, we see both multiple chemical sensitivity as well as peaking around a particular best stimulus. We think the peaks define labelled line clusters within each class but that across-fiber patterning provides spectra of stimulations that may signal subtle differences or nuances within different taste classes. There is therefore both labelled line coding and across-fiber patterning." (Pfaffmann, 1974)

Although Pfaffmann's statement is seen as a major concession to the neo-Müllerian view, many specifics about the mechanism are lacking from his description; this, in spite of the vast literature available on taste fiber response characteristics. It is the contention of the author that the major factor preventing such a detailed analysis is the failure of these earlier studies to undertake parametric variations of the concentration of their test solutions. The importance of this factor has previously been pointed out with regard to the discrepancies found between the data of Frank and Pfaffmann (1969), and Sato, et al., (1969). However, this problem is a general one in all of the electrophysiological work. Response spectra of cells obtained with one concentration of test solution will not necessarily resemble the response spectra obtained in the same cells, but with a different series of test

concentrations. An example of this problem would occur if the "true" thresholds for a fiber were 0.07 M for NaCl, 0.07 M for sucrose, 0.008 M for HCl and 0.005 M for QSO_4. By testing with solutions of 0.1 M NaCl, 0.1 M sucrose, 0.05 M HCl, and 0.0005 M QSO_4, one would conclude that this fiber was primarily responsive to acid, somewhat responsive to NaCl and sucrose, but insensitive to QSO_4. However, by testing with 0.5 M NaCl, 0.1 M sucrose, 0.005 M HCl and 0.008 M QSO_4, one would conclude that the fiber was primarily responsive to NaCl, somewhat responsive to sucrose and QSO_4, and insensitive to HCl. Such a situation demands that single fiber studies employ complete concentration series during testing; yet, up to now, relatively few of these studies have been undertaken.

Although the electrophysiological data on quality coding in lower mammalian species provide a rather confusing picture, the psychophysical data in man are no less so. Here again, discrepancies in data appear, primarily between the work of von Bekesy (1964a, 1966) and that of later investigators (Harper, et al., 1966; McCutcheon and Saunders, 1972; Plattig, 1972; and Smith and Bealer, 1975).

Of the modern literature on single-papilla sensitivity in man, the work of von Bekesy (1964, 1966), and of Dzendolet and Murphy (1964) stand alone in support of a rigid quality specificity. Although this type of specificity is not the most common type to be found in other species, a recent estimate (Pfaffmann, 1974) of the proportion of units responding to only a single class of chemical compounds in other species

is one-fourth. Given the large phylogenetic difference between man and most of the species from which such units were obtained, as well as the long-established differences in taste responses among species (Beidler, Fishman and Hardiman, 1955), it is quite possible that a much larger proportion of such highly specific units could occur in man. This possibility is further reinforced by the fact that the phylogenetically-advanced squirrel monkey appears to have a greater specificity of fiber responses than do lower species (Frank, 1974; Pfaffmann, 1974).

Also in keeping with the idea that von Bekesy's results are not, necessarily, inconsistent with the results found in lower species, is the fact that his data are psychophysical in nature, whereas the animal data are primarily electrophysiological. That such different methodologies should produce different results is not unlikely. In the words of Lord Adrian, "Comparing the impulse discharges in an eel's optic nerve and the brightness of a visual image in man may be like the comparison of chalk with cheese" (Granit, 1955, p. 283). Lord Adrian did go on to say that this procedure could be justified on the likeness of the sets of curves, but in the situation under consideration no "likeness in the curves" is present. Dzendolet (1969) has also written on this problem as it applies to gustatory quality coding, and he has concluded that "we are obviously dealing with separate experimental conditions, and it is inefficient use of our efforts to ask if one view is correct and the other incorrect." His position, and the one taken by the present author, parallels Niels Bohr's principle of complementarity which states that "Evidence obtained under different conditions and

rejecting comprehension in a single picture must, notwithstanding any apparent contrast, be regarded as complementary in the sense that together they exhaust all well-defined information about the object."

Passing from the discrepancy between von Bekesy's results and the electrophysiological data in animals, we encounter the data obtained by psychophysical methods in man which show multiple sensitivity in single papillae (Harper, et al., 1966; McCutcheon and Saunders, 1972; Plattig, 1972; Plattig and Innitzer, 1976; Smith and Bealer, 1975). Although these data were obtained through both electrical and chemical stimulation of the papillae, it is the opinion of the author that the electrical data is somewhat less relevant to the problem, since it is still not clear whether the receptors or first-order neurons are being stimulated. Nevertheless, the fact that Dzendolet and Murphy (1974) were able to replicate the electrical results of von Bekesy (1964) indicates that the phenomenon is real. Plattig's (1972, 1976) failure in this regard, has already been attributed to a probable hydrolysis occurring as a result of his stimulating procedure.

Concerning the chemical stimulation data, the early work of Oehrwall (1891) and of Kiesow (1898) appear to be invalidated by their crude brush stimulator, which probably resulted in the stimulation of more than one papilla. Yet, in spite of this, even these investigators reported 50% of the papillae to be specific to a single taste quality. Later investigators (Harper, et al., 1966, McCutcheon and Saunders, 1972; Smith and Bealer, 1975) have reported a much smaller proportion of such highly specific papillae, but much of their data is complicated by a high

degree of response ambiguity. A number of factors appear to exist for the discrepancy between their data and that of von Bekesy (1966). To begin, von Bekesy (1966) used near-threshold concentrations of his four test solutions and stimulated the sides of fungiform papillae. Both of these aspects of his procedure are different from those employed by the later investigators, and each has drawn considerable attention and criticism. The primary criticism has centered on his stimulation of the sides of fungiform papillae. Most investigators agree that taste buds occur only on the dorsal surface of these papillae. It is interesting to note, however, that relatively little histological evidence is available on this point. In fact, Harper, et al., (1966) resorted to two rather old histological studies (von Skramlik, 1926; Kolmer, 1927) in order to support this contention. More recent histology on fungiform papillae in humans has left open the possibility that such buds do exist. Henkin (1967) presented drawings of histological sections which show taste buds on the sides of human fungiform papillae. More recently, Paran, Mattern, and Henkin (1975) in a detailed histological investigation of human fungiform papillae, while not supporting the existence of taste buds on the sides of these papillae, have also not specifically ruled them out.

With regard to von Bekesy's use of low concentration test solutions, it has been argued that such solutions would only stimulate the lowest threshold receptors on a papilla, making the papilla appear to have only a single sensitivity. However, higher concentrations of these test solutions would ensure that all stimulus sensitivities present in the

papilla are evoked. Such a problem is analagous to the example cited earlier in electrophysiological studies. In light of the above line of reasoning, Harper, et al., 1966), McCutcheon and Saunders (1972), and Bealer and Smith (1975) have all employed extremely concentrated test solutions in their studies.

Although the results of the latter investigators are in keeping with the theoretical analysis described above, the multiple sensitivity they found in individual papillae, as well as the ambiguous nature of the sensations produced in their subjects, is consistent with some of von Bekesy's (1966) early results, and may be in keeping with a neo-Müllerian mechanism of quality coding. In regard to the ambiguous sensation found in these studies, von Bekesy (1966, p. 5) notes that in his pilot work he stimulated the dorsal surface of fungiform papillae, and then stopped this procedure because "droplets placed on the top of the papillae did not produce, in general, clear taste sensations." Since the later investigators only stimulated the dorsal surface, the ambiguous taste sensations of their subjects are consistent with von Bekesy's findings. It is quite unfortunate, in light of this, that the later investigators did not attempt to stimulate the sides of papillae in their subjects.

The multiple sensitivity of papillae found in the studies by Harper et al. (1966), McCutcheon and Saunders (1972), and Bealer and Smith (1975) can also be accounted for within a neo-Müllerian mechanism because of the highly concentrated solutions they used. The explanation previously put forth is that such concentrations make possible the

stimulation of highly specific taste buds by non-adequate solutions, just as pressure on the eye will result in visual sensations. That such non-adequate stimulation of receptors may have occurred in the above investigations is evidenced by the large number of quality responses which were found to be "inappropriate" to the stimulating compound.

It appears to the author, that, as in the case of the electrophysiological data in animals, the major factor mitigating against a resolution of the psychophysical data on quality coding in man is the failure to undertake parametric variation of the concentration of test solutions. Such an undertaking, in conjunction with a comparison of dorsal vs. side stimulation of papillae would likely resolve the current discrepancies and provide an opportunity to test a number of other problems related to thresholds, intensity coding, intensity-quality interactions and concentration-area relationships.

Preliminary Experiments

Procedural variables in previous studies on chemical stimulation of human taste papillae have varied widely. These variables include 1) the method of drying the tongue prior to stimulus presentation, 2) the nature of the delivery system for presenting solution droplets, 3) whether or not feedback is given to S following his response, 4) whether or not a rinse is employed between trials, and 5) the length of the interstimulus interval (ISI). Since each of these variables can have a considerable effect on the outcome of single-papilla experiments, the following pilot

experiments were undertaken to assess the probable effect of a number of these variables on the current research.

Experiment 1A

In order to successfully stimulate a single papilla with a droplet of solution, it is necessary to dry the surface of the tongue. This is required to prevent the stimulus droplet from spreading to adjoining papillae. Von Bekesy (1966) achieved this end by allowing the tongue to remain in an atmosphere of 30% relative humidity for a short period of time before stimulation. The resulting evaporation of saliva was sufficient to allow stimulation of a single papilla without spread of the droplet. Bealer and Smith (1975) used the more expedient method of drying the tongue with a paper towel before stimulation.

While both procedures are adequate for drying the tongue surface, each has the potential to elevate the threshold to sapid solutions subsequently presented to the papillae. Allowing the tongue to dry by evaporation results in cooling of the tongue surface. Von Bekesy (1965), using electrical stimulation, has shown that, although the cooling of papillae does not affect their ability to mediate the "sour" and "salty" tastes, it does elevate the electrical thresholds for "sweet" and "bitter." Similarly, by patting the tongue dry with an absorbent material, the tactile stimulation may interfere with subsequent taste sensitivity. In addition, the nature of the absorbant material may be such as to leave minute particles or fibers on the surface of the tongue, thereby introducing a confounding taste stimulus.

Since the time consumed in drying the tongue by evaporation contributes to subject fatigue, a third alternative presents itself. This is to pass a controlled air stream across the tongue surface. This technique avoids the problems associated with patting the tongue with a foreign material, while shortening the length of time required to achieve a specified degree of dryness by the simple evaporation method. Obviously this technique does not avoid the problem of surface cooling, but rather, enhances it.

All of the above procedures possess the potential to elevate the threshold for a single papilla. Furthermore, even if the papilla is tested in its normal state, its threshold is likely to be well above the whole-mouth threshold due to the relative areas of receptor surface stimulated. Thus, the combined effect of these factors makes it difficult to estimate the practical range of solution concentrations to be used in single-papilla stimulation. The available literature is of little help in this regard since, as has already been pointed out, previous investigators have chosen extremes of the concentration range in their studies. In order to obtain an estimate of the practical range of concentrations to be used in the subsequent phases of this research, an experiment was undertaken to compare the sensitivity of a circumscribed area of the dorsal tongue surface to a small droplet of solution, with the concomitant whole-mouth sensitivity to the same volume droplet. In addition, a test of the effect of the three methods of drying the tongue on these sensitivities was carried out.

Subjects

Three females and one male, between the ages of 20 and 24, volunteered as subjects. All were either students at the University of Massachusetts at Amherst or were area residents. All aspects of their participation were in accordance with the rules set forth by the Subject Committee of the Department of Psychology and in accordance with the ethical standards maintained by the American Psychological Association.

Prior to participation each S was screened by the method reported in Meiselman and Dzendolet (1967) to insure a criterion level of taste sensitivity. This procedure required that each subject reach a criterion of 70% correct quality identification for each of four test solutions. The solutions were 25 mM sucrose, 0.008 mM quinine sulfate (QSO_4), 2 mM HCl, and 40 mM NaCl. In addition, none of the Ss were smokers, and none were under medication at the time of their participation.

Stimuli

The test solutions were chosen to be well above whole-mouth threshold, and consisted of 200 mM sucrose, 10 mM HCl (pH = 2.00), 1 mM QSO_4 and 2000 mM NaCl. These, as well as all solutions used in the experiments to follow were made from reagent grade chemicals, with the exception of sucrose, which was commercial grade. All solutions were mixed, within 1-3 days of their use, with distilled water obtained from the Botany Department at the University of Massachusetts. All were stored in glass containers at room temperature (25°C), with the exception of

sucrose, which was stored at 4°C. During testing, all solutions were at room temperature.

Procedure

Test sessions were conducted over a one-week period with each session lasting 60 minutes. At the start of each session S was seated at a small table adjacent to a sink, and his head positioned in a metal restraint. S was instructed to extend his tongue and to rest it on his lower lip, keeping his upper lip resting gently on the dorsal surface of the tongue, approximately 3 cm from the tip. After extending his tongue, S was exposed to one of three conditions for drying the tongue. In the "simple evaporation" condition S merely left his tongue extended for a period of 45 seconds. In the "air flow" condition a stream of air (25°C), produced by a blower, was passed across the dorsal surface of the tongue for 10 seconds. Finally, in the "pat dry" condition E gently patted the tongue with absorbant tissue paper. The extent of drying produced by each of these procedures was previously equated by visual inspection (under 10X magnification) of the spread of a 0.02 ml droplet of methylene blue, presented to the tongue with the aid of a medicine dropper.

Following exposure to one of the above three drying conditions, one of the four test solutions was presented to the dorsal surface of the tongue, using a 1.0 ml glass medicine dropper. The volume of the solution droplet was approximately 0.02 ml. Placement of the droplet was quasi-random across the anterior 3 cm of the tongue, with one droplet

of each test solution being presented to each quadrant of exposed surface. Each of the four test solutions was presented four times following each of the three drying conditions.

After presentation of the test solution S made two judgments of its taste quality. The first judgment was made immediately following presentation of the stimulus, while the tongue was still in an extended position. The responses available to S were those of "sweet," "salty," "sour," "bitter," "no taste," and "indistinct or vague" and were made by placing the appropriate side of a small labelled cube face-up on the experimental table.

After giving his quality response S retracted his tongue, moved the solution around in his mouth in a manner common to standard "sip and spit" methods, and gave a second quality judgment. S then rinsed his mouth with distilled water, expectorated, and awaited the next trial. An ISI of two minutes was maintained.

Results

Table I shows the percentages of correct quality identification for each of the three drying conditions and the two modes of tasting. Analysis of variance revealed significant effects due to drying condition ($F = 132.25$, $df = 2/6$, $p < .05$) and mode of tasting ($F = 38.92$, $df = 1/3$, $p < .05$). The interaction effect was not significant. Newman-Kuells contrasts among the means for the three drying conditions showed that the "simple evaporation" method produced significantly better quality discrimination ($p < .05$) than either the "air flow" or "pat dry" methods,

Table I

Percentage of correct taste quality identifications under 3 conditions of tongue drying and 2 modes of tasting

Mode of Tasting	Subject	Evaporation	Air-Flow	Pat Dry
Dorsal Tongue Only	SC	87.50	50.00	62.50
	MS	56.25	6.25	12.50
	DP	62.50	18.75	31.25
	DS	43.75	6.25	6.25
	*Combined Ss	62.50	20.31	28.13
Whole Mouth	SC	100.00	81.25	75.00
	MS	75.00	68.75	68.75
	DP	93.75	50.00	50.00
	DS	87.50	50.00	56.25
	*Combined Ss	89.06	62.50	62.50

Note: Each value represents the percentage of correct taste quality responses to four presentations of each of four test compounds. The test solutions were 200 mM sucrose, 1 mM QSO_4, 20 mM HCl, and 2000 mM NaCl.

*Combined percentages for all four subjects; each value based on 64 presentations.

but that the latter two did not differ from one another.

Discussion

It is clear from these data that the method of drying the tongue is an important variable affecting taste quality identification. Simple evaporation is far superior to streaming air across the tongue or patting the tongue dry. It is likely that the failure of the "pat dry" technique was due to interference by the tactile stimulation which preceded the taste stimulus. It may be possible to circumvent this problem by allowing a longer period of time to elapse between the time the tongue is patted and the time that the stimulus is presented. However, in view of the poor discrimination using this procedure, a very long waiting period would probably be required. The failure of the "air flow" method is most likely the result of the very rapid cooling of the tongue surface which occurs in this condition, as compared to the relatively gradual cooling which results from simple evaporation.

In light of the above results it is concluded that simple evaporation of the tongue for a period of 45 seconds is the best method of drying to use in single-papilla research, since it results in the least decrement in taste quality identification.

The relatively poor taste quality identification following dorsal stimulation of the tongue, compared to when Ss were allowed to retract their tongue and taste in a whole-mouth manner, was not an unexpected result. The cooling of the tongue even in the simple evaporation condition, combined with the smaller total area of stimulation could easily

account for this difference, even though solution volume was controlled between the two conditions by the repeated judgment procedure. However, the nature of the percentages in Table I, being percentages of correct quality identifications, do not allow for the assessment of whether the decrements among groups were due to a loss of sensitivity or a loss of discrimination. Table II contains a breakdown of the incorrect responses in each condition, that does allow for such an assessment. The values shown in Table II are the percentages of "errors of detection," i.e., S responded "no taste" or "indistinct or vague" to the test solution, and the percentages of "errors of recognition," i.e., S reported a taste quality which was not the characteristic one for that solution.

An examination of the data of Table II indicates that the type of errors differed among conditions. As a rule, regardless of drying method, the errors made in the "whole-mouth" condition were primarily those of detection. However, in the "dorsal tongue only" condition an equal number of errors of detection and errors of recognition occurred. This indicates that when the solutions were presented to the dorsal tongue surface, Ss frequently misnamed the taste of the solution; however, upon retracting the tongue and spreading the solution around in their mouth, Ss identified the solution correctly. The frequent misnaming of taste qualities in the "dorsal tongue only" condition may be the result of guessing on the part of S, or it may be due to a true taste confusion between two or more qualities. If such misnaming is the result of guessing, it would be important to establish this, so that appropriate precautions could be taken to avoid such guessing in the

Table II

Analysis of the errors made in each condition of Experiment 1A. Recorded values are the percentages of errors of detection and errors of recognition from the total number of errors made in each condition

	EVAPORATION		AIR-FLOW		PAT DRY	
Mode of Tasting	Errors of Detection	Errors of Recognition	Errors of Detection	Errors of Recognition	Errors of Detection	Errors of Recognition
Dorsal Tongue Only	50.0	50.0	45.1	54.9	52.2	47.8
Whole Mouth	71.4	28.6	75.0	25.0	83.3	16.7

single-papilla studies to follow. Similarly, if the misnaming is the result of a true psychological or physiological confusion, this fact would be important in the interpretation of the frequent misnaming of solutions reported in single-papilla studies by Harper et al. (1966), McCutcheon and Saunders (1972) and Bealer and Smith (1975).

Experiment 2A

In order to assess whether the misnaming of taste qualities in Experiment 1A was the result of guessing or the result of a more fundamental confusion, the following experiment was undertaken.

Subjects

All Ss were the same as in Experiment 1A.

Stimuli

The test stimuli were identifical to those used in Experiment 1A.

Procedure

Although the procedure was similar to that of Experiment 1A, it differed from it by employing only the "simple evaporation" method of drying the tongue. All other aspects of procedure were the same.

Each of the four test solutions was presented eight times to each S for a total of 32 presentations of each solution. Since S judged the taste of each solution twice, once after dorsal tongue stimulation and again when the solution was retracted and tasted whole mouth, each solution was judged a total of 32 times in each condition.

Results

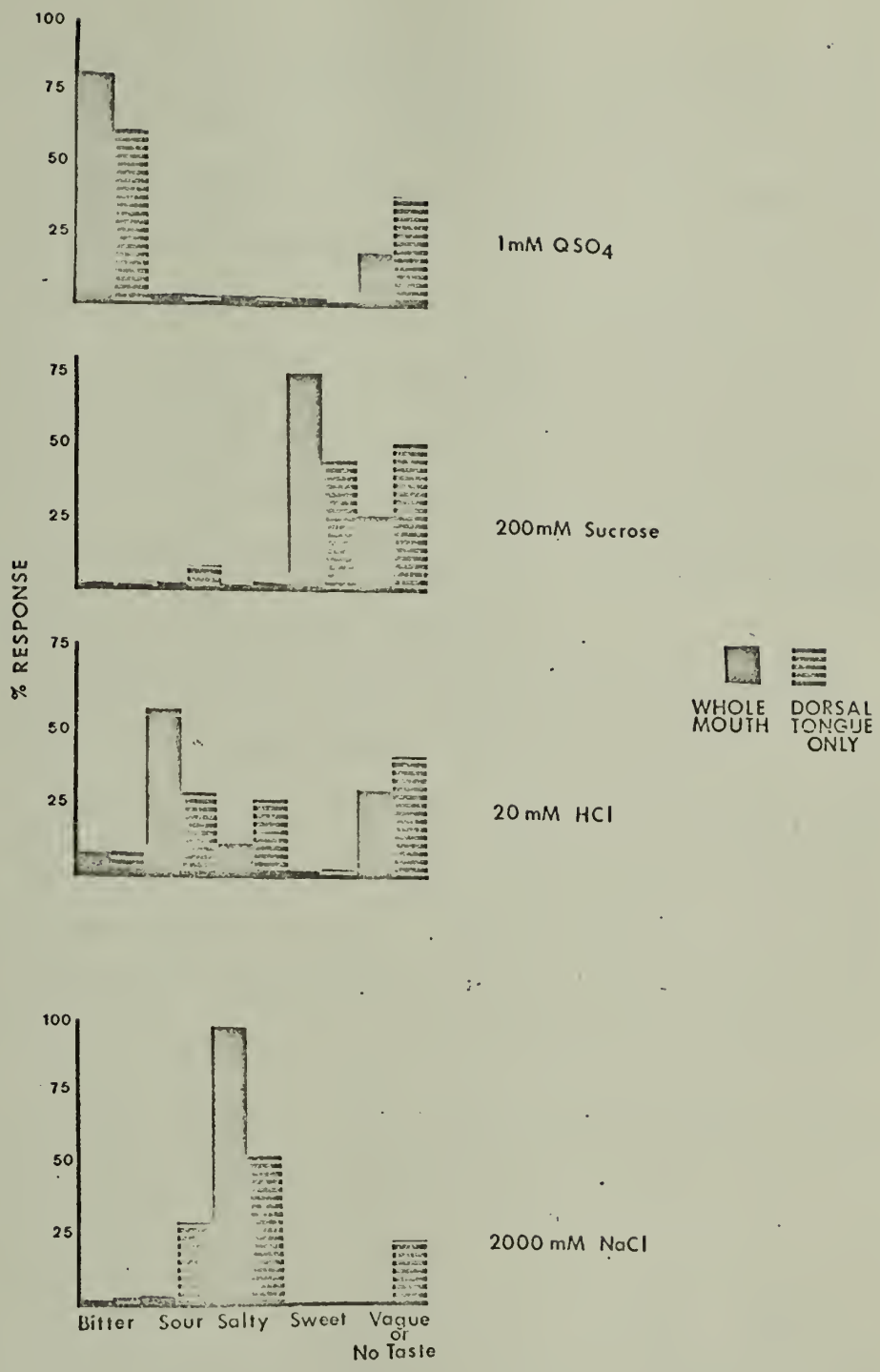
The data were plotted as histograms (Figure 1) showing the percentages of each taste quality response given to each solution under the two modes of tasting. Looking at these data it is clear that for all four solutions the percentage of "vague" and "no taste" responses were lower in the "whole-mouth" condition than in the "dorsal tongue only" condition. This indicates a difference in sensitivity between the two conditions. However, in looking at the difference in quality reports between the two conditions it is clear that for both HCl and NaCl there is a more frequent misnaming of the solutions in the "dorsal tongue only" condition. This misnaming is minimal in the whole mouth condition, and does not occur in any condition for sucrose or QSO_4. It can be seen from Figure 1 that the misnaming which occurs is that of calling HCl "salty" on numerous occasions and also that of calling NaCl "sour" on numerous occasions.

Discussion

If the misnaming of solutions in this condition was a result of guessing, then it would be expected that each solution would exhibit the same frequency of misnaming and that the misnaming would be random among qualities. This is clearly not the case in these data, and thus, points to some psychological or physiological confusion between the sour and salty qualities.

Although a sour-salty confusion has not been explicitly reported in the literature, as has been the case for the more common sour-bitter

Figure 1 Histogram of the percentages of each taste quality response under two different modes of tasting.


100
75
50
25
1mM QSO4
75
50
25
200mM Sucrose
% RESPONSE
75
50
25
20 mM HCl
WHOLE MOUTH
DORSAL TONGUE ONLY
100
75
50
25
2000 mM NaCl
Bitter
Sour
Salty
Sweet
Vague or No Taste

confusion (see Meiselman and Dzendolet, 1967; Robinson, 1970; Gregson and Baker, 1973; and McAuliffe and Meiselman, 1974), there have been allusions to such a confusion. Moncrieff (1967, p. 487) states that "the salt taste is often associated with the bitter and sour tastes" while von Skramlik (1926) states that "the taste description "salty-sour"....is not rare," and that "it is difficult to find salts that only taste salty and do not at the same time taste sour or bitter." In addition, the ionic nature of the stimuli for the sour and salty tastes, compared to those for bitter and sweet, lends itself readily to the suggestion of a sour-salty confusion.

Aside from such anecdotal support for a sour-salty confusion, much of the work by von Bekesy (1964b, 1965) points toward an integral relationship between these two qualities. Thus, his "duplexity theory of taste" (von Bekesy, 1964b) postulates that there exist two distinct groupings of taste qualities in man: "sour and salty" versus "sweet and bitter." The data upon which he bases his theory is his own work on the lateralization phenomenon on the tongue and on the electrical thresholds for single papillae. The first phenomenon occurs when equally intense solutions are placed on either side of the midline of the tongue. A similar phenomenon occurs for any pair of stimuli with the qualities of sweet, bitter, or warm. No interaction occurs between members of different groups. Von Bekesy concluded from this that there are two distinct groups of qualities with some common characteristics among members of each group. As further support for this theory, von Bekesy

(1964a) has shown that the frequency of maximal sensitivity to electrical stimulation of single papillae is about the same for "salty" and "sour" papillae, but much higher for "sweet" and "bitter" papillae. Similarly, von Bekesy (1965) has shown that cooling of "salty" and "sour" papillae does not affect the voltage threshold for these papillae, whereas cooling does affect the thresholds for "sweet" and "bitter" papillae.

Although all of the above are merely suggestive, the data of Experiment 2A argue strongly that such a confusion does, in fact, exist, at least in the subject population of this experiment.

Experiment 3A

Assuming that the sour-salty confusion of Experiment 2A is real, three questions immediately present themselves:

1) Is the confusion peculiar to the high concentration of HCl and NaCl used in Experiment 2A?

   This is a distinct possibility since "sting" is a common sensation reported in response to high concentrations of NaCl (Holway and Hurvich, 1937), and this trigeminal component may be confused with the "sting" of HCl at high concentrations.

2) Does the presence vs. absence of saliva affect the confusion?

   This is an important consideration in deciding whether or

not to use a rinse in the single-papilla research to follow.

3) Is the cooling of the tongue through evaporation responsible for the confusion?

This may be a possibility if cooling differentially effects different receptor types.

In order to answer these questions, the following experiment was undertaken.

Subjects

The subjects were the same as in Experiments 1A and 2A.

Stimuli

Solution concentrations were chosen to encompass the range in which both NaCl and HCl acquire a "stinging" or "biting" quality when tasted whole-mouth. These concentrations were 10, 15, 20, 25, 30, and 40 mM HCl (pH = 1.96, 1.82, 1.70, 1.60, 1.52, 1.40) and 500, 1000, 1500, 2000, 2500, 3000, and 3500 mM NaCl.

Procedure

Prior to each trial, S extended his tongue to expose approximately 3 cm of its dorsal surface in the same manner as Experiments 1A and 2A. Upon the instruction of E, S either rinsed his tongue with distilled water from a plastic squeeze bottle or did nothing. E then immediately presented a 0.02 ml droplet of solution, in the same manner as described in previous experiments. S was allowed to choose among the same quality

descriptors as before, and he made his response in a similar manner. After responding, S rinsed his tongue, retracted it, and awaited the next trial.

Whether S rinsed his tongue or not, prior to presentation of the stimulus, was random from trial to trial, as were the solutions presented on each trial. Each solution was presented 12 times under both the "rinse" and "no rinse" conditions for each S. A three-minute ISI was employed.

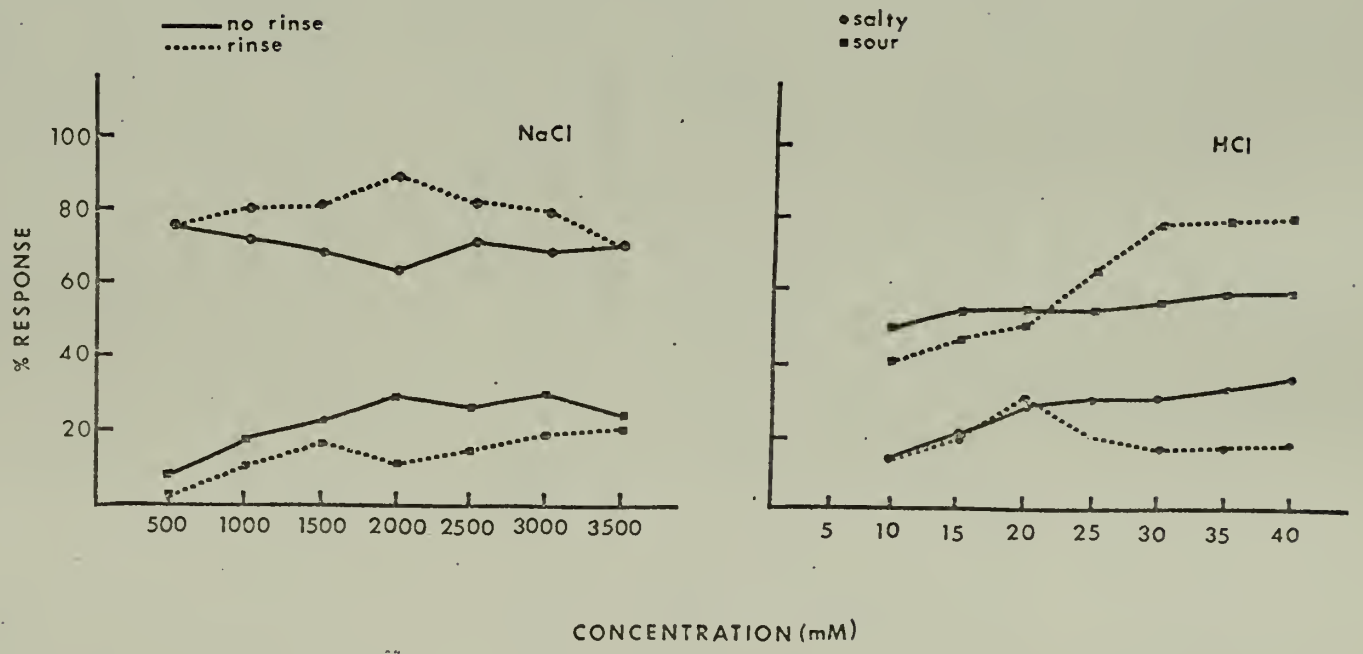
Results

The grouped data are plotted in Figure 2 as the percentage of sour and salty responses out of the total number of responses given to each solution concentration. Responses other than sour or salty were minimal across subjects and solutions, totalling 99 out of 1,248 presentations ($<7\%$). Most of these 99 responses were either "no taste" or "indistinct or vague" responses given at the lower concentrations in both the "rinse" and "no rinse" conditions. A small number (18) were bitter responses given to various concentrations of HCl by two of the Ss.

The solid lines in Figure 2 represent responses in the "no-rinse" condition, while the dashed lines represent responses in the "rinse" condition. It is clear from these data that a certain degree of confusion occurs at all concentrations of both test compounds and in both the "rinse" and "no rinse" conditions.

In order to assess the degree of confusion as a function of both concentration and rinse condition, a "discrimination index" was calculated

Figure 2 Plot of the percentages of sour and salty quality reports as a function of concentration of NaCl and HCl.


no rinse
rinse
NaCl
% RESPONSE
100
80
60
40
20
500
1000
1500
2000
2500
3000
3500
salty
sour
HCl
5
10
15
20
25
30
35
40
CONCENTRATION (mM)

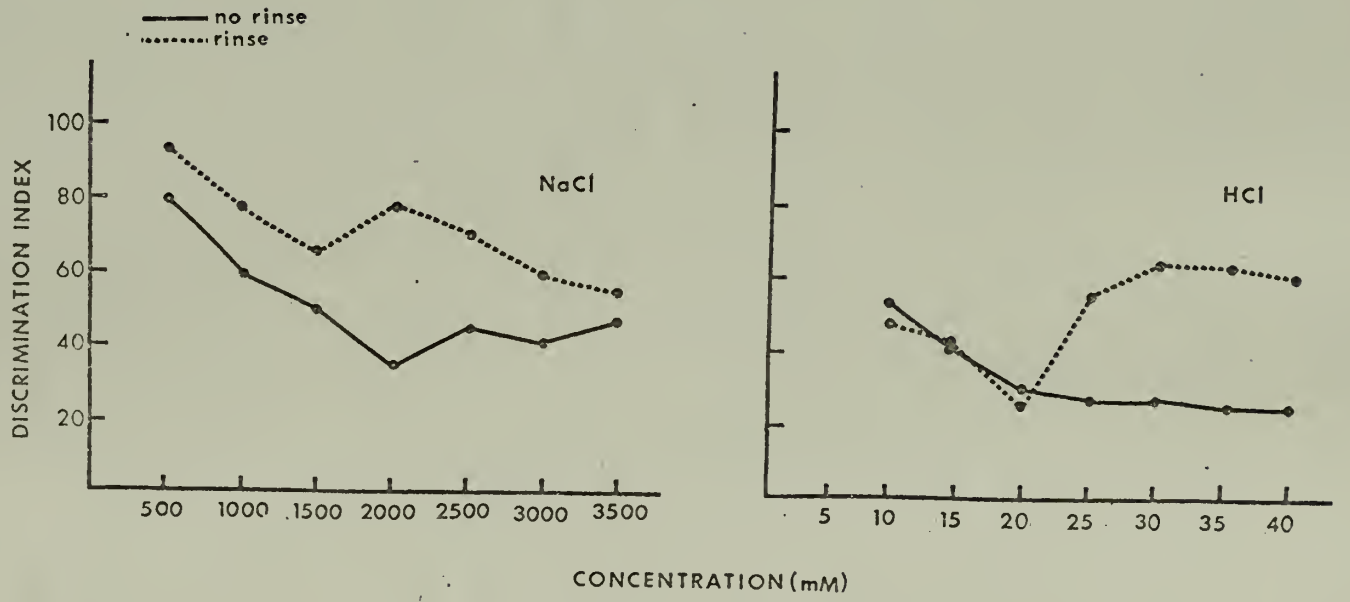
and the data re-plotted in Figure 3. The "discrimination index" of Figure 3 is defined as the difference between the percentage of sour and salty responses out of the total number of sour and salty responses given at any concentration. Thus, an index of 100 indicates complete discrimination of the two qualities, while an index of 0 indicates complete confusion between the qualities.

As is evident from Figure 3 there is a slight increase in confusion with increasing concentrations of NaCl and HCl in the "no rinse" conditions. For NaCl, the "rinse" condition shows a similar increase in confusion with increasing concentration, but the absolute level of discrimination is higher at all concentrations. For low concentrations of HCl the confusion in the "rinse" condition is no different from that in the "no rinse" condition. However, at the higher concentrations of HCl the "rinse" condition shows a marked decrease in confusion over that of the "no rinse" condition.

Discussion

Since the tongue was not dried in this experiment, yet the sour-salty confusion is as prevalent in these data as in the data of Experiments 1A and 2A, it can be concluded that the cooling of the tongue by evaporation in the previous experiments did not contribute significantly to the confusion. The fact that the confusion did tend to increase with increasing concentrations supports the notion that the trigeminal component of taste at these concentrations contributes, in some way, to the confusion. However, this is certainly not the entire basis of the

Figure 3 Plot of the "discrimination index" for "sour-salty" confusion as a function of the concentration of NaCl and HCl.


no rinse
rinse
DISCRIMINATION INDEX
100
80
60
40
20
NaCl
500
1000
1500
2000
2500
3000
3500
HCl
5
10
15
20
25
30
35
40
CONCENTRATION (mM)

confusion, since the saliva also appears to play some role, as is evidenced by the difference in confusion between the "rinse" and "no rinse" conditions.

A tenable explanation of the effect of rinsing on the sour-salty confusion depicted in Figures 1 and 2 derives from the chemical properties of saliva. As Bartoshuk (1964, 1968, 1974) and McBurney (1969, 1971, 1973) have shown in their work on cross-adaptation and "water taste," the sodium and chloride content of human saliva is sufficiently high (.0035 - .024 M Na and .0084 - .018 M Cl; Altman and Dittmer, 1961) so as to act as constant adapting concentrations for the tongue. Thus, concentrations of NaCl below this adapting concentration do not taste salty, but rather, bitter or sour. Similarly, the effective concentration of NaCl solutions above the salivary concentration are correspondingly reduced. This situation is analagous to that of presenting a visual stimulus under conditions of light adaptation. However, by rinsing the adapting saliva, as was done in the "rinse" condition of this experiment, the test solution of NaCl retains its total stimulating effectiveness. This would result in a more effective stimulation of salt receptors at all concentrations and account for the reduction in confusion found at all concentrations of NaCl in the "rinse" condition.

The effect of the rinse condition on the confusion to HCl is more difficult to explain. The fact that the effect is different at different concentrations implies that two separate factors may be operating. One possible combination of factors is the loss of both salivary chloride and salivary buffering agents in the "rinse" condition.

Since saliva is somewhat basic, it has a neutralizing effect on acids. If the saliva is removed by rinsing, it would be expected that acid solutions would become more effective in their ability to stimulate sour receptor sites. Thus, one would expect a general decrease in confusion at all concentrations of HCl. This is certainly the case at high concentrations in the present experiment, but is not the case at lower concentrations. However, if it is assumed that both the anion and cation of salts contribute to their overall taste, then there must exist receptor sites specifically sensitive to the chloride ion of salts. Since saliva also contains a large amount of chloride, these ions must bind to these receptor sites and contribute to the resting adaptation state of the tongue, as suggested by Bartoshuk (cited above). By rinsing the saliva, relatively more receptor sites responsive to chloride ions become available. If an HCl solution is then presented, the chloride ions of the solution should stimulate these receptors and contribute a salty component to the solution. This would obviously facilitate a sour-salty confusion. However, with more concentrated HCl solutions, the relative contribution of these "additional chloride sites" would be minimal when compared to the stimulation of sour receptors by the hydrogen ions. Whether the concentration range in which these mechanisms interact is actually the same as in the present experiment, is an empirical question. However, no other explanation for the differential effect of rinsing on the sour-salty confusion to HCl is readily apparent.

Whatever the mechanism(s) for the effect of rinsing in the present experiment, it is clear that a distilled water rinse has a generally

favorable effect on the sour-salty confusion of Ss. As such, a rinse following single-papillae stimulation should have little detrimental effect on subsequent trials, particularly if a reasonable length of ISI is employed.

While Experiments 1A, 2A, and 3A provide information about the conditions under which the sour-salty confusion occurs, they do not address themselves to the more fundamental problem of why this confusion only occurs when stimuli are restricted to the dorsal tongue surface. Neither do these experiments provide information about whether the confusion is psychological or physiological in nature, or some combination of both.

One plausible physiological explanation of the sour-salty confusion reported in these experiments derives from a Neural Pattern Interpretation view of quality coding. This explanation would hold that the distribution of receptor types on the tongue, compared to that of the entire oral cavity, is different. Thus, stimulation of only the dorsal tongue surface results in a different pattern of neural discharge than stimulation of the entire oral cavity, and a corresponding difference in quality is to be expected. Evidence for this view comes from the work on taste localization on the tongue, palate, and pharynx of man by Henkin and Christiansen (1967). By anesthetizing either the tongue or the palate of their subjects and then determining detection and recognition thresholds to sucrose, HCl, NaCl and urea, these investigators were able to show that anesthesia of the palate elevated only the thresholds for sour and bitter, while anesthesia of the tongue elevated only the thresholds for sweet and salty. These data suggest that

receptor types for each of the four taste qualities are, in fact, unevenly distributed between the tongue and palate of man.

The major importance of the sour-salty confusions found in these preliminary experiments involves the effect it will have on the single-papilla research to follow. However, the nature of the data do not permit one to predict beforehand what that effect might be. Certainly, if a similar confusion manifests itself in the single-papilla data, the results of Experiments 1A, 2A, and 3A will be of great importance in evaluating those results.

Single Papilla Experiments

Methodological Considerations

The original intent of the preliminary experiments was to obtain empirical information about the best procedures to be used in the single-papilla experiments. However, the unexpected occurrence of the sour-salty confusion led to a re-focusing of these experiments. Nevertheless, two major aspects of procedure were settled by these experiments, namely, the method to employ in drying the tongue, and whether or not to use a rinse following presentation of the stimulus. The remaining problems of methodology are those concerning the length of the ISI, whether feedback should be given to S, and the nature of the delivery system for presenting solution droplets.

The length of the ISI, while an important factor in single-papilla research, is relegated to secondary importance, once it has been decided that a rinse will be used. Von Bekesy, who did not use a rinse, chose

a 10-minute ISI. Later investigators, who have used a rinse, have chosen ISI's on the order of 20-60 seconds; however, the extremely high solution concentrations used by these investigators probably warrant a somewhat longer ISI. The ISI chosen for use in the experiments that follow (two minutes), reflects a compromise between the extremely long ISI used by von Bekesy and the much shorter ISI's used by later investigators.

With regard to subject feedback, McCutcheon and Saunders (1972) and Bealer and Smith (1975) both used a training procedure in their studies. Their procedure was to train their subjects by repeatedly presenting solutions representative of the four taste qualities, allowing the subject to give his quality response, and then informing the subject of the stimulus chemical applied. While such a procedure would obviously stabilize subjects' responses to a given chemical, it is not clear what problems a conditioning procedure of this nature would have on the interpretation of results. Certainly, the most obvious problem would be in determining whether the reported qualities are actually those that would have been chosen by the subject under normal conditions, or whether they are simply verbal labels that have been learned to be used in response to the overall sensation aroused by a particular chemical. It is certainly conceivable that a chemical which produces a particular sensation may have an ambiguous quality, i.e., it does not fall into one of the four primary taste categories of salty, sweet, sour, or bitter. However, telling the subject that the solution was a "salt solution" or a "sugar solution," would predispose the subject to respond "salty" or "sweet" to the next occurrence of that chemical, although the true

quality, as perceived by the subject may be neither. Perhaps a better training procedure to stabilize responses would be to give feedback of the form: "that was solution A" or "that was solution B." In this way the subject is trained to become aware of sensory aspects common to a given chemical without predisposing his description of their quality. However, even this procedure predisposes the subject to use only a specific number of taste names, determined by the number of test solutions. For this reason, no training procedure was used in the single-papilla experiments to follow.

The last methodological problem to be considered here is concerned with the type of delivery system to be used in presenting solution droplets to single papillae. As this issue is an important one for the research at hand, considerable time was spent deciding on a suitable system. Five different delivery systems were tested. Appendix A contains a discussion of the relative merits of each type of stimulator and the basis upon which the stimulator used in this research was chosen.

Experiment I

The initial experiment was designed to isolate in each S a number of fungiform papillae that would respond to chemical stimulation.

Subjects

Three of the four Ss were the same as in the preliminary experiments. One female from the original group of Ss was eliminated from further participation due to a marked change in her overall taste sensitivity.

This S had undergone a marked loss of body weight during the intersession between the end of the preliminary experiments and the start of the single-papilla experiments. Upon noticing a decrement in sensitivity during the initial stages of this experiment, this S was retested, using the original screening procedure, and failed to reach the established criterion for participation. As a result, she was eliminated from the study and replaced by another S. The final group of Ss used in all the single-papilla work consisted of two males (DP and EG) and two females (MS and SC) between the ages of 18 and 25. With the exception of one male (EG), all had participated in the preliminary experiments and none were on medication at the time of their participation. In addition, on test days, Ss were requested not to eat, drink, or smoke (one S, EG, was a light smoker) within one hour of the time of their participation.

Apparatus

The apparatus consisted of a series of disposable plastic 1 ml tuberculin syringes (Becton-Dickinson), fitted with 33-gauge (0.004" inner diameter, 0.25" shaft length) blunt stainless steel hypodermic needles (Vita Needle Company, Needham, Massachusetts). Solutions were drawn into the syringes from a series of 50 ml plastic containers and the loaded syringes were then held in a syringe rack built for that purpose. During testing, the syringes and syringe rack were hidden from S's view by a cardboard screen.

S sat at a small experimental table adjoining a stainless steel sink. During testing, S's head was positioned in a metal head-rest and

his/her hands folded on the experimental table to provide for greater stability of the tongue. Light was provided by overhead fluorescent room lights and by a small fluorescent lamp suspended above S and directed on the tongue surface.

E sat opposite and slightly above S at the experimental table. A wooden armrest, covered with non-skid material, was used to steady E's arm, and, thus, to aid in the positioning of droplets on the tongue. An adjustable binocular dissecting microscope (Nikon, Model Number 64213) with 12 - 60 x magnification was positioned between E and S. Focusing of the microscope could be effected with one hand while the other hand positioned the tip of the syringe needle onto a papilla. This arrangement provided for continuous focusing of the tongue surface under high magnification without interference from minute movements of the tongue.

After each session the test needles and syringes were washed, allowed to soak in water, and then rinsed thoroughly. In addition the same syringes and needles were used with the same solutions from one session to the next.

Further considerations about the apparatus (particularly the use of the syringe stimulator) can be found in Appendix A.

Stimuli

Test solutions consisted of 700 mM sucrose, 2 mM QSO_4, 30 mM HCl (pH = 1.52), and 2000 mM NaCl. All were mixed and stored in the same manner as described in previous experiments.

Procedure

During the initial sessions tongue maps of the fungiform papillae on the anterior 3 cm of the tongue were drawn for each S under slight magnification. These maps were drawn in order to make repeated observations on the same papillae, and they were used throughout all of the single-papilla experiments.

After assigning identifying numbers to the mapped papillae, testing began. Papillae to be tested were chosen quasi-randomly, with an attempt made to sample evenly across the anterior portion of the tongue. On each trial S would extend his tongue for a period of about 45 seconds to allow it to dry. (This time varied somewhat from session to session depending on the relative humidity of the atmosphere. The actual time of drying was determined empirically at the start of each session by placing a droplet of distilled H_2O on a random papilla and observing the amount of spread following a series of different drying times). After the tongue was dry, a 0.05 μl droplet of test solution was presented to the dorsal surface of the papilla. The procedure for doing this was to place the tip of the syringe needle directly over the papilla to be stimulated. Slight pressure on the syringe plunger would then cause a droplet of solution to appear at the tip. The volume of this droplet was varied by pressure changes on the plunger. After adjusting the size of the droplet to the desired volume, a slight lowering of the needle tip brought the solution droplet into contact with the dorsal surface of the papilla, allowing it to be deposited with a minimum of tactile interference. Immediately after its presentation the droplet was observed, in order to

insure that it remained on the papilla and did not spread to adjoining papillae or tissue. Occasional trials on which such spread occurred were invalidated, and the trial was repeated.

Following presentation of the stimulus S reported its taste quality. Available responses were those of "sweet," "sour," "salty," "bitter," "no taste," and "indistinct or vague," and were made by selecting the appropriate side of a small response cube and placing it face-up on the experimental table. In this manner S was able to make his response without retracting his tongue, in the same manner as in the preliminary experiments. An additional response alternative was provided by allowing S to write the words "complicated taste" on an erasable pad, and following this response with a written description of the taste. This alternative was provided to insure that responses were not restricted to the four primary taste qualities.

After making a response, S rinsed his/her tongue with distilled H_2O from a plastic squeeze bottle, retracted his/her tongue, and awaited the next trial. A two-minute ISI was employed.

Each papilla was tested twice with each solution. After any one papilla was stimulated it was not retested with a second solution until at least five other papillae had been tested. This procedure established an effective 10-minute ISI for each papilla. Solutions were presented in random order to all papillae. If on any trial, stimulation of a papilla resulted in a quality report of "sweet," "sour," "salty," "bitter," or "complicated taste" that papilla was designated as a "chemically responsive" papilla and no further testing was done on it. If stimulation of a

given papilla resulted in only "no taste" or "indistinct or vague" reports, then testing of that papilla continued until each of the four solutions had been presented twice. If at that time the papilla had not responded with a taste quality, then it was designated as a "chemically non-responsive" papilla. Testing continued until a total of 10 chemically responsive papillae had been identified in each S.

Results

Figures 4-7 are the tongue maps for each S, showing the relative size, location and distribution of fungiform papillae on the anterior 3 cm of the dorsal surface of the tongue. These maps do not show all of the fungiform papillae present on the tongue, but rather, those that were easily identifiable and relatively uncrowded by adjoining papillae. The numbers on Figures 4-7 are identifying numbers for the papillae.

Since testing of papillae was random and continued until 10 chemically responsive papillae were found, the relative number of chemically responsive and nonresponsive papillae found during this testing is an indication of the proportion of each to be found in the total population. Table III gives the identifying numbers of those papillae in each S which were found to be chemically responsive or nonresponsive. In addition, it gives the percentages of each type of papilla found in each S, and the total percentages across Ss.

In order to determine the distribution of responsive vs. nonresponsive papillae on the tongue, a composite map of the location of these papillae was made and appears as Figure 8.

Figure 4 Tongue map showing the relative size, location and distribution of fungiform papillae, and their identifying numbers for subject SC.

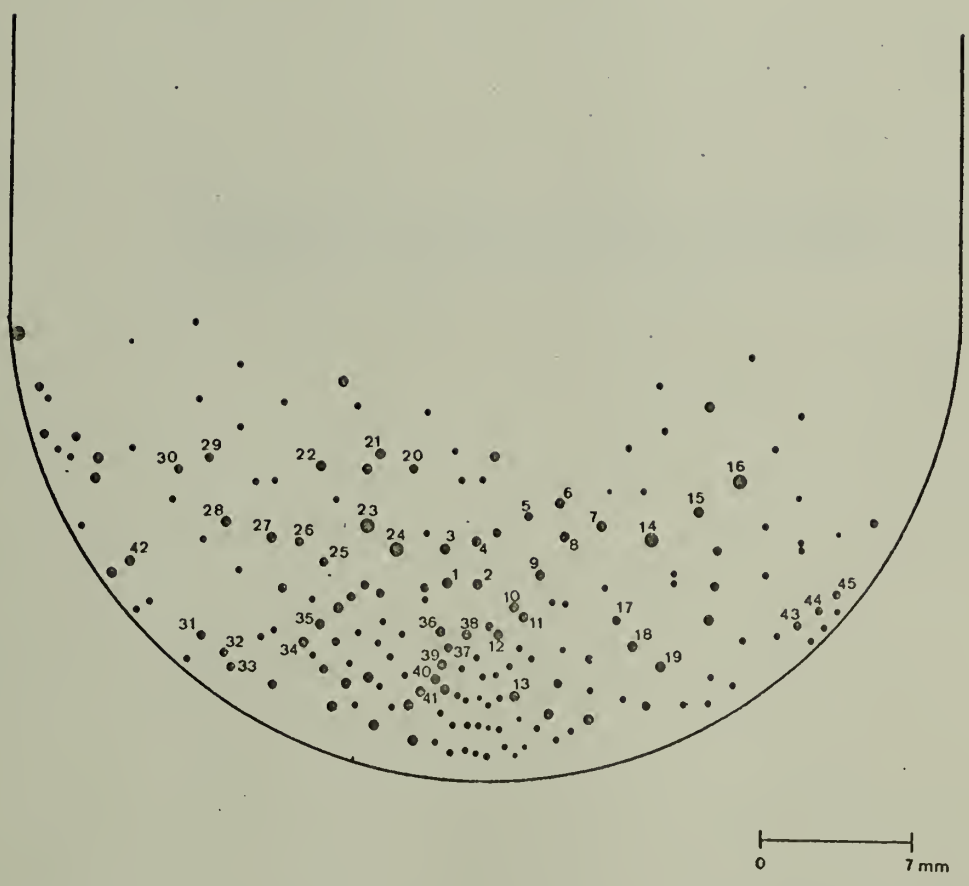

SC
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
0
7 mm

Figure 5 Tongue map showing the relative size, location and distribution of fungiform papillae, and their identifying numbers for subject MS.

MS

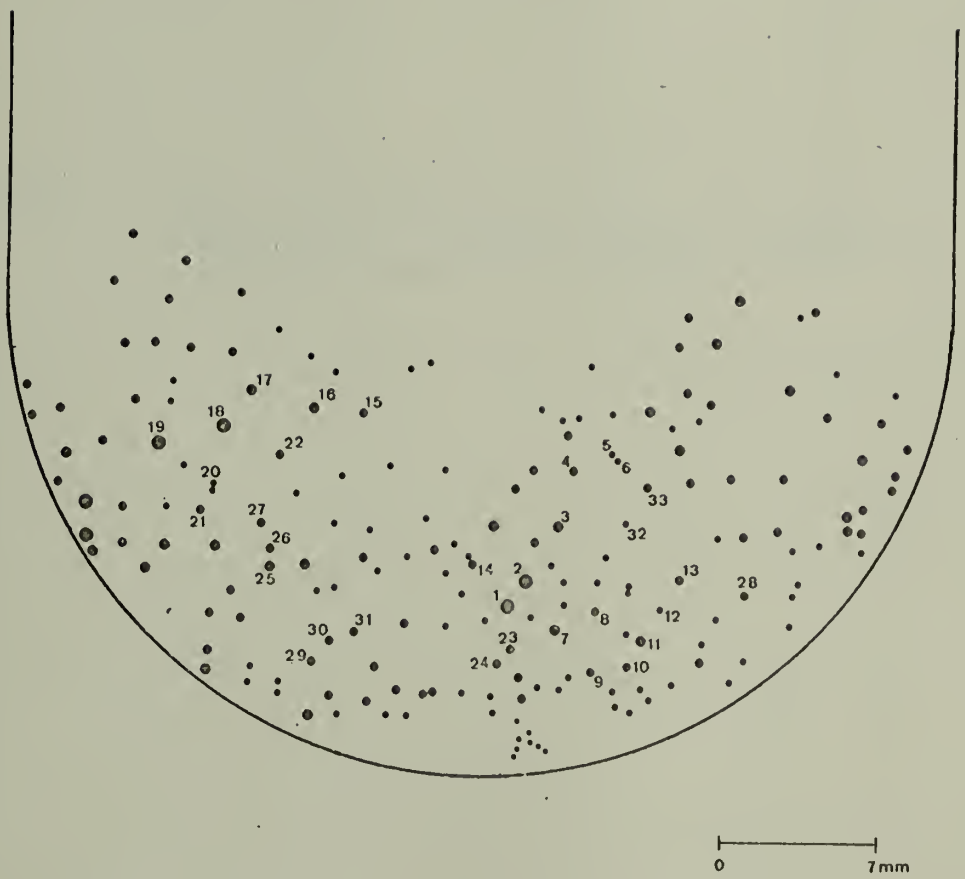
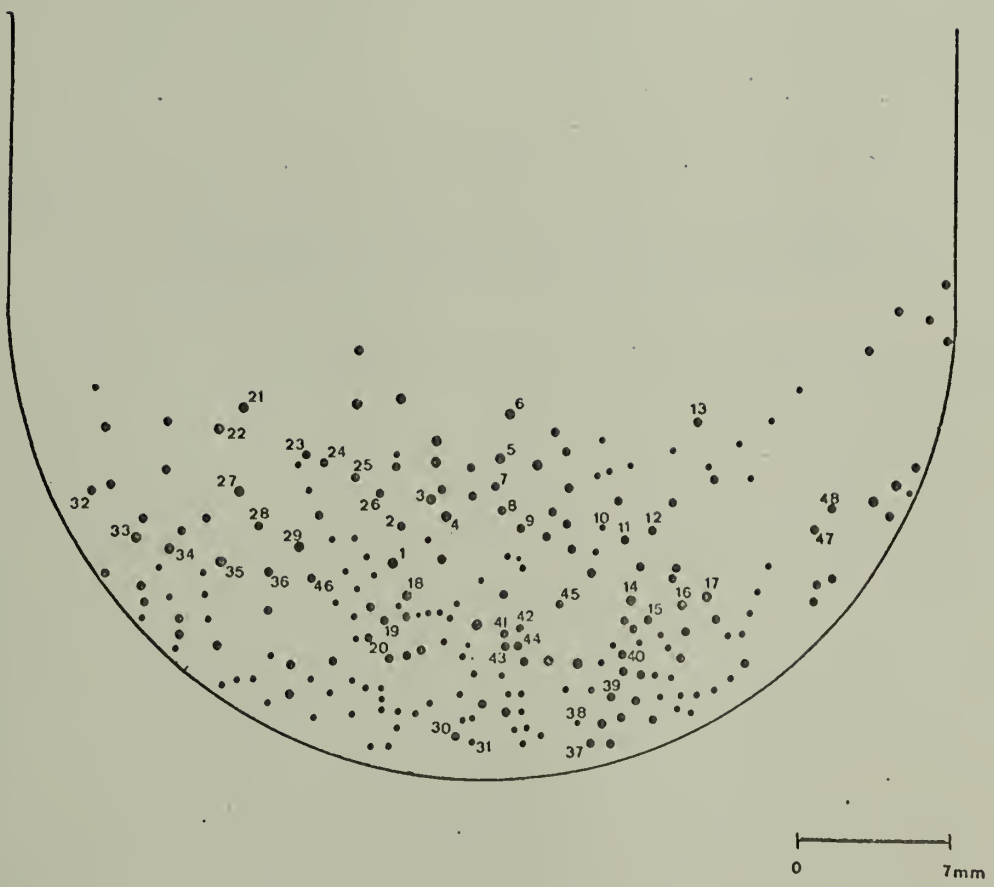

17
16
15
18
19
22
20
27
21
26
25
30
31
29
14
2
1
23
24
3
32
33
4
5
6
13
28
8
12
7
11
10
9
0
7mm

Figure 6 Tongue map showing the relative size, location and distribution of fungiform papillae, and their identifying numbers for subject DP.

DP


1
2
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4
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6
7
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9
10
11
12
13
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21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
0
7mm

Figure 7 Tongue map showing the relative size, location and distribution of fungiform papillae, and their identifying numbers for subject EG.

EG

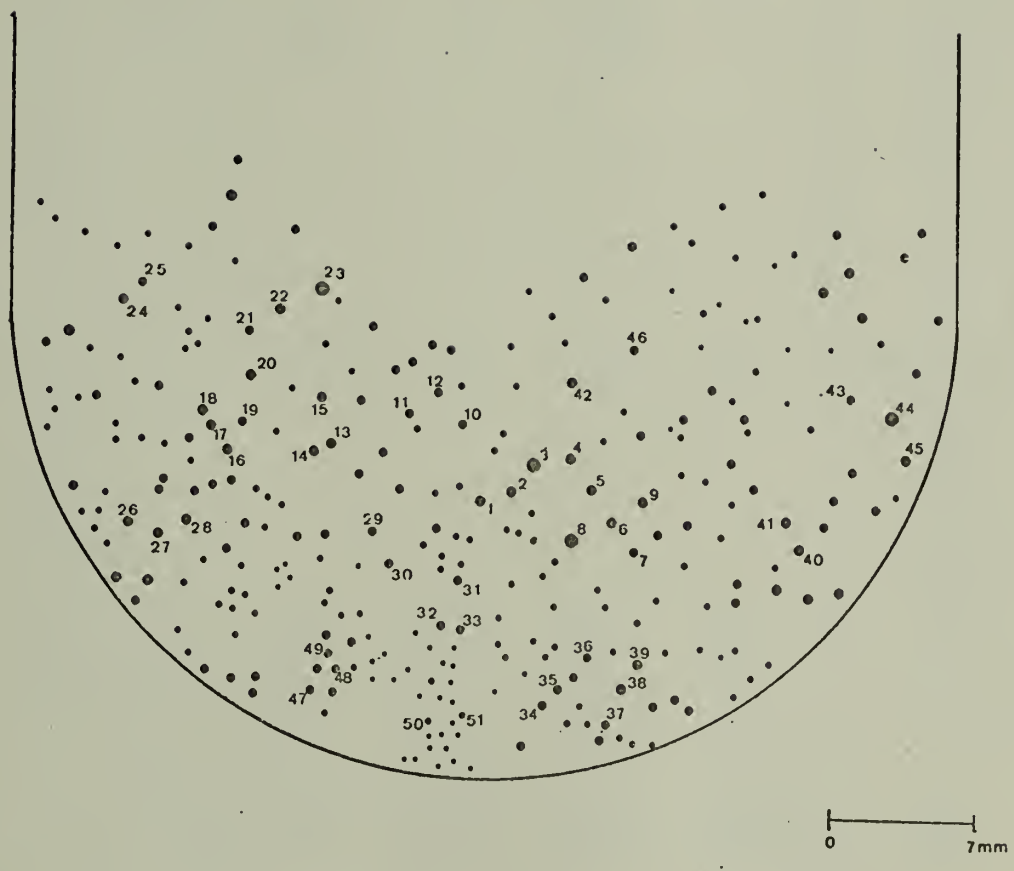

25
23
24
22
21
20
18
19
15
11
12
10
42
46
43
44
17
13
14
16
1
4
2
5
9
45
26
28
29
1
8
6
41
27
7
40
30
31
32
33
49
36
39
48
35
38
47
50
51
34
37
0
7mm

Table III

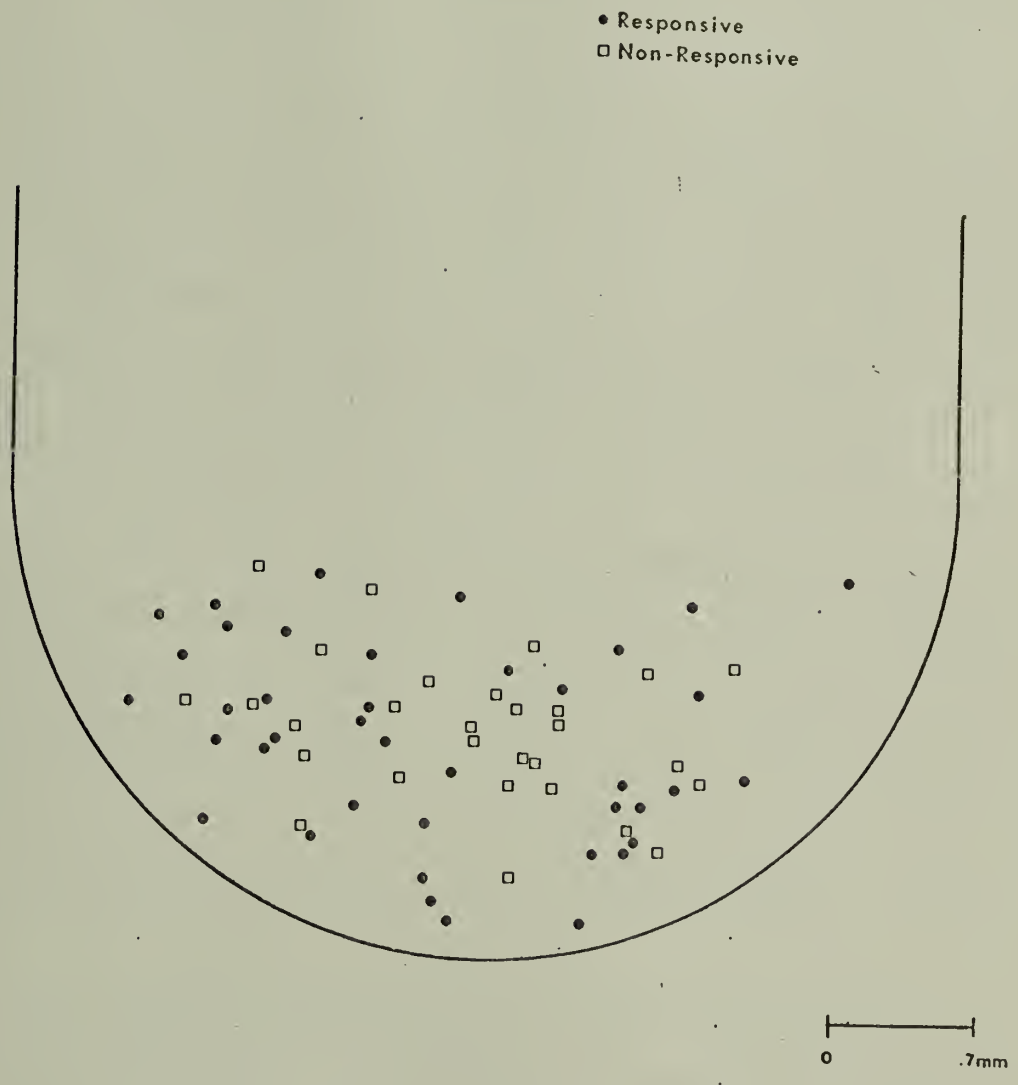
Percentages and identifying numbers of chemically responsive and non-responsive fungiform papillae for each subject

Subject	Chemically Responsive Papillae	Percentage	Chemically Non-responsive Papillae	Percentage
SC	* # 1, 30, 21, 15, 28, 41, 17, 23, 31, 6	52%	* # 22, 34, 19, 9, 18, 4, 8, 16, 13	48%
MS	# 29, 9, 28, 25, 19, 10, 27, 31, 22, 6	55%	# 1, 15, 14, 17, 3, 2, 33, 13	45%
DP	# 36, 30, 15, 22, 35, 37, 1, 16 13, 14	50%	# 2, 3, 9, 17, 29, 8, 18, 45, 46, 28	50%
EG	# 32, 15, 2, 39, 50, 16, 10, 26, 29, 43	83%	# 3, 28	17%
Combined Ss		58%		42%

Note: See text for definitions of responsive and non-responsive papillae.

*Numbers refer to identifying numbers on individual tongue maps (Figs. 4 - 7).

Figure 8 Composite tongue map showing the location and distribution of chemically responsive and non-responsive papillae across Ss.


• Responsive
□ Non-Responsive
0
.7mm

Discussion

Although Figures 4-7 do not show all of the fungiform papillae on a given S's tongue, the relative size, distribution, and density of papillae shown on these maps is proportional to that actually existing among Ss. It can be seen from these maps that, aside from subject EG, the distribution and density of these papillae is about the same among Ss. Subject EG, however, has an overall higher density of fungiform papillae, and they are present in larger numbers, further back on the tongue. Furthermore, observation of Table III indicates that, in addition to having a higher density of papillae, the percentage of these papillae that were chemically responsive is higher in subject EG. Interestingly, subject EG is the youngest S in these experiments (18 years old). Thus, both anatomically and functionally, subject EG's data support the commonly quoted reports that the number of papillae (Allara, 1939) and the number of taste buds per papilla (Arey, Tremaine and Monzingo, 1935) are greater in younger people. (Support for the latter case follows from the assumption that greater sensitivity is positively correlated with the presence of greater numbers of taste buds.)

Across subjects, the percentage of responsive papillae appears to be slightly greater than the percentage of non-responsive papillae. These percentages are well within the range of previously published single-papilla data (Kiesow, 1898; von Bekesy, 1966; Harper, et al., 1966; Bealer and Smith, 1975). Table IV shows the percentages of chemically responsive and nonresponsive papillae found in these previous single

Table IV

Summary and comparison of the percentages of chemically responsive and chemically non-responsive fungiform papillae found in previous single-papilla experiments

Source	Subjects	Number of Papillae Tested	Percent Responsive	Percent Non-responsive
Kiesow (1898)	S_1	37	90	10
von Bekesy (1966)	S_1	70	50	50
	S_2	118	87	13
	Total: 2 Ss	188	73	27
Harper, et al. (1966)	S_1	5	60	40
	S_2	6	17	83
	S_3	6	83	17
	S_4	6	17	83
	Total: 4 Ss	23	43	57
Bealer & Smith (1975)	4 Ss	15	87	13
Cardello* (1976)	S_1	19	52	48
	S_2	18	55	45
	S_3	20	50	50
	S_4	12	83	17
	Total: 4 Ss	69	58	42
All Studies Combined	15 Ss	332	73	27

* Reported herein

papilla experiments. The percentages for individual Ss can be seen to vary widely, probably reflecting both the differences in ages among the Ss and the differences in the criteria used by the investigators to categorize papillae as being responsive. However, taken as a whole, the data seem to point toward a relatively larger number of chemically responsive papillae. Combining all subjects and papillae observed in previous experiments with those of the present experiment, one arrives at an overall estimate of 73% chemically responsive fungiform papillae and 27% chemically nonresponsive fungiform papillae.

Although Ss differed in the number of responsive vs. nonresponsive papillae, there was no obvious pattern to the distribution of these papillae across the anterior tongue surface. Figure 8 is a composite tongue map showing the distribution of responsive and nonresponsive papillae. While there may appear to be a greater density of nonresponsive papillae near the mid-line, the relatively small number of papillae tested does not warrant such a conclusion. Rather, it appears that chemically responsive and nonresponsive fungiform papillae are evenly distributed across the anterior 3 cm of the tongue.

Experiment II

Having identified 10 fungiform papillae in each S that were responsive to at least one of the four test compounds, testing began in order to determine detection and recognition thresholds in each papilla for a wide range of chemicals. In addition, subjective estimates of the intensity of suprathreshold concentrations of each solution compound were

obtained for each papilla using the method of magnitude estimation.

Subjects and Apparatus

The subjects and apparatus were the same as described in Experiment I.

Solutions

Test solutions were chosen to include all of the major compounds used in previous single-papilla studies. In addition, at least two compounds representative of each of the four primary taste qualities were included to enable intraquality comparisons of the data. Table V compares the solutions used in previous studies with those of the present experiment. The concentration ranges shown for the compounds used in the present experiment were chosen to encompass almost the entire range of concentrations used by previous investigators.

The complete list of compounds and solution concentrations used in the current research appears in Table VI. In addition, distilled water was used as a control stimulus. All solutions were mixed as previously described. With the exception of the salts, all solutions were stored at 4° C, and all were at room temperature (25° C) at the time of testing.

Procedure

At the start of each session S was provided with written instructions concerning his task. These instructions were similar to those provided in Experiment I, with the exception of an additional paragraph concerning the magnitude estimation procedure. The complete instructions appear in

Table V

Compounds and solution concentrations used in contemporary studies of chemical stimulation of human taste papillae

Compound	von Bekesy (1966)	Harper, et al. (1966)	McCutcheon & Saunders (1972)	Bealer & Smith (1975)	Cardello (1976) (current research)
Sucrose	2.3-8.8 mM	1200 mM	400 mM	1000 mM	5-1000 mM
Dextrose	-	-	-	-	2.5-1500 mM
Dulcin	-	5 mM	-	-	-
Quinine Sulfate	.03-.1 mM	-	.3 mM	-	.01-3 mM
Quinine Hydrochloride (monohydrate)	-	41-60 mM	-	100 mM	.05-100 mM
HCl	.2-1 mM	-	-	-	.1-50 mM
Citric Acid	-	470-600 mM	100 mM	500 mM	.25-500 mM
NaCl	5-20 mM	2600-3600 mM	400 mM	5000 mM	1-5000 mM
LiCl	-	-	-	-	1-5000 mM
KCl	-	-	-	-	1-3500 mM

Table VI

Solutions Used in Experiment II

Sucrose	Dextrose	Quinine Sulfate	Quinine Hydrochloride (monohydrate)	HCl (pH)	Citric Acid (pH)	NaCl	LiCl	KCl
1000	1500	3	100	50 (1.30)	500 (1.66)	5000	5000	3500
700	1000	2	50	40 (1.40)	250 (1.83)	3500	3500	2000
500	500	1	25*	30 (1.52)	100 (2.06)	2000	2000	1000
250*	250*	0.5	10	20 (1.70)*	50 (2.24)	1000*	1000*	500
100	100	0.25*	5	10 (2.00)	25 (2.45)*	500	500	250*
50	50	0.10	2.5*	5 (2.30)	10 (2.62)	250*	250*	100
25*	25*	0.05	1.0	1 (3.00)	5 (2.81)	100	100	40
10	10	0.025*	0.5	0.5 (3.30)	2.5 (2.98)*	40	40	10
5*	5	.01	0.25*	0.25 (3.60)*	1.0 (3.20)	10	10	5
	2.5*		0.1	0.1 (4.00)	0.5 (3.36)	5	5	2.5*
			0.05		0.25 (3.53)*	2.5*	2.5*	
						1.0*	1.0*	

Note: All solution concentrations are expressed in millimoles (mM).

* Solutions not used in Experiment III.

Appendix B.

Most aspects of the procedure concerning the presentation of stimuli were the same as in Experiment I. Each of the 10 papillae were tested quasi-randomly, with five trials separating any two presentations to the same papilla. A two-minute ISI was employed, but this again translated into an effective 10-minute ISI for any one papilla, because of the aspect of procedure stated above. A 45-second drying period preceded each presentation of the stimulus, and S rinsed with distilled water after each trial.

Stimuli were presented using a modified method of constant stimuli. The modification was necessitated by the wide range of thresholds among papillae. In order to reduce the number of subthreshold solutions that were presented, each papilla was first tested with an intermediate concentration of each chemical solution. If a papilla did not respond to this concentration, the next presentation of that compound to the papilla would be at some random but higher concentration. If the papilla again did not respond, then a still higher concentration was presented on the next trial for that compound and papilla. Once a papilla did produce a quality response (something other than "no taste" or "indistinct or vague") subsequent presentations of that compound were random, but always at or above the concentration which last produced a null response. This procedure continued until: 1) a concentration was found at which stimulation of the papilla failed to produce a subjective quality response on two successive presentations of that solution, and 2) until all solution concentrations above this lowest concentration had

been presented twice.

Two control procedures were instituted to insure against guessing. The first was to stimulate each papillae five times with distilled water. The second was to stimulate various locations on the dorsal tongue surface where no papillae were present. The solutions used in this second control procedure were the same as used in Experiment I, and each was presented 10 times to each S. All control trials were indistinguishable from test trials and were presented randomly during each session.

After presentation of a stimulus S was required to give two responses before retracting his/her tongue. The first was a judgment of its quality. Response choices were "salty," "sweet," "sour," "bitter," "no taste," "indistinct or vague," and "complicated taste." With the exception of the last alternative, all responses were made using a response cube as described in Experiment I. An erasable pad was once again provided for written descriptions of "complicated tastes."

After making a quality response, S was required to judge the subjective intensity of the solution by the method of magnitude estimation. No modulus was assigned, and "no taste" responses were automatically assigned a zero magnitude estimate. Responses were made by writing the numerical judgment on the erasable pad. After E recorded the number, the pad was erased so that no physical record of past responses was available to S. Since no modulus was used and testing continued for a period of four months, it was necessary to provide a method for equalizing the magnitude estimates from session to session, both within and among Ss. In order to do this, four "standard" solutions were presented

every day. Each of these solutions was presented twice to a papilla that had been shown to respond reliably to that solution in Experiment I. The standard solutions were the same as those that were used in Experiment I (700 mM sucrose, 2 mM QSO_4, 30 mM HCl, and 2000 mM NaCl).

Sessions were conducted on alternating days and at random times throughout the day. Average session length varied from one to two hours, with a 5-10 minute break every 45 minutes. Not all compounds or concentrations were tested during any one session; however, test solutions within a session always included at least one series representative of each of the four primary tastes. The average number of solutions tested in any one session was 16, with a range from eight to twenty-seven. A total of $\approx$ 6000 presentations were made over a period of four months of testing.

Data Analysis

Threshold data: Detection and recognition thresholds were determined for each papilla, compound and subject. The procedure for calculating the detection threshold for a given papilla was to perform a least-squares linear regression on the percentages of response as a function of concentration. This regression procedure included all solution concentrations between the last concentration at which there were 100% "no taste" responses and the first concentration at which there were 100% "indistinct or vague" and/or some other taste quality responses. The solution concentration that was detected 50% of the time was then calculated from this regression equation and recorded

as the detection threshold. A similar procedure was performed to calculate recognition thresholds, except the solution concentrations used in the regression procedure were those between the last occurrence of 100% "no taste" and/or "indistinct or vague" responses and the first occurrence of 100% true quality responses. An exception to the above procedure was made in the case of subject EG, who for reasons to be discussed later, gave a large number of "sour" and "bitter" quality responses to low concentrations of sucrose and dextrose. For this reason his recognition thresholds for these two compounds were calculated between the last occurrence of 100% "no taste" and/or "indistinct or vague" responses and the first occurrence of 100% "sweet" quality responses.

After thresholds had been calculated for each papilla, solution, and subject, each was converted to a decibel measure for ease of comparison. As is the case with both auditory and visual stimuli, the definition of decibel that was used was that for energy, and is defined as:

$$dB = 1/10 \log (E1/E2)$$

where E1 is the energy level to be converted to decibels, and E2 is the reference energy level.

The reference value for the data of this experiment was the average detection (or recognition) threshold ($\overline{AL}$) across all papillae and subjects for a given compound.

Suprathreshold data: Magnitude estimates were equalized across subjects and sessions by calculating the geometric mean of the magnitude

estimates for the eight trials that the standard solutions were presented in each session. These "session means" were then pooled and the grand geometric mean calculated. Each estimate in a given session was then multiplied by the ratio of the grand mean to the session mean. The resulting "equalized" magnitude estimates were then used in all further analyses.

Since each solution concentration was judged twice, some measure of central tendancy was required to summarize the magnitude estimates. The measure of choice for magnitude estimates is the geometric mean, because the distribution of log magnitude estimates to a given stimulus approximates normality. In lieu of the geometric mean, the median is the second measure of choice, and it is normally used in those cases where there are magnitude estimates of zero. However, the data of this experiment pose a problem, because, although there are zero magnitude estimates, a median of two scores is equivalent to an arithmetic mean, and an arithmetic mean is inappropriate for magnitude estimation data. The compromise was to calculate geometric means in all cases where there were two non-zero magnitude estimates and medians in those cases where one score was a zero. Although the use of two measures of central tendency is not a commonly accepted practice, it is justified in the present circumstance on the grounds that only 10-15% of the magnitude estimates were zero, and that, when plotted on full logarithmic axes as a function of concentration, the magnitude estimates showed no marked discontinuity at those concentrations where zero magnitude estimates were present. In summary, the procedure was to calculate geometric means for the data, using the median

as the best estimate in those cases where a zero was present in the data.

Results

Control trials: The frequency of quality reports during control trials were calculated and appear in Tables VII and VIII. Table VII contains the frequencies of response to control presentations of the four standard solutions to areas of the tongue where papillae were not present. Responses other than "no taste" or "indistinct or vague" were minimal for all Ss, totalling only 6.25%. Table VIII contains the same frequencies, but for control trials in which distilled water was presented to the papillae being tested. For the female subjects (SC and MS) responses other than "no taste" or "indistinct or vague" were minimal and random as to quality. However, for the male subjects (DP and EG) there were a large number of taste quality responses to distilled water. These responses were primarily sour and bitter, and they were independent of the papilla being stimulated.

Single papillae responses: Most of the fungiform papillae in all Ss responded to chemicals representative of more than one primary taste quality. Table IX shows that the number of papillae which responded to a particular solution did not vary greatly among Ss, with the possible exception of NaCl. Similarly, the number of responding papillae did not vary greatly as a function of the test compound, either within or across Ss.

By designating papillae according to whether or not they responded

Table VII

Frequencies of quality reports to control presentations of test solutions to areas of the tongue where fungiform papillae are not located

Subject	Control Solution	No Taste	Indistinct or Vague	Sweet	Bitter	Sour	Salty
SC	700 mM CHO *	9	0	1	0	0	0
	2 mM QSO_4	10	0	0	0	0	0
	30 mM HCl	9	0	0	0	1	0
	2000 mM NaCl						
MS	700 mM CHO *	9	0	0	0	1	0
	2 mM QSO_4	9	1	0	0	0	0
	30 mM HCl	10	0	0	0	0	0
	2000 mM NaCl	9	0	0	0	0	1
DP	700 mM CHO *	7	2	0	0	1	0
	2 mM QSO_4	7	2	0	1	0	0
	30 mM HCl	9	1	0	0	0	0
	2000 mM NaCl	7	2	0	0	0	1
EG	700 mM CHO *	8	1	1	0	0	0
	2 mM QSO_4	10	0	0	0	0	0
	30 mM HCl	9	1	0	0	0	0
	2000 mM NaCl	8	1	0	0	0	1

Note: Frequencies are based on a total of 10 presentations of each solution to each subject

*Denotes sucrose.

Table VIII

Frequencies of quality reports to control presentations of distilled water to test papillae

Subject	Control Solution	No Taste	Indistinct or Vague	Sweet	Bitter	Sour	Salty
SC	Distilled H_2O	40	4	1	2	2	1
MS	Distilled H_2O	37	10	1	0	2	0
DP	Distilled H_2O	29	9	0	5	7	0
EG	Distilled H_2O	14	11	1	4	20	0

Note: Frequencies are based on a total of 50 presentations for each S.

Table IX

Number of papillae in each subject
which responded to the various test compounds of Experiment II

Subject	Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
SC	9	8	7	9	8	10	7	7	9
MS	8	8	7	9	8	9	10	8	10
DP	7	7	8	6	8	9	4	7	8
EG	7	8	10	10	9	9	9	9	9
Combined	31	31	32	34	33	37	30	31	36

Note: All frequencies for individual subjects are out of a total of 10 chemically responsive papillae that were tested. Correspondingly, the "combined" frequencies are out of a total of 40 chemically responsive papillae in all Ss.

to compounds representative of a given taste quality, it was possible to categorize papillae according to the particular combination of taste qualities that they mediated. Table X shows the various combinations of qualities which were mediated by each papilla in this experiment. In addition, Table X gives the percentage of the total number of papillae which exhibited each particular combination of response qualities. It is clear from this table that the majority of papillae in all Ss were capable of responding to chemicals representative of all four primary taste qualities. In addition, there were a number of papillae which responded with three qualities and one papilla which was responsive only to salts. No papillae were found which responded to a combination of two qualities. Figure 9 is a composite map showing the location of each of these papilla types on the dorsal tongue surface.

Threshold data: The detection and recognition threshold for each papilla, compound, and subject appear in Table XI. All thresholds are expressed in millimolar (mM) concentrations. In most cases the detection threshold was lower than the recognition threshold; however, the two often coincided.

In Figures 10-13 response profiles for the 10 papillae tested in each subject are presented. These profiles are based on the recognition thresholds of Table XI, expressed as decibels. As previously stated, in order to provide a relative sensitivity measure across compounds, the decibel measure for a papilla was defined as one-tenth the common logarithm of the ratio of the threshold for that papilla to the average threshold across all papillae and subjects. However, in order to plot

Table X

Combination of taste qualities mediated by single papillae, and their percentages in the total population of chemically responsive papillae

	Sw-B-So-Sa	B-So-Sa	Sw-So-Sa	Sa
SC	* # 1, 30, 21, 15, 41, 17, 23, 28, 21, 6			
MS	# 29, 9, 28, 25 19, 10, 27, 31	# 22		# 6
DP	# 36, 30, 15, 22, 35, 37	# 1, 16	# 13, 14	
EG	# 32, 15, 2, 39, 50, 16, 10, 26	# 29, 43		
Percentage of total number of responsive papillae	80%	12.5%	5%	2.5%

* Numbers refer to topographic tongue maps for each S.

Figure 9 Composite tongue map showing the location of papillae mediating the different quality combinations noted in Table X.

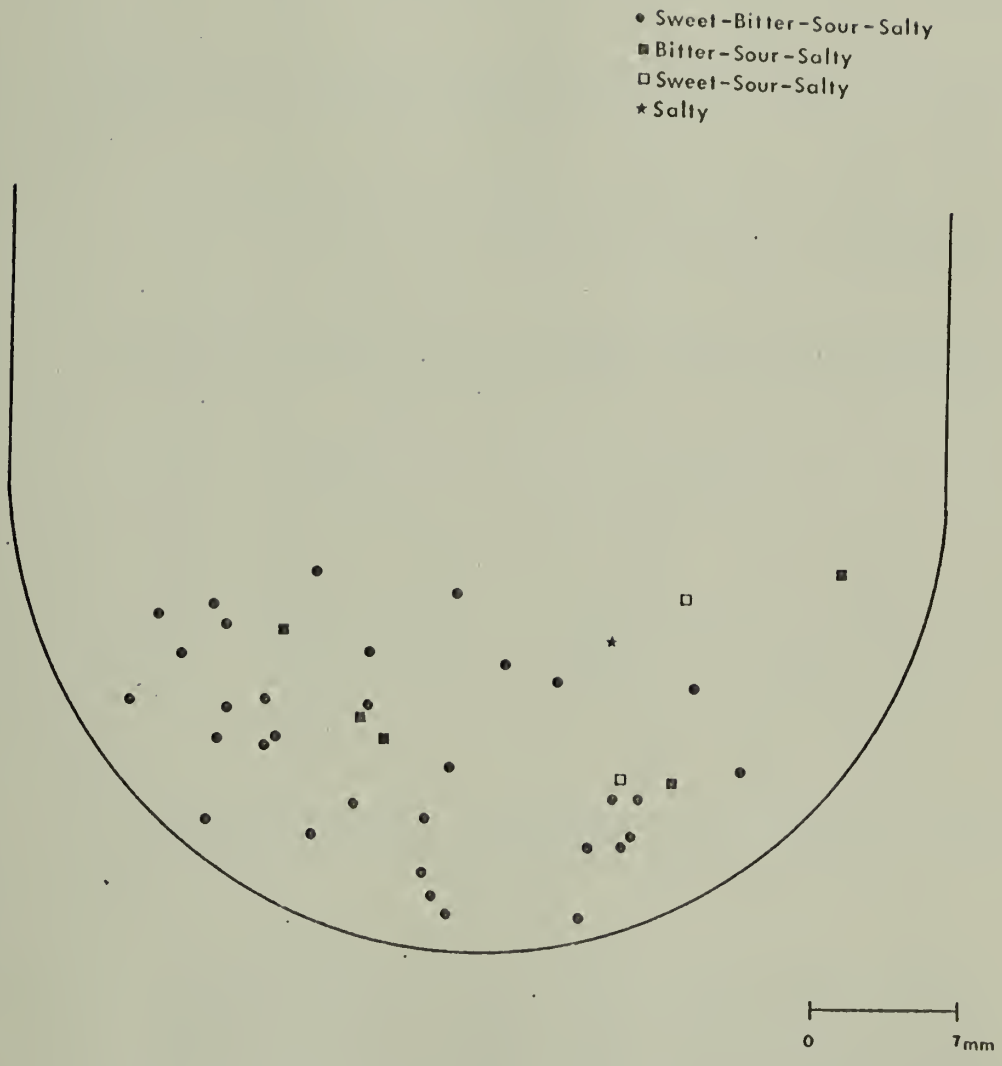

• Sweet-Bitter-Sour-Salty
■ Bitter-Sour-Salty
□ Sweet-Sour-Salty
★ Salty
0
7mm

Table XI

Detection and recognition thresholds for each papilla, solution, and subject. Thresholds are expressed in milliMoles (mM).

Subject: SC

Papilla Number		Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
1	Detection	821	-	-	4.63	25	432	-	3500	750
	Recognition	821	-	-	5.83	25	432	-	3500	750
30	Detection	388	750	.583	37.5	40	28	463	175	-
	Recognition	510	1333	.583	58.3	40	28	463	175	-
21	Detection	320	813	2	37.5	20	175	750	-	2800
	Recognition	387	1000	3	87.5	50	175	3842	-	2800
15	Detection	510	-	3	-	47	500	-	1500	3071
	Recognition	760	-	3	-	47	500	-	1500	3071
28	Detection	038	1222	1.5	.375	7.5	75	938	175	70
	Recognition	133	1222	2	.375	20	133	1167	175	130
41	Detection	38	18	.075	.175	30	1.33	70	5.83	70
	Recognition	106	46	.075	2.22	35	1.75	223	5.83	70
17	Detection	600	813	2.5	17.5	-	28	463	-	2166
	Recognition	600	1222	2.5	17.5	-	362	583	-	3070
23	Detection	175	75	-	100	50	28	-	-	938
	Recognition	175	75	-	100	50	28	-	-	1450
31	Detection	28	58	-	1.75	-	1.33	5.33	2166	2166
	Recognition	28	75	-	3.75	-	3.8	7.5	2166	2166
6	Detection	-	1250	1.35	87.5	25	375	750	5000	2625
	Recognition	-	1250	1.35	87.5	30	500	750	5000	2625

Table XI-Continued

Subject: MS

Papilla Number		Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
29	Detection	175	175	.133	283	9	7.33	70	25	378
	Recognition	175	175	.133	1.56	9	7.33	70	25	378
9	Detection	75	1098	.075	.283	2.16	.583	3	7.5	175
	Recognition	375	1136	.133	1.85	13.2	6.32	18	7.5	175
28	Detection	38	175	.133	.075	20	10.6	100	18	463
	Recognition	58	283	.463	.463	20	22.5	130	25	463
25	Detection	850	175	2.44	78.4	20	13	2166	750	750
	Recognition	1000	283	2.66	78.4	20	13	2166	750	750
19	Detection	760	375	-	18.5	20	23	25	-	1166
	Recognition	760	375	-	32.1	25	28	50	-	1166
6	Detection	-	-	-	-	-	-	4100	-	3071
	Recognition	-	-	-	-	-	-	4100	-	3071
10	Detection	75	75	1.5	.175	25	1.06	70	100	151
	Recognition	733	225	1.5	.175	30	1.33	70	130	151
27	Detection	87	58	.175	13.3	25	10.6	2166	7.5	375
	Recognition	106	225	.175	46.3	30	17.5	2166	7.5	375
31	Detection	175	283	.021	1.06	5.33	106	2166	70	81
	Recognition	388	283	.029	2.25	15	106	2166	70	81
22	Detection	-	-	-	37.5	-	13	583	3500	750
	Recognition	-	-	-	37.5	-	18	583	3500	750

Table XI-Continued

Subject: DP

Papilla Number		Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
1	Detection	-	-	1.63	75	-	500	-	2875	-
	Recognition	-	-	2.67	100	-	500	-	4500	-
16	Detection	-	-	2	100	16.3	75	-	283	-
	Recognition	-	-	2	100	16.3	175	-	875	-
36	Detection	483	813	1.17	-	25	-	-	2875	2750
	Recognition	483	1333	1.17	-	25	-	-	2875	3500
30	Detection	18	23	1.17	-	25	13.3	-	-	1167
	Recognition	700	134	2.67	-	25	38.0	-	-	1167
15	Detection	600	18	.075	2.83	3	2.83	175	70	130
	Recognition	1000	87	.225	5.83	7.5	3.75	283	223	378
22	Detection	-	1000	2.67	58.3	50	10.6	-	50	175
	Recognition	-	1000	2.67	87.5	50	18.5	-	223	463
35	Detection	75	283	1.35	88	30	87	3842	-	223
	Recognition	133	463	1.35	100	30	87	4500	-	463
13	Detection	600	-	-	-	35	375	583	-	1500
	Recognition	914	-	-	-	40	375	938	-	2167
37	Detection	38	567	.75	13.4	.175	28.3	2167	1500	25
	Recognition	73	670	1.63	32.1	.375	46.3	2167	2167	25
14	Detection	375	375	-	-	-	75	-	3.75	283
	Recognition	821	1222	-	-	-	75	-	315	750

Table XI-Continued

Subject: EG

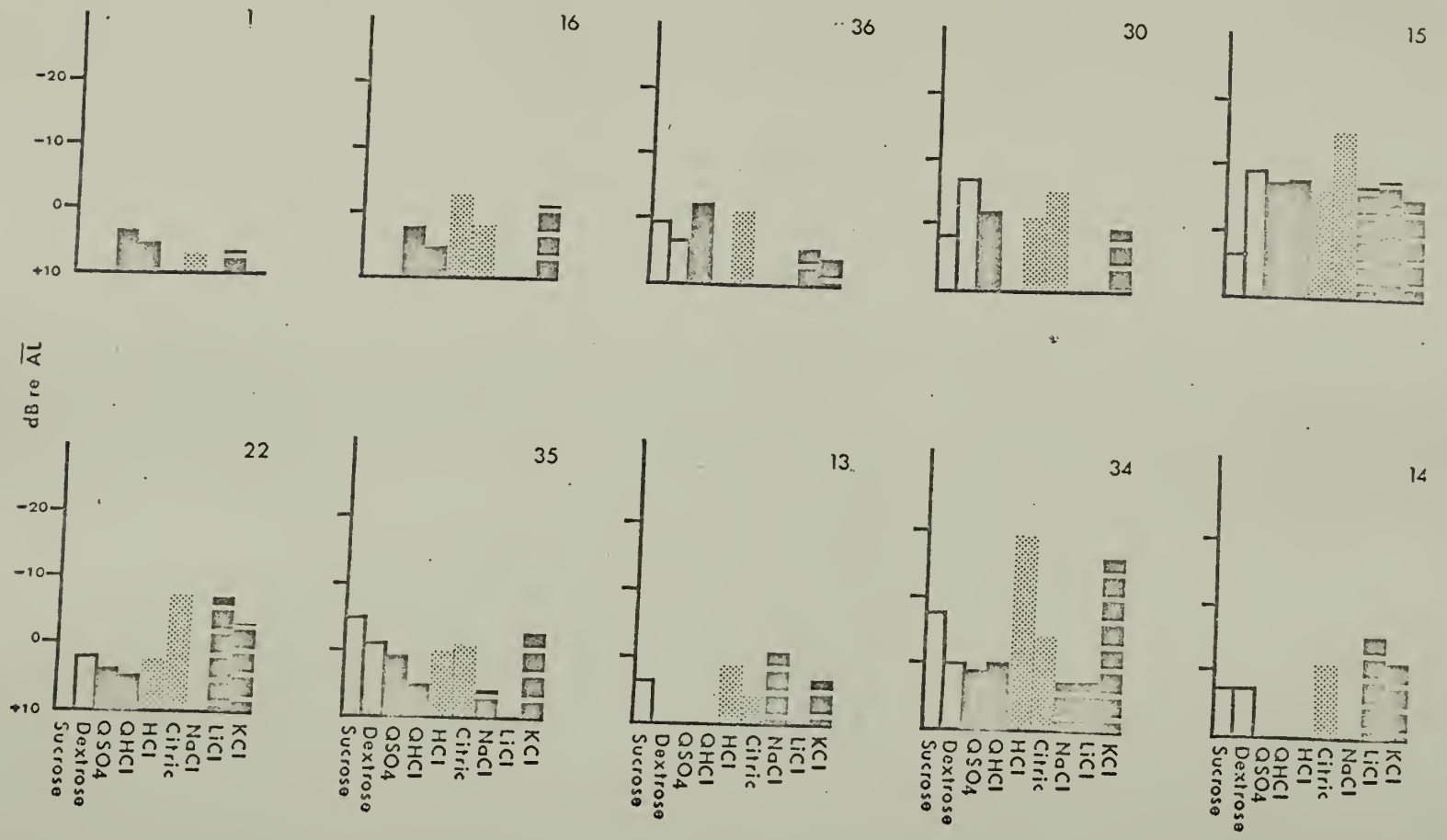
Papilla Number		Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
32	Detection	7.5	10.6	.125	.380	12	2.83	25	2.83	70
	Recognition	58.3	380	.125	.730	12	2.83	70	2.83	70
15	Detection	600	7.5	.185	.870	45	156	50	25	32
	Recognition	733	1222	.225	.870	50	156	50	70	32
2	Detection	-	3.75	.375	.375	-	13.3	1.75	2042	100
	Recognition	-	1136	.375	.75	-	75	4.63	2875	100
29	Detection	-	-	.583	17.5	25	5.83	75	283	100
	Recognition	-	-	.750	17.5	25	5.83	183	583	100
39	Detection	17.5	28.3	.075	.283	45	13.3	25	175	70
	Recognition	375	1500	.175	1.06	45	17.5	100	175	283
43	Detection	-	-	.75	5.83	15	28.3	1500	-	-
	Recognition	-	-	.75	1.06	43	46.3	2750	-	-
50	Detection	46.3	243	.25	5.83	25	1.85	1.75	5.83	7.5
	Recognition	58.3	276	.77	7.50	25	3.8	1.75	81	7.5
16	Detection	37.5	87	.075	3.8	35	17.5	317	1500	283
	Recognition	58.3	583	.283	4.63	45	28.3	557	1500	283
10	Detection	17.5	.106	.0583	1.06	25	-	-	100	378
	Recognition	375	-	.321	1.06	25	-	-	100	463
26	Detection	28.3	46.3	.106	2.83	15	2875	2875	18.3	70
	Recognition	46.3	75	.125	3.75	15	3500	3500	25	70

Figure 10 Sensitivity profiles for papillae of subject SC. The measure of sensitivity is the decibel equivalent of the ratio between the recognition threshold for the papilla and the mean recognition threshold across all papillae and subjects.

Figure 11 Sensitivity profiles for papillae of subject MS. The measure of sensitivity is the decibel equivalent of the ratio between the recognition threshold for the papilla and the mean recognition threshold across all papillae and subjects.

19
22
KCl
LiCl
NaCl
Citric
HCl
QHCl
QSO4
Dextrose
Sucrose
25
34
28
27
9
10
29
6
-20
-10
0
+10
dB re AL
Subject MS

Figure 12 Sensitivity profiles for papillae of subject DP. The measure of sensitivity is the decibel equivalent of the ratio between the recognition threshold for the papilla and the mean recognition threshold across all papillae and subjects.


dB re $\overline{AL}$
-20
-10
0
+10
1
16
36
30
15
22
35
13
34
14
Sucrose
Dextrose
QSO4
QHCl
HCl
Citric
NaCl
LiCl
KCl

Subject DP

Figure 13 Sensitivity profiles for papillae of subject EG. The measure of sensitivity is the decibel equivalent of the ratio between the recognition threshold for the papilla and the mean recognition threshold across all papillae and subjects.

39
26
KCl
LiCl
NaCl
Citric
HCl
QHCl
QSO4
Dextrose
Sucrose
29
10
2
16
Subject EG
15
50
34
43
-20
-10
0
+10
dB re Δl

sensitivity profiles rather than threshold profiles, the decibel measures in Figures 10-13 were plotted from highest to lowest, rather than vice-versa. Thus, looking at one of these profiles, the zero-decibel point on the ordinate reflects the average recognition threshold across all papillae for a given compound. Points above this (negative decibels) reflect lower thresholds and points below it (positive decibles) reflect higher thresholds.

Apparent from Figures 10-13 is the fact that papillae often responded to only one of two (or more) compounds representative of the same taste quality. Also, regardless of the number of compounds to which each papilla responded, the level of sensitivity to those compounds did not vary greatly within a single papilla. As an example, papilla #21 in subject SC responded to eight test compounds, and all eight had recognition thresholds of about +4 dB re $\overline{AL}$. Similarly, papilla #41 in the same S responded to all nine compounds, and the thresholds to all nine were about -10 dB re $\overline{AL}$. Thus, it is as if the sensitivities to all compounds for a papilla are controlled by a common gaining mechanism.

The fact that the relative sensitivities among compounds are fairly constant within a papilla, suggests a general process occurring within the papilla. One possibility is that, as a function of time, various papillae and their associated taste buds and receptor cells undergo a process of slow degeneration, similar to that which affects auditory receptor cells (Gulick, 1971). If that is the case, then it may be likely that those papillae which do not respond to compounds

representative of a particular taste quality, fail to do so because they have reached a stage of functional degeneration, whereupon they are no longer sensitive to those particular compounds. Under such circumstances the sensitivities of these papillae to other compounds should also be low. To test this hypothesis, all papilla thresholds were converted to ratios relative to the average recognition threshold across all papillae in that subject. Then, in order to compare the levels of sensitivity among the four classes of papillae shown in Table X, the arithmetic mean of the ratios (expressed as decimals) were calculated for each papilla type. Since all Ss possessed papillae which mediated all four taste qualities, comparisons were made between these "sweet-bitter-sour-salty" papilla and each of the other types. However, depending on the particular comparison, the mean threshold ratio for the "Sw-B-So-Sa" type was calculated without including the threshold ratios for compounds representative of the taste quality which was not mediated by the other papilla type.

Table XII contains the mean threshold ratios for the papillae involved in each comparison, as well as the probability that such a distribution of ratios would occur if there were no differences in the underlying population of papilla types. These probabilities derive from Mann-Whitney U-tests (one-tailed) performed on the data. Although the probabilities are low, they do not reach the .05 level, due primarily to the lack of a sufficient number of scores in one or both groups.

Spearman rank-order correlation coefficients between the recognition thresholds for all papillae in a subject were calculated for all possible pairs of solution compounds and appear in Table XIII. The variability in

Table XII

Within subject comparisons of mean threshold ratios for different papilla types

Subject	Papilla Types			
	Sw-B-So-Sa		B-So-Sa	
MS	9.474	3.721	.724	
	23.766	24.658		
	12.121	12.060		(p = .222)
	.816	7.756		
	Sw-B-So-Sa		Sa	
MS	13.655	7.890	.174	
	47.802	8.556		
	11.004	25.902		(p = .222)
	.755	5.892		
	Sw-B-So-Sa		B-So-Sa	
DP	.480	2.598	.283	
	.857	1.026	.797	(p = .142)
	33.417	16.733		
	Sw-B-So-Sa		Sw-So-Sa	
DP	.509	2.468	.602	
	1.628	1.583	1.334	(p = .286)
	9.006	17.553		
	Sw-B-So-Sa		B-So-Sa	
EG	36.409	6.482	2.222	
	5.730	1.050	1.317	(p = .178)
	26.047	2.243		
	3.397	5.999		

Table XIII

Correlation matrix of Spearman rank-order coefficients for all possible pairs of test solutions. Correlations were calculated for recognition thresholds across all papillae in a given S.

S	Solution	Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
SC										
MS	Sucrose		.813*	-.012	.523	-.268	.896*	.497	.332	.438
DP			.644	.728*	.571	.697*	.274	.296	.862*	.596
EG			.429	.299	-.173	.370	-.030	.276	-.417	.456
			.766*	.563	-.118	.634	.640	-.025	.763*	.431
SC										
MS	Dextrose			.04	.319	-.372	.775*	.464	-.040	.440
DP				.552	.475	.430	.488	.110	.488	.536
EG				.461	.391	.426	.791*	.353	.143	.783*
				.376	-.142	.287	.620	.337	.558	.694*
SC										
MS	QSO_4				.256	.424	.269	.503	.550	.170
DP					.468	.770*	.295	.160	.826*	.833*
EG					.521	.697*	.111	.315	.181	.303
					.235	.211	.274	-.219	.604	.126
SC										
MS	QHCl					.327	.505	.560	.519	.604
DP						.465	.491	.683*	.428	.602
EG						.443	.551	.432	.553	.580
						-.330	-.325	.374	.018	-.055
SC										
MS	HCl						-.218	-.235	.506	.480
DP							.502	.345	.565	.540
EG							.293	.453	.111	.365
							.689*	-.339	.597	.193
SC										
MS	Citric							.599	.381	.376
DP	Acid							.548	.524	.468
EG								.280	.505	.762*
								.152	.479	.459
SC										
MS	NaCl								.398	-.037
DP									.245	.222
EG									-.045	.574
									.103	.661
SC										
MS	LiCl									.284
DP										.693*
EG										.331
										.685*
SC										
MS	KCl									
DP										
EG										

*significant at .05 level

these coefficients among Ss is sufficient to obscure any pattern which may be present among them. In order to summarize the coefficients in each cell of the matrix, all coefficients for each subject were rank-ordered and the mean rank across subjects for each solution pair was calculated. These mean ranks appear in Table XIV.

As a final analysis of the threshold data, all the papillae in a subject were grouped together and the sensitivity profiles for each subject plotted in Figure 14. It is clear from this figure that single-papillae sensitivities differ among subjects. Furthermore, subject EG, who had been previously shown to possess the greatest number of fungiform papillae and the greatest number of chemically responsive papillae, also exhibited the greatest sensitivity to compounds of any subject.

Suprathreshold data: The geometric mean of the magnitude estimates were plotted as a function of concentration for each papilla, solution, and subject. Since this involved a total of 360 psychophysical functions, only a representative sample of these functions are presented here. Figures 15-19 show a sample of three single-papilla psychophysical functions for each of the nine test compounds. They are plotted on full logarithmic axes. An examination of these functions reveals that in many instances the functions reach an asymptote at a high concentration and then, either remain at that level or begin to decline. This "ceiling" effect has been reported previously in various contexts (Moskowitz, 1970a, b, 1972; Bartoshuk, 1975; Smith, 1971), and has the effect of decreasing the slope of the functions, as well as the fit of the data to various standard functions.

Table XIV

Table of mean ranks for the correlation coefficients of Table XIII

Solution	Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
Sucrose		7	18	21.25	17	18.25	25	15.25	15
Dextrose			17.5	24.25	25	8.62	22.75	24.12	9.5
QSO_4				20.62	12.25	27.37	25.75	12.25	20
QHCl					24.5	18.25	11.75	18	12.25
HCl						20.5	28	16.12	18.5
Citric Acid							17.75	15.5	15.87
NaCl								28.25	19.25
LiCl									14.75
KCl									

Figure 14 Sensitivity profiles for individual Ss, based on the average thresholds across all papillae in a subject.

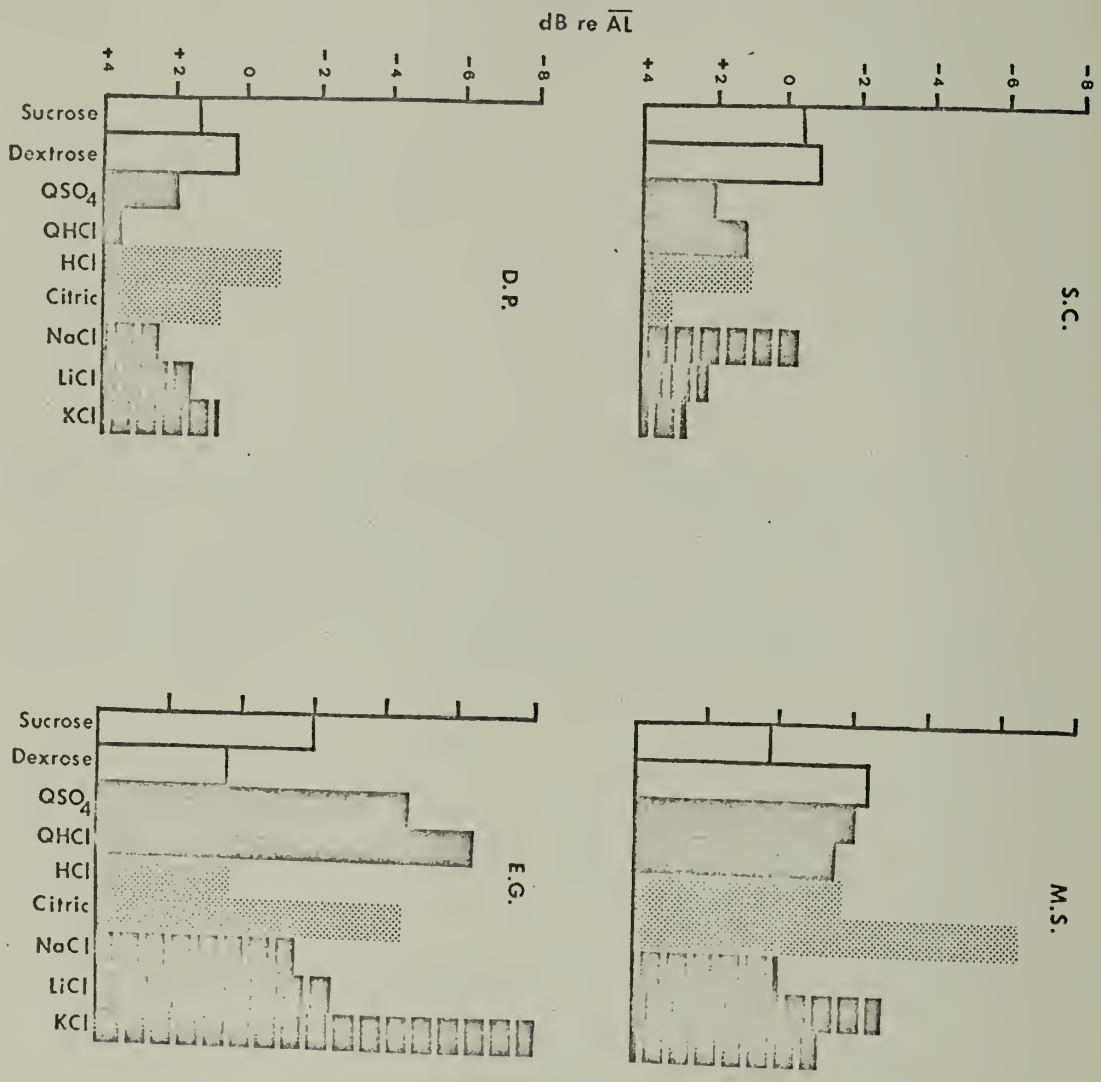

dB re $\overline{AL}$
+4
+2
0
-2
-4
-6
-8
Sucrose
Dextrose
QSO_4
QHCl
HCl
Citric
NaCl
LiCl
KCl
D.P.
S.C.
E.G.
M.S.

Figure 15 Representative single-papilla psychophysical functions for sucrose and dextrose. Papillae are designated by the first initial of the subject followed by the identifying number of the papillae from Figs. 4 - 7. The number under the papilla designation is the slope of the regression line on log-log coordinates, and is, therefore, the exponent of the best-fitting power function.

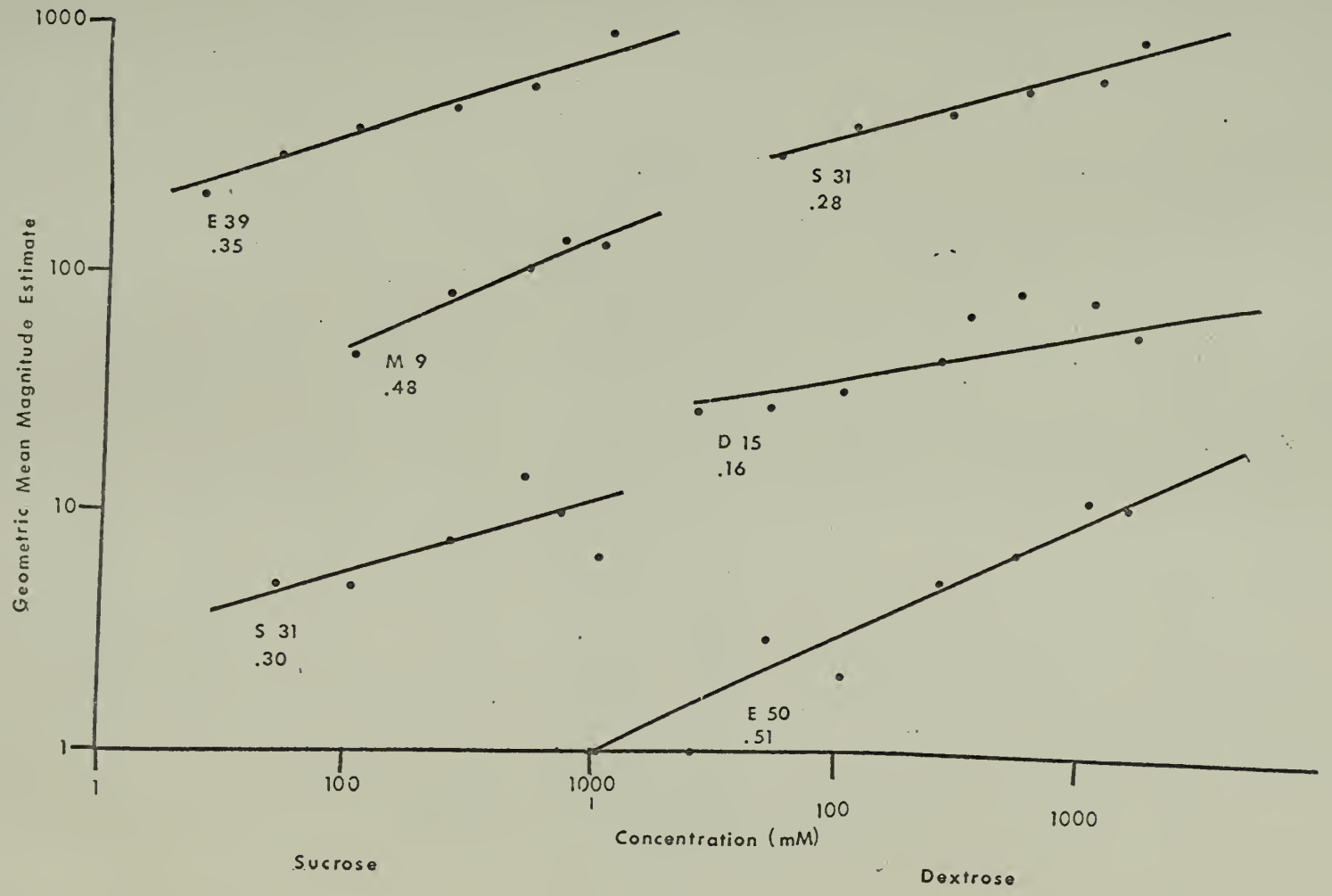

1000
100
10
1
Geometric Mean Magnitude Estimate
E 39
.35
M 9
.48
S 31
.30
S 31
.28
D 15
.16
E 50
.51
1
100
1000
1
100
1000
Concentration (mM)
Sucrose
Dextrose

Figure 16 Representative single papilla psychophysical functions for QSO_4 and QHCl. Papillae are designated by the first initial of the subject followed by the identifying number of the papillae from Figs. 4 - 7. The number under the papilla designation is the slope of the regression line on log-log coordinates, and is, therefore, the exponent of the best-fitting power function.

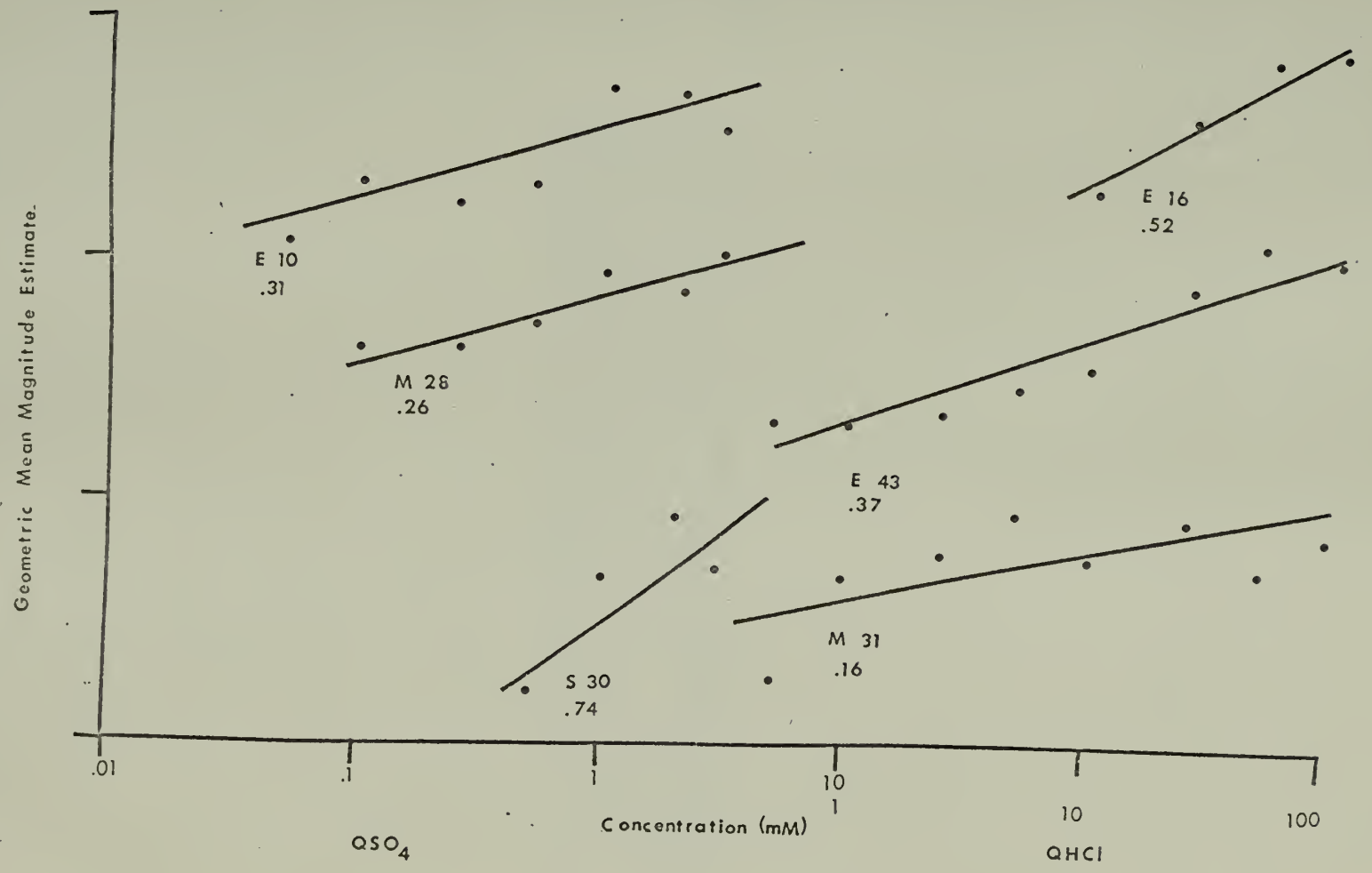

Geometric Mean Magnitude Estimate
E 10
.31
M 28
.26
E 16
.52
E 43
.37
M 31
.16
S 30
.74
.01
.1
1
10
1
10
100
Concentration (mM)
QSO4
QHCl

Figure 17 Representative single papilla psychophysical functions for HCl and Citric acid. Papillae are designated by the first initial of the subject followed by the identifying number of the papillae from Figs. 4 - 7. The number under the papilla designation is the slope of the regression line on log-log coordinates, and is, therefore, the exponent of the best-fitting power function.

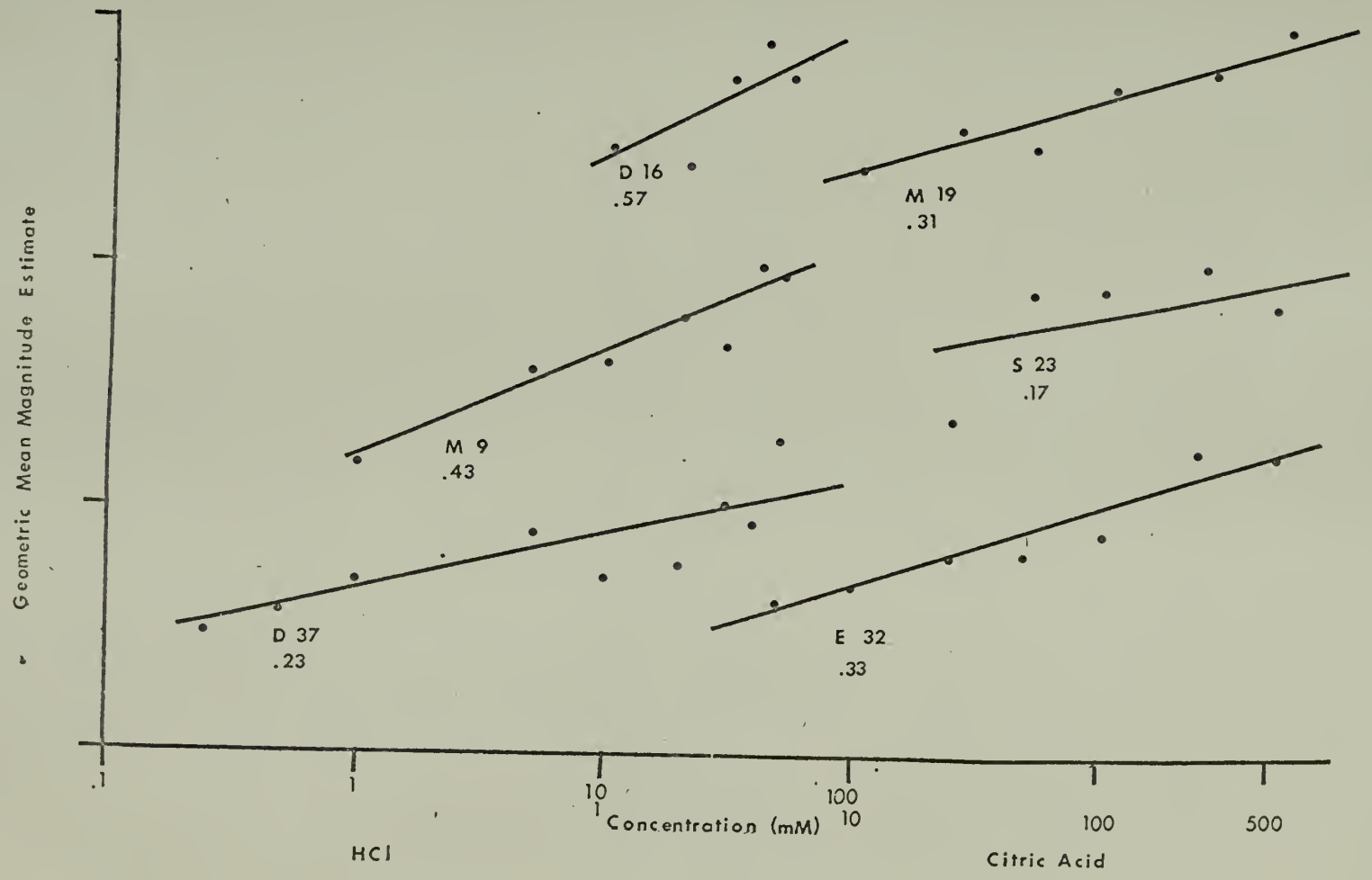

Geometric Mean Magnitude Estimate
D 16
.57
M 19
.31
M 9
.43
S 23
.17
D 37
.23
E 32
.33
.1
1
10
1
100
10
100
500
Concentration (mM)
HCl
Citric Acid

Figure 18 Representative single papilla psychophysical functions for NaCl and LiCl. Papillae are designated by the first initial of the subject followed by the identifying number of the papillae from Figs. 4 - 7. The number under the papilla designation is the slope of the regression line on log-log coordinates, and is, therefore, the exponent of the best-fitting power function.

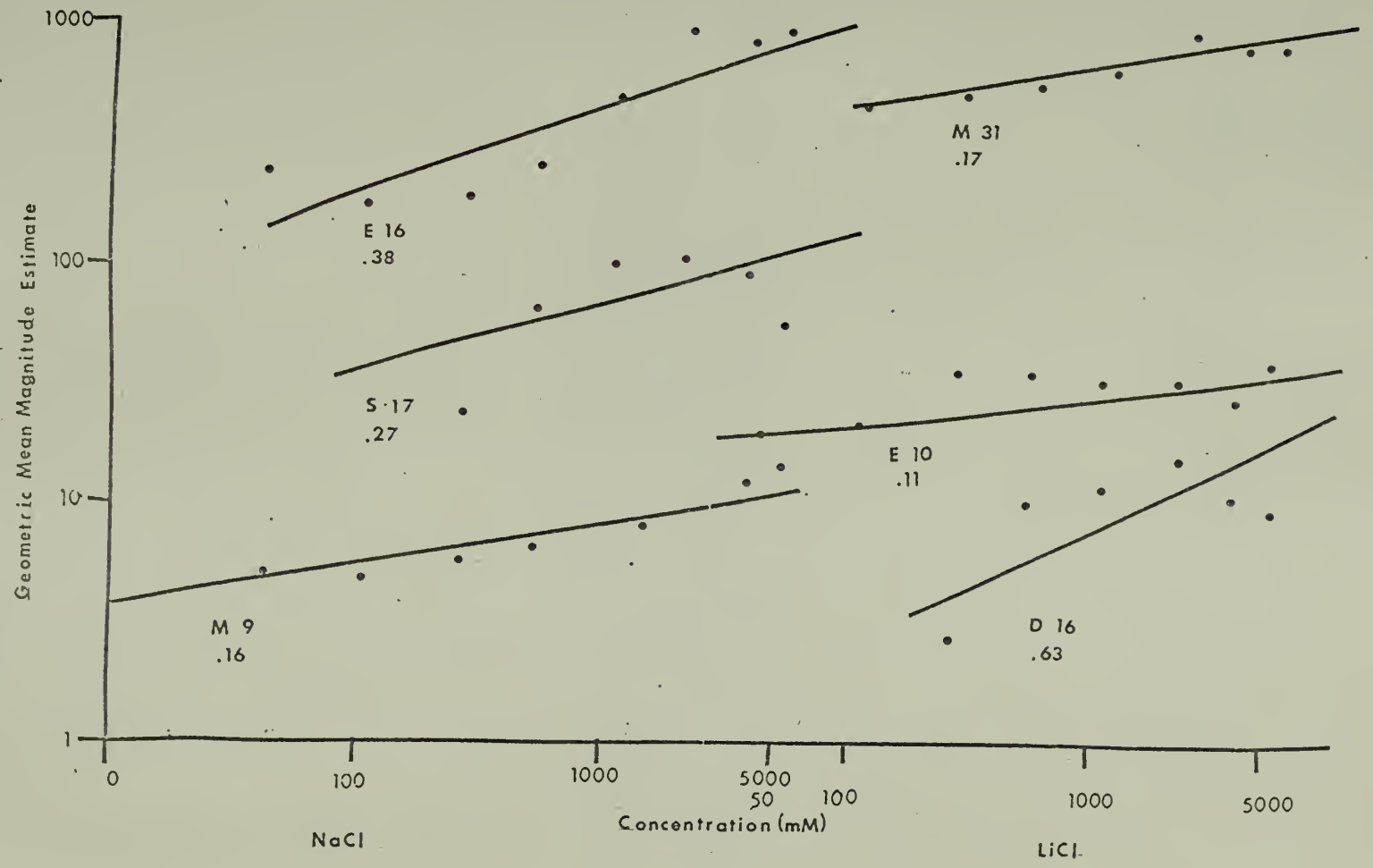
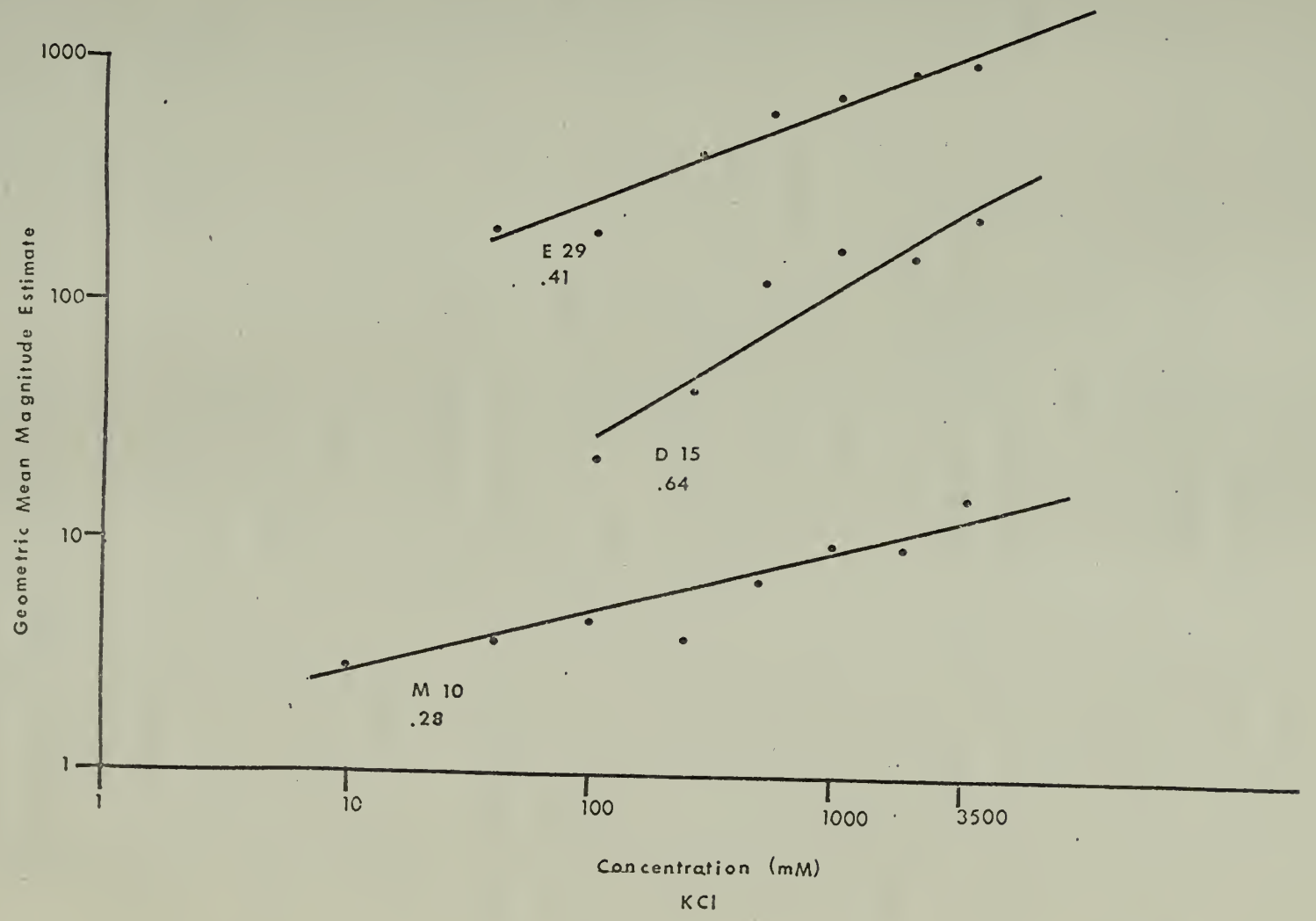

1000
100
10
1
Geometric Mean Magnitude Estimate
E 16
.38
M 31
.17
S·17
.27
E 10
.11
M 9
.16
D 16
.63
0
100
1000
5000
50
100
1000
5000
Concentration (mM)
NaCl
LiCl

Figure 19 Representative single papilla psychophysical functions for KCl. Papillae are designated by the first initial of the subject followed by the identifying number of the papillae from Figs. 4 - 7. The number under the papilla designation is the slope of the regression line on log-log coordinates, and is, therefore, the exponent of the best-fitting power function.


1000
100
10
1
Geometric Mean Magnitude Estimate
E 29
.41
D 15
.64
M 10
.28
1
10
100
1000
3500
Concentration (mM)
KCl

All of the single-papilla functions that were comprised of at least five data points were fit to linear, logarithmic, and power functions by a least-squares regression computer program. The correlation coefficients for these fits were then converted to Z-scores using the Fisher r to z transform and the arithmetic mean of the Z-scores calculated for each solution and subject. A two-way repeated-measures analysis of variance on these data was then performed to determine whether, either the solutions, or the functions to which the data were fit, affected the regression coefficients (r). The results of the analysis indicated that neither the function to which the data were fit, nor the solution, significantly affected the r values. The conclusion warranted by this is that, taken as a group, the single-papilla functions are not significantly better fit to either a linear, a logarithmic, or a power function. However, the relative order of the mean r values for each of the three fits was such that the fit to a power function was somewhat better than that to either a linear or a logarithmic function.

In fitting the above data to power functions, exponents of these functions were obtained, and the median exponent was calculated for each solution. These median exponents appear in Table XV, along with the number of single-papilla exponents upon which they were based.

Quality responses in salts: Figures 20-22 show the percentage of each quality response at each concentration of NaCl, LiCl, and KCl. These data were collapsed across papillae and subjects, because the number of responses for individual papillae and/or subjects were too few to be considered separately. These data show similar shifts in taste

Table XV

Median exponents of single-papilla psychophysical functions for each test solution.

	Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
Median Exponent	.22	.28	.17	.28	.41	.34	.18	.19	.38
Number of papillae upon which medians are based	(17)	(17)	(14)	(19)	(8)	(28)	(20)	(21)	(21)

Figure 20 Percentage of each quality response as a function of concentration for NaCl. Data are collapsed across papillae and subjects.

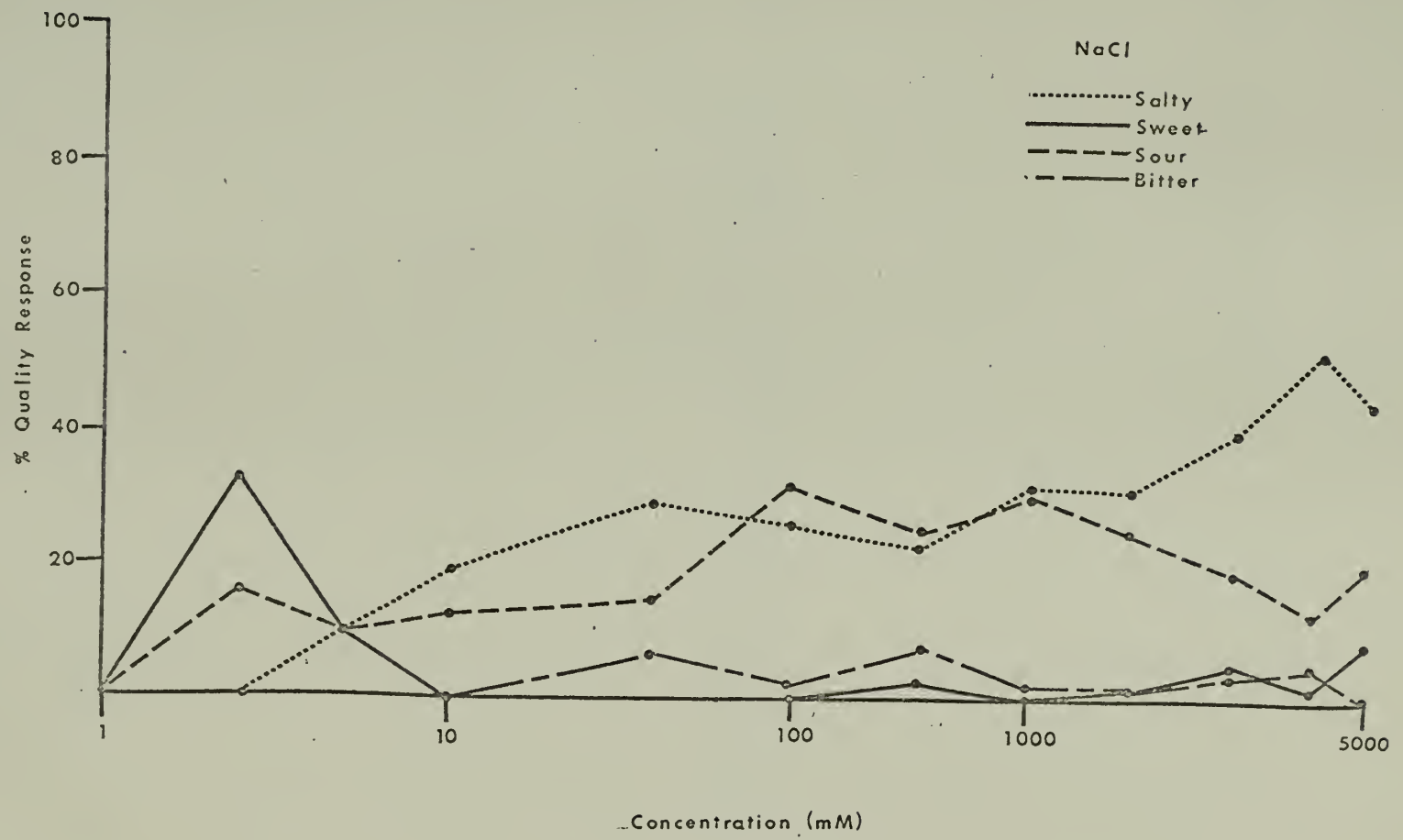

NaCl
Salty
Sweet
Sour
Bitter
% Quality Response
100
80
60
40
20
1
10
100
1000
5000
Concentration (mM)

Figure 21 Percentage of each quality response as a function of concentration for LiCl. Data are collapsed across papillae and subjects.

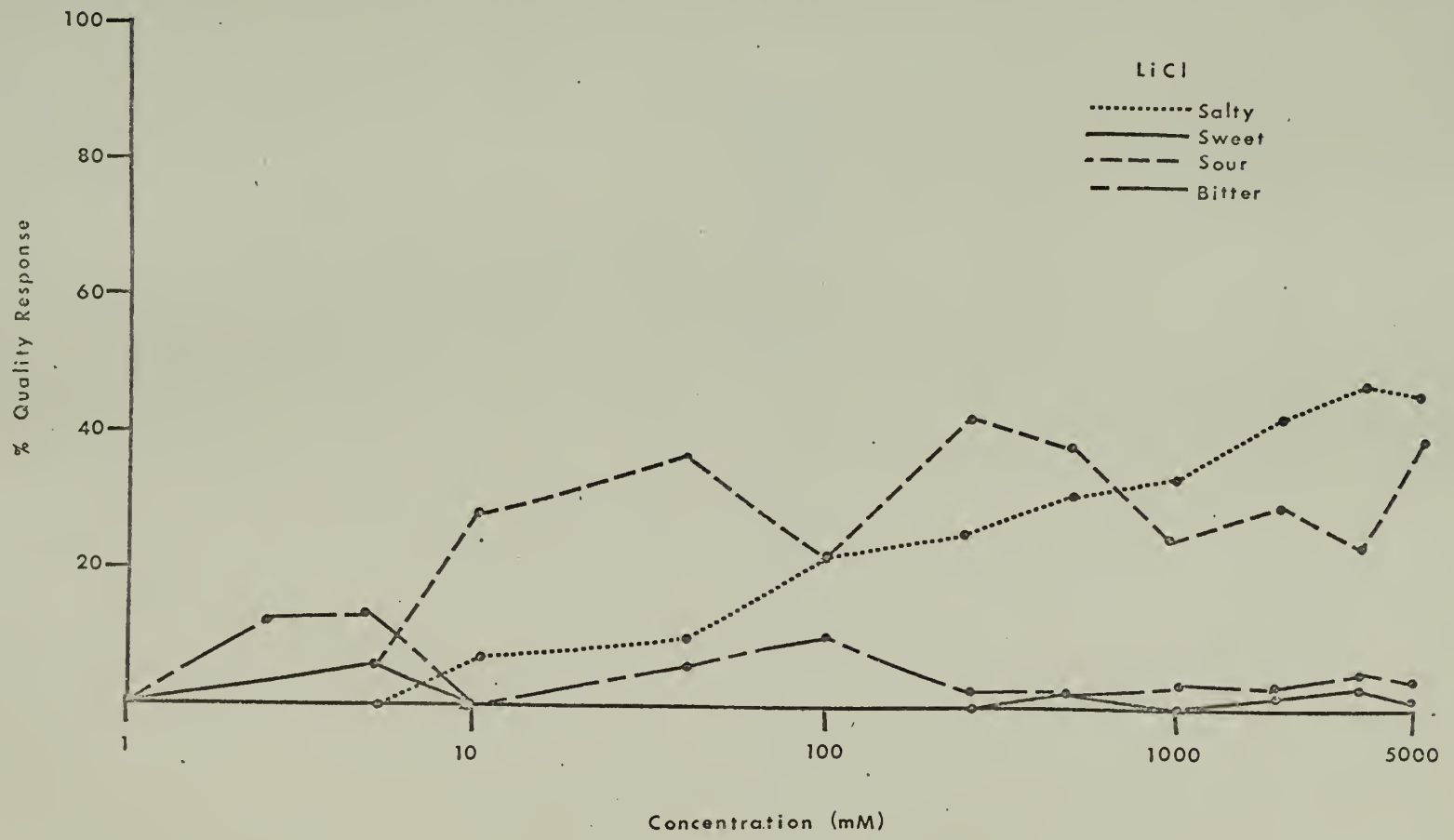
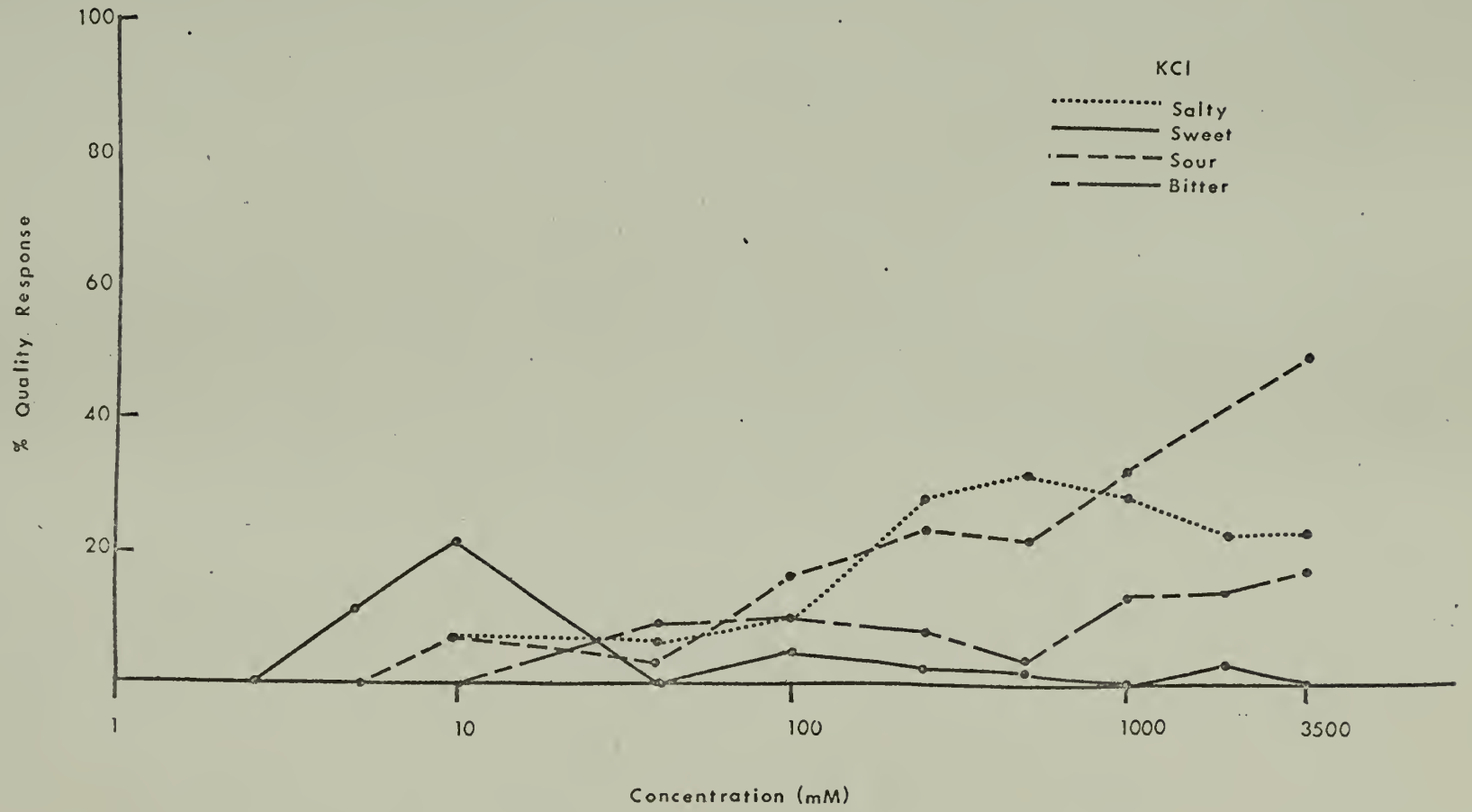

LiCl
Salty
Sweet
Sour
Bitter
% Quality Response
100
80
60
40
20
1
10
100
1000
5000
Concentration (mM)

Figure 22 Percentage of each quality response as a function of concentration for KCl. Data are collapsed across papillae and subjects.


KCl
Salty
Sweet
Sour
Bitter
% Quality Response
100
80
60
40
20
1
10
100
1000
3500
Concentration (mM)

quality as a function of concentration as have been previously reported for the whole mouth.

Discussion

Control procedures and support of a "water taste" at the single papilla level: The results of the control procedures indicate that guessing by the subjects was not a problem in these experiments. Over 93% of subject responses to stimulation of control areas of the tongue fall into the "no taste" or "indistinct or vague" categories (Table VII). Furthermore, the majority of the quality responses in the other 7% of the cases were appropriate for the solution presented, indicating that on these trials undetected papillae may have been stimulated in these "control" areas, or minute spread of the solution may have occurred to papillae adjoining the control area. Table VIII presents a similar picture, with 77% of the responses to distilled water falling into the null categories. However, of the remaining responses, over 78% were sour or bitter responses given by subjects DP and EG. This fact is interesting for two reasons. First, these responses do not appear to be the result of guessing, as neither subject showed a similar propensity for making sour or bitter guesses in the control procedure discussed previously (Table VII). Secondly, subjects DP and EG are both males. The conclusion suggested by these data is that these Ss were responding to the taste of the distilled water.

That distilled water is reported to have a sour or bitter taste has been known for some time. The recent investigations of this "water

taste" and of the effects of adaptation on taste function by Bartoshuk (1964, 1968, 1974) and McBurney (1969, 1971, 1973) indicate that this phenomenon is probably the result of adaptation to the sodium and chloride constituents of saliva. This conclusion is based on the fact that, following adaptation to NaCl, all solution concentrations of NaCl below the adapting concentration taste sour or bitter. That this may be the explanation for the sour and bitter responses of subjects DP and EG is a distinct possibility. However, this explanation does not account for the fact that only two of the four Ss showed this phenomenon. If it were the result of salivary adaptation it would be expected to occur in all Ss. Furthermore, the fact that the responses to water occurred only in the males suggests a possible sex difference. McCutcheon and Saunders (1972) reported a "few weak, sour or bitter responses" to distilled water in their single-papilla data, but they failed to state if these responses occurred in their male or female subjects, or in both. Data on individual differences in the occurrence of "water taste" have not been reported in the literature, however the data of this experiment suggest that this may be a fruitful area of investigation. It may, in fact, be the case that males and females differ in the amount of salivary sodium they possess, thus, allowing for the sex differences in this experiment to be resolved within the context of the "water taste" mechanism proposed by Bartoshuk.

Specificity vs. non-specificity: The fact that the majority of fungiform papillae in all subjects responded to chemicals representative of all of the four primary taste qualities supports the previous findings of Harper, et al., (1966), McCutcheon and Saunders (1972), and Bealer and

Smith (1975). Since an extremely large concentration range was used in this research, an explanation of this multiple sensitivity based on non-adequate stimulation of receptors by high concentration solutions is ruled out. The unequivocal conclusion from this research is that single human fungiform papillae possess multiple sensitivity to compounds representative of the four primary taste qualities.

As concerns the mechanisms of quality coding, these data indicate that, specificity, if it exists, must be found at the level of single taste buds or single receptor cells. However, since there are only two to five taste buds on a single human fungiform papilla (Paran, et al., 1975) and the vast majority of papillae in this experiment mediated all four taste qualities, it is highly unlikely that there can be specificity among taste buds. If there were, then all papillae with less than four taste buds would not be able to mediate all four qualities, and in addition, even those that did have four or five taste buds would probably not have one of each type of bud, given any degree of randomness in their distribution among papillae. Thus, it seems clear that any specificity to be found at the extreme periphery of the human taste system, must occur at the level of the individual receptor cells. Taste papillae are not a fundamental unit in the mechanism of quality coding. Rather, they appear to be only anatomical structures, whose functional role appears to have been lost in phylogeny.

The distribution of taste sensitivities among papillae was such that 80% of the tested papillae mediated all four qualities, 17.5% mediated some combination of three qualities, none mediated two qualities,

and only 2.5% (one papilla) were specific to a single quality. Furthermore, the response profiles for individual papillae (Figures 10-13) show that the sensitivities to the various test compounds were about constant for any given papilla, but the level of sensitivity differed among papillae. A similar finding was reported for the 15 papillae tested by Bealer and Smith (1975). Comparison of the overall sensitivity of papillae which mediated either four, three, two, or one taste quality (Table XII) suggests that those papillae which mediated less than the full number of taste qualities have lower overall sensitivities. The above facts combine to suggest that under normal circumstances human fungiform papillae have multiple sensitivity to the four primary taste qualities. However, some general process or characteristic of the individual papillae regulates the level of sensitivity to all compounds. In those papillae which have lower overall sensitivites, the responsiveness to any one class of compounds may be absent. Papillae with still lower sensitivities may be unresponsive to two, three, or all classes of compounds. The process which regulates the sensitivity of the papillae, may be a degenerative one, effecting all taste buds on a given papilla or it may be developmental, determined by the absolute number of taste buds and/or cells innervating a particular papilla. Some support for the former interpretation comes from the work on human taste buds by Arey et. al., (1939). These investigators suggested the existence of a "variable susceptability of neighboring sets of taste buds to the obscure forces responsible for progressive atrophy" to account for the large variability in the number of taste buds they found among papillae in their subjects.

It should be pointed out, however, that these researchers were investigating circumvallate papillae in older subjects than were tested here; and in addition, Jurisch (1922) found evidence of papillary degeneration only after the 40th year.

Regardless of the mechanism responsible for the variable sensitivity among papillae, the lower sensitivity in papillae which responded with fewer qualities accounts for the relative number of each papilla type found in this experiment. It is quite possible that if still higher concentrations of test solutions were employed. a larger number of papillae mediating only one or two qualities may have been found. The results of von Bekesy (1966), who found quality-specific papillae using extremely low concentrations, can be accounted for by his having stimulated papillae which were capable of mediating all four qualities, but having reached threshold with only one compound. An alternative explanation is that, by presenting solutions to the sides of papillae in his experiments, he stimulated taste buds and/or receptors that are more sensitive and more quality-specific than those found on the dorsal surface of papillae. Experiment IV of this research addresses itself to this possibility.

The profiles of Figures 10-13 also reveal that some papillae respond with a high level of sensitivity to one compound representative of a given quality but not at all to another compound representative of that quality. Similarly, the correlation matrices of thresholds for the various compounds (Tables XIII and XIV) show little correlation between compounds of the same taste quality, with the possible exception of sucrose and dextrose, for which the correlation coefficients for all Ss

are high. Such a situation is perplexing, especially if it is assumed that there are only four different types of receptor sites to which chemical structures can bind, and that all chemical solutions representative of a given quality bind to the same receptor site. This view is almost certainly incorrect, and it has been specifically suggested that, for both salts (Dzendolet and Meiselman, 1967b) and acids (Dzendolet, 1969b), the anion and cation affect different receptor sites. If this is the case, then the failure to find correlations among the thresholds for HCl and citric acid or between NaCl and LiCl may be due to the fact that different papillae have different numbers of each type of receptor site. Thus, although one papilla may respond more to NaCl than LiCl because of a greater number of receptor sites for Na^+, another papilla with more Li^+ sites may respond more to LiCl than NaCl. Such a situation would prevent any significant correlation of thresholds between NaCl and LiCl across papillae. A similar argument may be used to explain the failure to find correlations among the other pairs of solutions in Table XIII. The one case in which there does appear to be some degree of correlation for all subjects is that between sucrose and dextrose. This may indicate that these two sugars act on similar receptor sites, or the correlations may be spurious, due to the large number of correlations that were calculated. The latter explanation is probably applicable to at least some of the significant correlations in Table XIII.

Primary taste qualities: The subjective primacy of the taste qualities of sweet, salty, sour, and bitter is supported by the data of this experiment. Of over 6000 stimulus presentations in this experiment,

subjects chose to use the "complicated taste" category on only 10-15 occasions. Furthermore, the taste qualities they gave on these occasions were primarily combinations of the above four. Thus, a subject would occasionally report that quinine had a "sour-bitter" taste or that NaCl had a "sour-salty" taste. In addition, subjects would sometimes use this category to describe high concentrations of QSO_4 or KCl as being "stinging" or "burning." The bulk of these data suggests that subjects distinguish among only four different categories of taste experience and these categories are the classical four--sweet, salty, sour, and bitter. Whether this is due to lack of an adequate vocabulary for taste experience or the result of a true physiological primacy for these qualities is an empirical question which cannot be answered with the data at hand.

Single-papilla psychophysical functions: The psychophysical functions of Figures 15-19 exhibit two major characteristics. First, in many cases, there is a peaking of response magnitude at high concentrations. Secondly, the slopes of these functions are much lower than have usually been found in whole-mouth scaling of these same solutions. The former aspect of these data might be expected, since with the small subset of receptors involved in single-papilla stimulation, a very high solution concentration would cause the receptors to be maximally stimulated; however, once this point is reached, no increase in subjective intensity could be expected as a result of contribution by other stimulated receptors, as is the case in whole-mouth stimulation. The fact that all papillae did not exhibit this effect probably again reflects the sensitivity and operating range differences among papillae.

The rather low slopes of the functions in Figures 15-19 partially reflect the above "ceiling" effect at high concentrations. The median exponents for the various test solutions (Table XV) are well below the values usually reported for whole-mouth testing. The importance of this fact and its relevance to the literature will be discussed in Experiment III.

Although the average r values for least-squares fits to power functions were greater than the corresponding values for linear and logarithmic fits, there was no significant difference among them. This fact probably again reflects the asymptotic aspects of the functions for many of the papillae. If the data points at the highest concentrations of these papillae are ignored, the remaining points appear to fall more nearly along a straight line in full logarithmic coordinates. Whether this would significantly effect the fit of the data to a power function is an empirical question. However, by arbitrarily choosing the data points to be included in the regression, the impartiality of the data analysis would be seriously compromised. Thus, at best it can be said that a power function is a somewhat better description of the relationship between subjective intensity and physical magnitude in a single papilla, than either a linear or a logarithmic function. However, the latter two may also be used to describe the data.

Quality changes in salts as a function of concentration: The taste quality changes that occur as a function of solution concentration in many inorganic salts also occur within a single papilla. Figures 20-22 show clearly that at their lowest concentrations NaCl and KCl are sweet.

LiCl also shows a greater percentage of sweet responses at the lower concentrations, but a strong bitter component is simultaneously present. At higher concentrations there is an increase in both sour and salty responses, so that, for LiCl, the predominant taste in the mid-concentration range is sour. At the highest concentrations, NaCl and LiCl assume their characteristic salty taste, while KCl acquires a strong sour taste, with some salty and bitter also present. The above taste quality changes are identical to those found with whole-mouth procedures (Dzendolet and Meiselman, 1967a; Cardello and Murphy, 1976), with the exception that the sour component in each of the curves at higher concentrations is greater than has been previously found. This greater percentage of sour responses is probably related to the same mechanism(s) responsible for the sour-salty confusion found in the preliminary experiments, and will be returned to in the discussion of taste confusions to follow.

Concerning the mechanism of taste quality changes in salts, the combined results of this experiment support Dzendolet's (1968) hypothesis, with one slight modification. Since Dzendolet assumes that certain concentration-dependent physico-chemical structures of the salt solutions are responsible for the stimulation of different receptor types, these structures must also be present in solutions presented to a single papilla. Thus, stimulation of different receptors types at different concentrations would be expected even within a single papilla. However, Dzendolet's hypothesis assumes that the mechanism by which one quality replaces another is through a process of inhibition among papillae. Since only one

papilla was stimulated in this experiment, Dzendolet's inhibitory mechanism cannot be operating. The problem lies in Dzendolet's assumption that individual papillae are quality specific. At the time that Dzendolet (1968) proposed his theory, von Bekesy (1964a, 1966) had just completed his work on chemical and electrical stimulation of single papillae. Thus, his assumption was not unreasonable at the time. In light of the present research, as well as that of Harper, et al., (1966), McCutcheon and Saunders (1972) and Bealer and Smith (1975), it is clear that this assumption is false. However, by modifying Dzendolet's theory slightly, so that the inhibition is assumed to occur between individual taste cells, rather than between papillae, Dzendolet's theory can adequately account for taste quality changes of salt solutions for both whole-mouth and single-papilla stimulation.

Taste confusions

As pointed out in the previous section, the salt data (Figures 20-22) exhibit a higher percentage of sour responses at the higher concentrations than have been reported with whole-mouth procedures. This finding parallels the results of Experiment 3A, in which it was found that the percentage of sour responses to NaCl increased with increasing concentration (Figures 3 and 4). Thus, it appears that the sour-salty confusion found with dorsal tongue stimulation also manifests itself during single-papilla stimulation. An examination of the quality responses to HCl and to citric acid in this experiment further supports this contention. Of the total number (200) of single-papilla quality responses to HCl, 60%

were sour, 30% were salty, 2% were sweet and 8% were bitter. For citric acid the percentage of the total number of responses (300) were almost identical, with 60% being sour, 30% salty, 2% sweet, and 7% bitter. Looking at Figure 3, the 30% salty responses in the single-papilla responses to acid are approximately the same as were found for HCl in Experiment 3A. Thus, the same mechanism(s) which were operating to produce the sour-salty confusions in the preliminary experiments, are also operating at the single-papilla level.

This sour-salty confusion found in both the single-papilla experiments and the preliminary experiments involving small-area stimulation of the dorsal tongue, is interesting for a number of reasons. First, McCutcheon and Saunders (1972), in their work on chemical stimulation of single papillae, were unable to find consistent salty responses to NaCl. They reported that:

> Sodium chloride gave stable "sour" responses in one papilla for both subjects. Although the two subjects occasionally gave "salty" responses to sodium chloride stimulations, the predominant response was "sour"....Our failure to obtain the reliable "salty" responses to a strong concentration of NaCl is perplexing. It is possible that simultaneous stimulation of several papillae will be necessary to obtain a clear "salty" response. (McCutcheon and Saunders, 1972, p. 216)

The "failure" that McCutcheon and Saunders reported, appears not to be a "failure" in any sense of the word. Rather it appears to be a fact of human taste discrimination under conditions of small-area dorsal tongue stimulation. Furthermore, their suggestion that stimulation of several papillae may be necessary to obtain the stable "salty" response is precluded by the data of Experiments 2A and 3A, since in those

experiments a large number of papillae were stimulated simultaneously, yet the confusion still occurred.

In addition to their "failure" with NaCl, McCutcheon and Saunders also reported that "salty" responses were often given to HCl stimulation. Again, the "sour-salty" confusion is apparent.

The existence of a "sour-salty" confusion may also account for the numerous "inappropriate" quality responses found in other single-papilla studies (Harper, et al., 1966; Bealer and Smith, 1975). It is unfortunate that these investigators chose not to analyze the quality responses given to each of their test compounds, but rather, reported only "hits" and "misses."

Although the percentages of quality responses to HCl and to citric acid, reported above, were almost identical, a very apparent sex difference was observed among subjects. This difference was related to the percentage of bitter responses. In particular, although there were no major differences in the percentages of sour, salty, or sweet responses to HCl and citric acid, over 94% of all bitter responses to HCl were made by the male subjects (DP and EG), while 100% of the bitter responses to citric acid were made by the males. Furthermore, these bitter responses occurred throughout the entire range of these compounds, as well as throughout the entire range of the three salts. Frequent bitter and sour responses were also given at the lower concentrations of sucrose, dextrose, QSO_4 and QHCl.

The explanation of these data appears to be related to the fact that males have a greater propensity to confuse the sour and bitter taste

qualities (Meiselman and Dzendolet, 1967). This accounts for the higher percentage of bitter responses at all concentrations of HCl and citric acid. The greater percentage of bitter responses throughout the concentration range of the salts is probably related to the fact that the salts are often tasted as being sour. Thus, there may be an interaction of confusions with males, such that dorsal stimulation with a salt solution elicits a sour-salty taste, with the sour component sometimes being confused with a bitter taste.

The frequent bitter and sour responses made by the male subjects at the lower concentrations of the sugars and quinine compounds suggests that they may be responding to the distilled water of these solutions. This explanation derives from the fact that the males frequently called distilled water bitter or sour when it was presented alone to the papilla (Table VIII). It would follow directly that solutions of low concentration would also be called bitter or sour because of the large amount of distilled water compared to the small amount of solute in the solution.

As mentioned in the results section, subject EG's sour and bitter responses to low concentrations of sucrose and of dextrose were so numerous that his recognition thresholds had to be calculated in a different manner from the other Ss, in order to insure that his recognition thresholds were for sugar and not for water. That the calculation of EG's thresholds for acids and quinine compounds were also effected by the response to water, is a definite possibility. However, since sour and bitter are the "appropriate" quality responses for these compounds, it is impossible to say whether or not this was the case. Thus, subject EG's

thresholds for these compounds should be viewed with the reservation that they may be spuriously low.

The fact that this "water taste" was so pronounced in the data for the males, but not in the data for the females, suggests a fruitful avenue for future research.

Experiment III

In order to compare the single-papilla thresholds and psychophysical functions of Experiment II with their whole-mouth counterparts in the same individual, the following experiment was undertaken at the completion of the single-papilla work.

Subjects and Stimuli

Subjects and stimulus solutions were the same as in Experiment II.

Procedure

Thresholds: S sat at the experimental table. At the start of each trial, S was presented with 10 ml of test solution in a 50 ml plastic cup. S was instructed to sip the entire contents of the cup, hold the solution in his/her mouth for three seconds and then expectorate. S then reported the taste quality of the solution, using the same response categories as were available in Experiment II. After making his response, S rinsed his mouth with distilled water from an eight ounce cup and awaited the next trial. An ISI of two minutes was employed.

Stimuli were presented using a modified method of constant stimuli. The modification was analagous to that described in Experiment II, with

the exception that testing began with solution concentrations near threshold and was not continued above the concentration at which two taste quality responses were given. All solutions were presented twice, so that detection and recognition thresholds could be determined in the same manner as for single papillae.

Scaling data: After the threshold data had been collected, each S returned on the following day to undergo testing with suprathreshold solutions. The test solutions included all of those listed in Table VI with the exception of those noted by an asterisk.

At the start of each trial S was presented with 2 ml of solution in a 50 ml plastic cup. S sipped the entire contents of the cup, held the solution in his/her mouth for three seconds, and then expectorated. S then gave both a taste quality response, as before, and a magnitude estimate of the subjective intensity of the solution. No modulus was used. After making his response, S rinsed voluminously, as required by the extremely concentrated solutions that were used. A three-minute ISI was employed.

All solutions were presented randomly, and each was presented only once. This was done to reduce the total number of solution presentations, and, thereby, minimize the effects of adaptation. The use of only a single presentation of each solution is acceptable in scaling methodology, since repeated judgments of the same stimulus adds little information to that already obtained on the first judgment (Stevens, 1971).

Results

Thresholds: Detection and recognition thresholds were determined

for each of the nine test compounds using the same least-squares regression procedure used for the single-papilla thresholds. These thresholds appear in Table XVI along with the average of the single-papilla thresholds for each S. Not unexpectedly, the whole-mouth thresholds are consistently below the average single-papilla thresholds.

Psychophysical functions: Whole-mouth psychophysical functions were fit to linear, logarithmic, and power functions, and the resultant r values were compared by a two-way repeated-measures analysis of variance. Again, as with the single-papilla data, none of the fits were significantly better than one another, although the average r value suggested that the fits to power functions were somewhat better than the fits to either of the other two functions. This may again be accounted for by the fact that the response curves tended to asymptote at the higher concentrations, although not to the extent found within single papillae. The median exponents across subjects, determined for the best-fitting power functions, appear in Table XVII, along with the median single-papilla exponent for each test compound. A two-way repeated-measures analysis of variance showed a significant difference in the exponents for single-papilla vs. whole-mouth stimulation ($F = 12.54$ df = 1/3, $p < .05$) and for solution ($F = 4.165$, df = 8/24, $p < .05$).

Discussion

The whole-mouth thresholds for each S are well below the average single-papilla thresholds. This is to be expected since the relationship between stimulus concentration and area of stimulation is described by

Table XVI

Detection and recognition thresholds for whole mouth stimulation vs. average detection and recognition thresholds for single papilla stimulation. All thresholds are expressed in milliMoles (mM).

			Sucrose	Dextrose	QSO_4	QHCl	HCl	Citric Acid	NaCl	LiCl	KCl
SC	Detection	Single Papilla	324	625	1.57	31.9	31	164	491	1789	1628
		Whole Mouth	.375	13.3	.00375	.00375	.0283	.0583	1.33	.75	2.83
	Recognition	Single Papilla	391	778	1.83	40.3	37	216	1005	1789	1793
		Whole Mouth	.75	13.3	.00583	.00583	.0463	.075	1.33	1.75	2.83
MS	Detection	Single Papilla	279	302	.64	16.6	15.8	20.6	1145	560	736
		Whole Mouth	17.5	75	.0133	.0175	.0075	.175	1.75	3.75	1.75
	Recognition	Single Papilla	449	373	.728	22.3	20.3	24.4	1152	564	736
		Whole Mouth	17.5	75	.0133	.0175	.0075	.175	11.7	3.75	2.83
EG	Detection	Single Papilla	108	66.6	.258	5.90	27	27	534	461	123
		Whole Mouth	10.6	28.3	.00225	.00583	.0075	.0225	25	5.83	4.63
	Recognition	Single Papilla	267	739	.390	7.27	32	37.7	784	601	156
		Whole Mouth	10.6	28.3	.00225	.00583	.0075	.0225	25	5.83	4.63
DP	Detection	Single Papilla	313	440	1.35	56.3	23.1	122	1692	1094	782
		Whole Mouth	4.63	58.3	.00225	.00075	.00583	.0463	3.75	1.33	11.7
	Recognition	Single Papilla	589	701	1.80	70.9	24.3	129	1972	1525	1114
		Whole Mouth	7.5	58.3	.00375	.00175	.0075	.375	5.83	11.7	11.7

Table XVII

Median exponents of the best-fitting power functions for whole-mouth psychophysical functions compared to the median exponents for single-papilla psychophysical functions (Experiment III)

Solution	Median exponents for whole-mouth	Median exponents for single-papilla
Sucrose	.610	.219
Dextrose	.930	.284
QSO_4	.474	.173
QHCl	.417	.280
HCl	.443	.413
Citric Acid	.328	.344
NaCl	.677	.181
LiCl	.656	.188
KCl	.738	.383

the equation (Smith, 1971):

$$I = C^n \times bA^p$$

where I is perceived taste intensity

C is the concentration of the stimulus

n is the exponent of the power function relating perceived taste intensity to stimulus concentration

A is the area stimulated

p is the exponent of the power function relating perceived taste intensity to area stimulated

and b is a constant of proportionality.

Smith (1971) has also provided equal intensity functions for NaCl, QHCl, citric acid, and saccharin as a function of both area of stimulation and number of papillae stimulated. The latter functions were determined by counting the number of papillae present per unit area of stimulation. (Smith does not state whether his counts were of fungiform papillae only; but since he stimulated the anterior dorsal tongue surface, it can be assumed that the majority of papillae were fungiform.) The interesting aspect of Smith's functions are that they show a differential effect of the number of papillae on taste intensity for each of the four solutions he tested. Extrapolating from his data, it can be predicted that for QHCl and saccharin the threshold for whole-tongue stimulation should be approximately two log units lower than the threshold for a single papilla. Similarly, the whole-tongue threshold for citric acid should be approximately one log unit lower than the single-papilla threshold, and that for NaCl approximately .5 log units lower. Examination of Table XVI reveals that, in this experiment, the whole mouth

detection and recognition thresholds were lower than their single-papilla counterparts. For QHCl this difference was 3.5 log units, for citric acid it was 2.5 - 3.0 log units, and for NaCl it was 2.0 log units. The relative order of these thresholds by solution is the same as that predicted from Smith's data; however, the absolute differences are greater. The reason for the latter discrepancy derives from the fact that Smith's data were obtained from stimulation of the dorsal tongue only; therefore his functions only allow accurate extrapolation for areas of stimulation on the tongue surface. Thus, the maximum range of extrapolation that can be made is between a single papilla and the whole tongue. These were, in fact, the two areas used to predict the differences in threshold concentrations. The problem is that in the present experiment the reported differences in threshold concentrations are for single-papilla stimulation vs. whole-mouth stimulation. Therefore, the larger differences between thresholds in this experiment are consistent with having stimulated a larger area than that for which the predictions were made.

Although saccharin was not a test compound in this experiment, as it was in Smith's (1971) study, a comparison of the differences between whole-mouth and single-papilla thresholds for sucrose and for dextrose indicates that the whole mouth thresholds were only 1.0 - 1.5 log units lower. These differences are smaller than that predicted for saccharin (2.0 log units) from Smith's data. This suggests that the distribution of receptors responsive to saccharin is different from that for sucrose or for dextrose. This is in keeping with the similar finding by Moskowitz (1970b) that the exponent for the subjective sweetness

function of saccharin (.6 - .8) is different from that for sugars (1.0 - 1.3), and that this is probably related to the fact that saccharin stimulates bitter receptors in addition to sweet receptors.

Psychophysical functions

The whole-mouth psychophysical functions exhibit the same characteristic as do the single-papilla functions, namely a tendency to reach asymptote at the higher solution concentrations. However, the exponents for the whole-mouth functions are consistently higher than for the single-papilla functions. Meiselman (1971) has shown that the method of presentation of solution to the tongue can effect the exponent of the psychophysical function. In particular, whole-mouth sip procedures produce larger exponents than do dorsal-tongue flow procedures. Furthermore, two studies that have restricted stimulation to a small area of the dorsal tongue surface have reported some of the lowest exponents in the literature (Feallock, 1965; Collings, 1974). Yet, the single-papilla exponents found in Experiment II are even lower than the exponents reported in either of these two studies. Smith (1971), in his study of the interaction of concentration and area, found no significant difference among the exponents of the psychophysical functions for any test compounds, as a function of area of stimulation. However, re-examination of his data shows that there is a trend in the direction of lower exponents for smaller areas of stimulation, at least in the cases of NaCl and citric acid. These combined facts indicate that the exponent of the psychophysical functions for taste may be dependent upon the total area

of stimulation. The lower exponents found when using flow procedures may be partly related to the fact that flow procedures involve stimulation of only the dorsal tongue surface, and therefore, a smaller area is involved than with sip procedures. One possible mechanism for small-area stimulation producing lower exponents is the following. For any given concentration, the solution presented to a small area of the tongue is focused on that area, and individual receptors are stimulated at some rate that is related to the concentration of the stimulus. This is also true when the whole mouth is stimulated, except that the effective concentration of the solution is reduced in proportion to the area over which the solution is allowed to spread. Thus, for the same concentration, the effect on each individual receptor is less. Such a situation would allow for a wider range of concentrations to be coded by the firing rate of cells, before the upper limit of response rate is reached for any one receptor. This means that with higher concentrations, stimulation of a small area would not allow as great an increase in total discharge as large area stimulation would. This compression at higher concentrations would result in lower exponents for small area stimulation. The possibility of this, as exemplified by the data of this experiment, suggests that a systematic examination of area affects on the slope of psychophysical functions may prove fruitful in the evaluation of exponent invariance and the underlying physiological basis of the power law.

Experiment IV

A major controversy of single-papilla research has arisen from the report by von Bekesy (1966) that he was able to obtain clear taste sensations from his subjects by stimulating the "sides" of papillae. Many investigators have doubted this claim, because available histology of human fungiform papillae has not established the existence of taste buds on the sides of these papillae. However, single-papilla research to date has failed to examine this question. Its importance for the interpretation of von Bekesy's results is obvious. If stimulation of the sides of papillae produces a greater magnitude of response than stimulation of the dorsal surface of the papillae, then the low solution concentration used by von Bekesy may have been adequate to stimulate these papillae. Moreover, there is the possibility that the specificity of response found by von Bekesy was a result of his having stimulated only the sides of papillae. In order to compare the responses resulting from stimulation of the dorsal surface of papillae with those resulting from stimulation of the sides, the following experiment was undertaken.

Subjects and Apparatus

The subjects and apparatus were the same as in Experiments I and II.

Stimuli

The test solutions consisted of the four standard solutions used in Experiments I and II, namely 700 mM Sucrose, 2mM QSO_4, 30 mM HCl, and 2000 mM NaCl.

Procedure

In order to stimulate the "sides" of a papilla, a method had to be devised to lift the papilla from the tongue surface so as to expose its circumferential surfaces. The method developed was to use a small piece of polyethelene tubing as a prod to lift the papilla into an erect position. If the piece of tubing was then immediately removed, the papilla would return to its original resting position. In order to prevent this, the papilla was held in an upright position for approximately 30 seconds. During this time, the base of the papilla dried through evaporation. When the tubing was then pulled away, the papilla remained in an upright position of its own accord. The advantage afforded by this procedure, over that of holding the papilla upright during stimulation, is that all tactile interference is eliminated at the time of stimulation.

At the start of each trial S extended his tongue in the manner previously described. Depending on whether the tested papilla was to be stimulated on its "side," or on the "top," E did one of two things. If the papilla was to be stimulated on the side, E manipulated the papilla in the manner described above for a period of 30 seconds, leaving the papilla in an upright position. If the papilla was to be stimulated on its dorsal surface, then E merely moved the papilla with the tubing for a period of 30 seconds. This was done to prevent S from discriminating between those trials on which the side or top of the papilla was to be stimulated. Following one of the above two procedures, the tongue was allowed to dry for an additional 15 seconds, after which time the

stimulus was presented.

Each solution was presented to one of four papillae. Each papilla had been chosen on the basis of its being highly responsive to one of the four test compounds. The papilla which was stimulated, as well as the location of stimulation, was random from trial to trial. Each papilla was stimulated eight times on the top and eight times on the side with the same solution.

S gave both quality responses and magnitude estimates after each presentation, in the same manner as previously described. S then rinsed his tongue with distilled water and awaited the next trial. A two-minute ISI was employed.

Results

The percentage of quality responses (those other than "no taste" or "indistinct or vague") were calculated for each solution, subject, and location of stimulation. These data appear in Table XVIII. A two-way repeated-measures analysis of variance showed a significant effect for locus of stimulation ($F = 14.28$, $df = 1/3$, $p < .05$). In addition the geometric means of the magnitude estimates for each solution, subject, and locus of stimulation were calculated for those trials on which a non-zero magnitude estimate was given. These data appear in Table XIX. A two-way repeated measures analysis of variance again showed a significant effect due to locus of stimulation ($F = 76.95$, $df = 1/3$, $p < .05$).

Table XVIII

Percentages of taste quality responses to stimulation of the "topside"*and "underside"* of single human fungiform papillae

Subject	Solution	Percent Quality Response Topside	Underside
SC	700 mM CHO**	87.5	87.5
	2 mM QSO_4	62.5	62.5
	30 mM HCl	62.5	25.0
	2000 mM NaCl	62.5	50.0
	Combined	68.75	56.25
MS	700 mM CHO**	87.5	12.5
	2 mM QSO_4	37.5	25.0
	30 mM HCl	100.0	50.0
	2000 mM NaCl	100.0	75.0
	Combined	81.25	40.62
DP	700 mM CHO**	37.5	25.0
	2 mM QSO_4	100.0	12.5
	30 mM HCl	87.5	12.5
	2000 mM NaCl	50.0	0.0
	Combined	68.75	12.50
EG	700 mM CHO**	75.0	0.0
	2 mM QSO_4	50.0	50.0
	30 mM HCl	62.5	0.0
	2000 mM NaCl	62.5	50.0
	Combined	62.50	25.00

Note: Percentages based on eight presentations of each solution to each S.

*See text for definition of "topside" and "underside."

**Denotes sucrose.

Table XIX

Geometric means of the magnitude estimates given in response to stimulation of the "topside" and "underside" of fungiform papillae

Subject	Solution	Geometric Mean Magnitude Estimates Topside	Underside
SC	700 mM CHO*	9.463	7.047
	2 mM QSO_4	12.870	6.435
	30 mM HCl	9.754	5.105
	2000 mM NaCl	8.994	8.994
	Combined	10.215	6.755
MS	700 mM CHO*	7.595	4.797
	2 mM QSO_4	7.364	5.775
	30 mM HCl	10.563	7.708
	2000 mM NaCl	18.401	10.227
	Combined	10.211	6.836
DP	700 mM CHO*	7.577	5.382
	2 mM QSO_4	10.900	4.701
	30 mM HCl	13.871	2.621
	2000 mM NaCl	9.493	7.023
	Combined	10.212	4.645
EG	700 mM CHO*	9.467	0.0
	2 mM QSO_4	11.583	10.422
	30 mM HCl	7.576	6.160
	2000 mM NaCl	13.115	10.126
	Combined	10.216	8.668

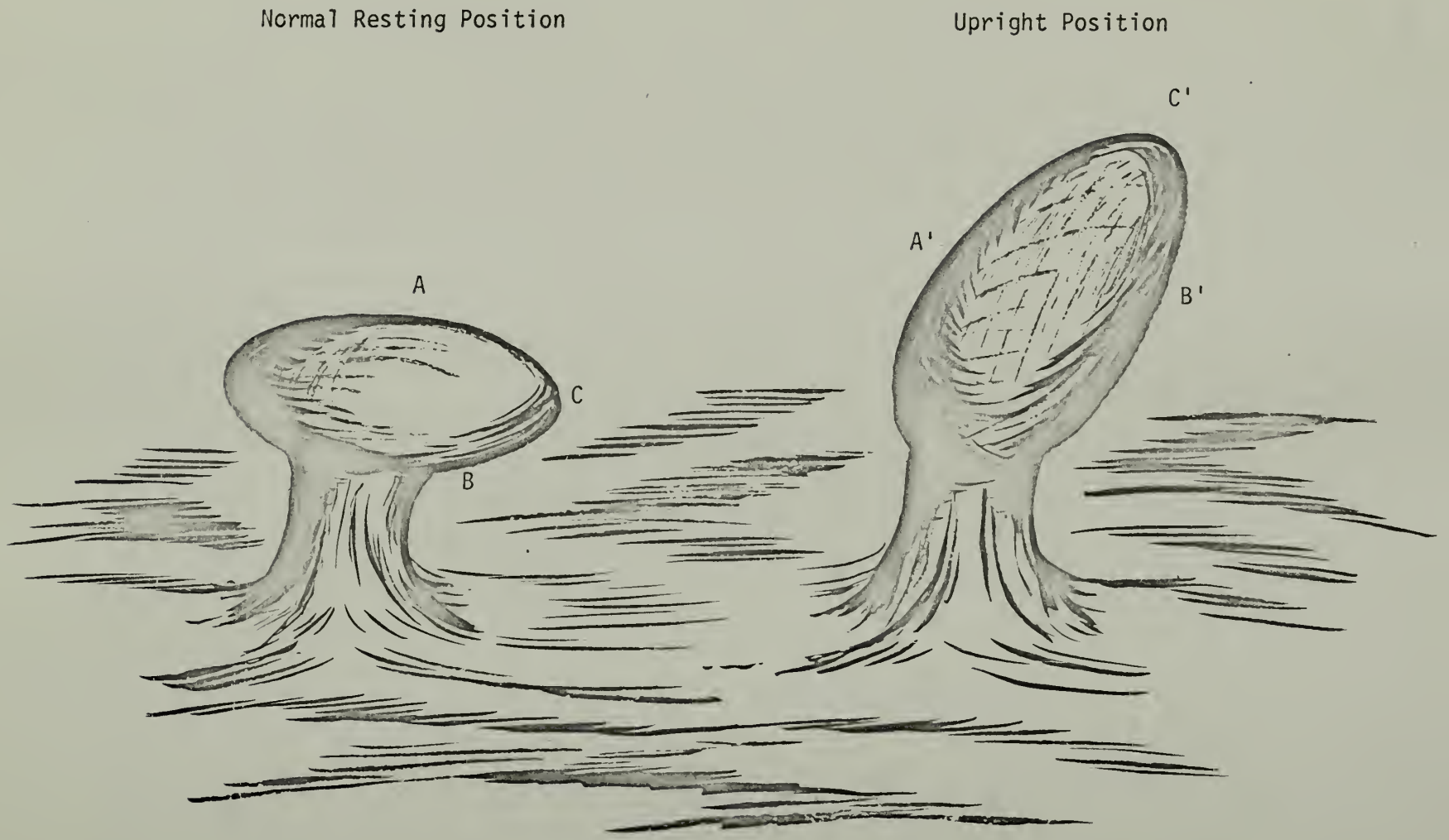
Note: Geometric means are for those trials in which a response other than "no taste" was given.

*Denotes sucrose

Discussion

At the outset of this experiment it became obvious that the terminology used in the literature to describe the two loci of stimulation was inappropriate and misleading. The reason for this is that in the majority of cases, the fungiform papillae on the dorsal surface of the tongue rest in a position which is slightly bent relative to the perpendicular. (Those papillae near the tip and margins of the tongue do not show such bending, as they are usually shorter in height and stand more erect in the resting position.) In addition, their shape is such as to present a flattened surface to the external environment. The left side of Figure 23 shows a fungiform papilla in this normal testing position. When such a papilla is lifted into an upright position it takes on the shape shown on the right-hand side of Figure 23. Comparing these two sketches it is clear that surface A, which is normally considered to be the "top" of the papilla, is identical to "side" A' of the uprighted papilla. Thus, this surface may more accurately be described as the "topside" of the papilla. Similarly, the surface that is opposite the topside, namely surface B (or B'), is more properly called the "underside" of the papilla. Surface C (or C') should most properly be called the "apical" end of the papilla. As such it is the "topside" of the papilla which is stimulated under normal circumstances, and it is this surface that other authors refer to as the "top" of the papilla. Similarly it is the "underside" of the papilla that von Bekesy was probably stimulating, but since he had uprighted the

Figure 23 Sketch showing the relative location of surfaces of a fungiform papilla when in the normal and the upright positions.


Normal Resting Position
Upright Position
A
B
C
A'
B'
C'

papilla, it appeared to him to be merely the "side." Thus, the comparison made in this experiment was between the "topside" and "underside" of fungiform papillae and will be so designated through the rest of the discussion.

The fact that both the percentage of quality responses and the geometric mean of the magnitude estimates were greater in response to stimulation of the "topside," indicates that this is the more effective receptor surface for the papilla. This is what one would expect from a phylogenetic view, since it is more advantageous for an organism to be more chemically sensitive on those surfaces which face out to the world, than on those surfaces that do not. The fact that responses were obtained at all on the "underside" indicates that some taste buds must, in fact, be present on "circumferential" surfaces of fungiform papillae.

The results of this experiment cast further doubt on the ability of von Bekesy's solution concentrations to have reached threshold in any, but a very small number of fungiform papillae. Furthermore, after testing had been completed in this experiment the underside of each papilla was randomly tested with each solution. In almost all cases these trials resulted in correct quality responses. This multiple sensitivity eliminates the possibility that the specificity found by von Bekesy (1966) was attributable to his having stimulated the undersides of the papillae.

Experiment V

In addition to the work on chemical stimulation of papillae, von

Bekesy also found specificity of response in human fungiform papillae using electrical stimulation (von Bekesy, 1964a, 1965). Furthermore, he found complete agreement between the taste qualities elicited in the same papilla by chemical and electrical stimulation.

In order to compare the quality responses resulting from the chemical stimulation of Experiment II with those resulting from electrical stimulation of the same papillae, the following experiment was undertaken.

Subjects

The subjects were the same as in previous experiments.

Apparatus

The apparatus for electrical stimulation was identical to that used by Dzendolet and Murphy (1974). It consisted of a stimulator (Model 54, Grass Instrument Company, Quincy, Massachusetts) which was adjusted to produce 0.5 msec monophasic positive, rectangular pulses. The stimulating electrode was a length of gold wire (0.3 mm in diameter) coated with an insulating material and presenting a stimulating surface of 0.07 mm^2. The return electrode was a common disk-shaped silver electrode (Grass Instrument Company), similar to that used in the recording of galvanic skin responses. A 1 megohm resistor was placed in series with the stimulating electrode to produce a constant current source and to protect S against a current surge.

Procedure

S was seated at the experimental table in the same manner as for

chemical stimulation. The return electrode was placed under S's tongue and the lead wire allowed to extend from the corner of the mouth. S could then extend his/her tongue as in the previous experiments. At the start of each trial S extended his tongue, and it was allowed to dry for a period of 45 seconds. The stimulating electrode was then placed on a papilla under 30x magnification. After five seconds S was told that the current would soon be presented. Within the next 5-10 seconds the current was presented for approximately five seconds. The stimulating electrode was then removed, S rinsed his tongue with distilled water and made his/her response. A two-minute ISI was employed.

S made two responses. One was a description of the sensation produced by the stimulating electrode during the initial five seconds, while the current was off. This response was obtained to use as a control in determining whether S was actually responding to the current or merely to the touch of the gold wire of the stimulating electrode. After making this initial response, S gave a description of the sensation produced by the electrode when the current was on. S was not restricted in his response choices and could choose any descriptor he deemed appropriate for the sensation. Further, introspective reports were also accepted if S felt that they were necessary in order to adequately describe the sensation.

At the start of the experiment a period of pilot testing was required to obtain a voltage-frequency combination which was appropriate to use with each S. The criterion for choice of a voltage-frequency combination was that the sensation produced by it was strong, but not so strong as to be

disagreeable. After an appropriate combination had been chosen for each S, testing began.

Each of the 10 chemically responsive papillae in each S was stimulated five times in random order, for a total of 50 presentations in each S.

Results

Table XX catalogues the various descriptions given to electrical stimulation of single papillae and their frequency of occurrence across Ss. A breakdown of responses for individual Ss appears in Appendix C.

In order to compare the responses to electrical stimulation with those to chemical stimulation, a criterion of three taste quality responses out of five stimulus presentations was adopted in order to classify a papilla as being responsive to electrical stimulation. The particular quality combinations that were elicited by electrical stimulation were then compared to the quality combinations elicited by chemical stimulation of these papillae in Experiment II. However, since chemical stimulation almost always elicited all four taste qualities, the quality of the chemical stimulus which was found to be most effective for that papilla (from Figures 10-13) was noted for comparison. The various quality responses to chemical and electrical stimulation of these papillae appear in Table XXI. It is clear from these data that there is very little correlation between the quality (-ies) elicited by electrical stimulation in a pipilla and the quality (-ies) elicited by chemical stimulation of the same papilla.

Table XX

Frequencies of responses given by subjects to describe the sensations resulting from electrical stimulation of single fungiform papillae. The "current off" condition shows responses given during the control period before the current was turned on, but while the stimulating electrode was touching the papilla. The "current on" condition shows responses given while the current was on.

Sensations	Current Off		Current On	
Gustatory	Sour	10	Salty	40
	Sour, buzz	4	Salty, sharp	5
	Sour, metallic	1	Salty, vibration	2
	Salty	1	Salty, strong	1
	Salty, tingly	1	Sour	19
	Sweet	3	Sour, buzz	5
	Bitter	1	Sour, strong	4
			Sour, metallic	1
			Sour-salty	1
			Sweet	8
			Sweet, cool	2
			Sweet, tingly	1
			Sweet, buzz	1
			Sweet, metallic	1
			Sweet-salty	1
			Bitter, peculiar	1
			Bitter, buzz	1
Tactile	Metallic	52	Buzz	21
	Brassy	26	Buzz, strong	2
	Buzz	23	Vibration	15
	Tingly	9	Vibration, strong	2
	Vibration	6	Metallic	13
	Shock	3	Metallic, strong	12

Table XX - Continued

Sensations	Current Off		Current On	
Tactile (cont.)			Shock	8
			Brassy	3
			Indistinct,vague	2
			Burning	1
			Tingly, strong	1
Thermal	Cold	16	Cold	4
	Cool	9	Cold, buzz	1
			Cool, tingly	1
No Sensation	--	35	--	19
	Current Off: Total Number of Presentations = 200		Current On: Total Number of Presentations = 200	

Table XXI

Comparison of the quality responses elicited by chemical and electrical stimulation of the same papillae

Subject	Papilla Number	Chemical Responsiveness	Maximum Chemical Sensitivity	Electrical Responsiveness
SC	30	Sw-B-So-Sa	So-Sa	Sw-Sa
	28	Sw-B-So-Sa	B	Sa
	41	Sw-B-So-Sa	So-Sa	Sa
	17	Sw-B-So-Sa	B-Sa	Sw-Sa
	31	Sw-B-So-Sa	Sa	So-Sa
MS	9	Sw-B-So-Sa	Sa	So-Sa
	28	Sw-B-So-Sa	B-Sa	Sa
	25	Sw-B-So-Sa	So	Sw-Sa
	10	Sw-B-So-Sa	B-So	Sw-Sa
	19	Sw-B-So-Sa	Sa	So-Sa
	27	Sw-B-So-Sa	Sa	Sa
	31	Sw-B-So-Sa	B	Sa
	22	B-So-Sa	So	Sa
DP	36	Sw-B-So-Sa	B-So	So
	15	Sw-B-So-Sa	So	So
	35	Sw-B-So-Sa	Sw-Sa	So
EG	32	Sw-B-So-Sa	Sa	So-Sa
	39	Sw-B-So-Sa	B	So-Sa
	50	Sw-B-So-Sa	Sa	So
	26	Sw-B-So-Sa	So-Sa	B-So-Sa

Note: Maximum chemical sensitivity was determined from Figs. 10-13. The quality (-ies) listed under this column are the characteristic quality (-ies) of the solution(s) with the highest relative sensitivity in the papilla.

Discussion

Looking at Table XIX, one can see that thermal, tactile and gustatory sensations were all elicited by the stimulating electrode, whether or not the current was on. The thermal and tactile responses under both conditions were expected, given the metallic nature of the electrode. However, the gustatory responses which were elicited by the electrode when the current was off were not expected. Similar gustatory responses to tactile stimulation of papillae have been reported previously by Dzendolet and Murphy (1974). In fact, these authors could elicit such responses by touching papillae with a piece of polyethelene tubing. Thus, these responses appear to be the result of tactile stimulation, rather than chemical stimulation by electrolytic processes related to the use of a metal electrode.

The gustatory responses elicited prior to stimulation with current are much fewer in number than those elicited while the current was on. The percentages of gustatory responses, out of the total number of responses, was 10% in the former case and 47% in the latter case. Furthermore, the distribution of taste qualities differed between the two conditions. Prior to initiating the current, the percentages of quality responses were 51% salty, 31% sour, 14% sweet, and 2% bitter. While the current was on, the percentages were 10% salty, 75% sour, 15% sweet, and 5% bitter. If the former percentages are viewed as control values, then the absence of change in the percentages of sweet and bitter responses indicates that these responses are not related to the presence of the current. If such is the case, then the sweet and

bitter responses found by previous investigators may also be spurious and unrelated to the process of electrical stimulation.

Although frequency was not varied in the present experiment, other investigations of electrical stimulation in single taste papillae have also revealed low percentages of sweet and bitter responses, whereas those for sour and salty responses have been high. In addition not one of these investigations (von Bekesy, 1964a; Plattig, 1972; Dzendolet and Murphy, 1974; Plattig and Innitzer, 1976) employed a control procedure to insure that subject responses were the result of current being applied to the papilla. The need for such procedures is obvious from the present data, in order to establish if electrical stimulation does, in fact, elicit true sweet and bitter responses.

The comparison of the qualities elicited by chemical and electrical stimulation of the same papilla (Table XX) raises the question of whether these two types of stimulation are acting on the same neural elements. Although it is true that every quality elicited electrically in a papilla was also elicited chemically, there appears to be no obvious relationship between the quality elicited by electrical stimulation and the maximum quality responsiveness elicited by chemical stimulation. This, combined with the fact that control procedures indicated that only sour and salty responses were elicited by electrical stimulation, indicates that the current in this experiment may have been acting directly on the neuronal axons, rather than on receptor cells. Bujas and Pfaffmann (1971) have made a similar analysis of the effect of electrical stimulation by noting that potassium gymnate did not block the sweet responses resulting from

electrical stimulation, but did block the sweet responses elicited by chemical stimulation.

Introspective reports

Subjects in this experiment reported a general difficulty in assigning taste names to the sensations they experienced. However, if required to do so, as was implied by the simple fact that they were in a "taste experiment" then they would do so, and do so consistently for a given papilla. As examples of some of the comments, subject SC reported that "the tingle of some of these (electrical stimulations) was like the tingle of salt at high concentrations." Similarly, she reported that she could "relate the sensations (of electrical stimulation) to the sensations of chemicals, but the taste was not the same." Subject DP reported that he could "tell the difference between this (electrical) sour and the chemical sour." Perhaps, subject EG summarized it best when he said, "it's like you showing me the color green, and I say it's peppermint flavored."

The failure to find dependable quality reports in response to electrical stimulation in this experiment may reflect either a skepticism of the procedure on the part of the subjects, or a simple failure to achieve a suitable set of parameters for stimulation. In either case, the conclusion to be reached is that, at least for these subjects and this experiment, the sensations and taste qualities elicited by electrical stimulation of a papilla did not coincide with those elicited by chemical stimulation. This failure may be due to the procedure or to a true lack

of correlation between the two modes of stimulation.

General Discussion

As stated at the outset, the conflicting data on the specificity of single human taste papillae has, up to now, defied resolution. The major factors contributing to this situation have been the differences in the experimental procedures and the solution concentrations used by previous investigators. The experiments described herein have attempted to resolve these discrepancies by using the best possible combination of experimental procedures, and a range of concentrations which encompasses the entire range of concentrations used in previous studies. The fruitfulness of this approach is reflected in the number of questions to which this research has been able to address itself.

The major question that this research has resolved is the direct one, concerning the specificity of fungiform papillae in man. The unequivocal conclusion from these experiments is that single human fungiform papillae can mediate more than one primary taste quality. Furthermore, since those papillae that mediate less than the total number of possible taste qualities are few in number, and have generally higher thresholds, the results of von Bekesy must be attributed to his having stimulated multi-sensitive papillae with solutions that were too weak to reach threshold for all but a single compound. The possibility that his results were due to his having stimulated the "sides" of these papillae has been eliminated by the fact that stimulation of the sides of papillae in Experiment IV of this research elicited more than a single

taste quality, even though the overall effectiveness of the stimulation was less.

The failure to find sizeable correlations between the thresholds for compounds which have the same taste quality poses an interesting problem, which can only be resolved when more is known about membrane biophysics and the action of chemical structures on these membranes. Undoubtedly, this step will be the key to resolving the problem of gustatory quality coding at the receptor level.

Since stimulation of a single papilla involves only an extremely small fraction of the total number of receptors in the human taste system, it is not unexpected that the thresholds for single papillae would be much higher than corresponding whole mouth thresholds. The data of this experiment are consistent with the predictions made by Smith (1971) for such areal summation, however, the lower exponents of the single-papilla functions suggest that differences in the number of responding receptors can effect subjective taste intensity functions. Such a possibility raises serious questions about exponent invariance and the physiological basis of the power law.

The demonstration of a "water taste" phenomenon at the single-papilla level is consistent with the explanation of such water tastes as described by Bartoshuk (1964, 1974). However, the appearance of these water tastes in only the two male subjects of this experiment suggests a possible sex difference. Future studies of "water taste" should be directed toward the question of individual differences, since the mechanism behind such differences must necessarily be integral to

the overall mechanism of "water taste."

The data on quality changes in inorganic salts at the single-papilla level is again important, as an extension of our knowledge of the range of conditions under which this phenomenon occurs. Furthermore, concerning the mechanism for such quality changes, these data provide support for Dzendolet's (1969) theory of physico-chemical changes occurring in the salt solutions themselves. However, the basic finding of these experiments, namely, that related to the multiple sensitivity of single papillae, requires that a modification of Dzendolet's inhibitory mechanism be made. Once made, however, this theory adequately accounts for the quality changes found with both single-papilla and whole-mouth stimulation.

The ubiquity of the "sour-salty" confusion throughout this research indicates that this is a very robust phenomenon. The fact that it only occurs in response to small-area dorsal tongue stimulation indicates that there probably is a physiological basis to this confusion, although a psychological confusion cannot be ruled out. The increased use of dorsal flow techniques of stimulation in the past decade warrants a systematic study of the cause of this confusion, in order to eliminate possible misinterpretations of quality data obtained with these techniques.

The failure to find a correspondence between the qualities mediated by chemical and electrical stimulation in the same papilla raises questions as to the locus of effect for electrical stimulation. Clearly, before any final conclusions can be made about the effectiveness of electrical stimulation, proper controls must be instituted to insure that the

qualities elicited are truly the result of the electrical stimulus and not the result of simple tactile stimulation or verbal associations of gustatory labels to non-gustatory sensations.

As a final comment, this research forces the search for specificity in neural coding to the level of the single taste bud or single receptor cell. Based on considerations already presented, it appears that the human taste bud is not likely to be the location of such specificity. Thus, the focus of future research for answering questions of quality coding in man should be turned toward the single receptor cell. An effective combination of psychophysical and electrophysiological techniques at this level may resolve, once and for all, the debate over specificity in the human gustatory system.

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Appendix A

Considerable time was spent on pilot research to determine the best method of stimulus presentation to be used in these experiments. Five different stimulating apparatus were tested. The criteria adopted for selection of the best stimulator were (1) the ease and accuracy of positioning a solution droplet on a single papilla, (2) minimum tactile stimulation of the papilla during presentation of the droplet, and (3) accurate control of droplet volume.

The first stimulator which was tested was a small circular loop (0.5 mm inner diameter) constructed from fine platinum wire (0.127 mm diameter) and attached to the end of an innoculating loop holder. This type of stimulator is similar to that employed by Bealer and Smith (1975) and also to one used in pilot research by von Bekesy (1966).

While this type of stimulator was the simplest to use of those tested, and provided constant droplet volume from one trial to the next, two major problems were encountered in its use. First, the chosen diameter (0.5mm) was too large to enable accurate placement of the solution droplet on any but the largest papillae; and second, the nature of the stimulator required that the loop be touched to the surface of the papilla in order to deposit the droplet. Although the former problem was eliminated by using smaller diameter loops, Ss consistently reported a strong tactile component upon placement of the droplet, even when special care was taken while positioning the droplet. The Ss' awareness of the tactile component was judged as sufficient reason to eliminate the use of this type of stimulator in the experiments.

The second type of stimulator to be tested consisted of a 1 cc disposable plastic tuberculin syringe (Becton, Dickinson and Company; Rutherford, New Jersey) in conjunction with a 33 gauge (0.004" inner diameter) stainless steel blunt hypodermic needle (Vita Needle Company, Needham, Massachusetts).

This type of stimulator provided excellent positioning of the droplet on a papilla and eliminated any tactile interference, since the solution droplet could be formed at the tip of the needle and then touched to the papilla without any contact between needle and papilla. Droplet volume was controlled by visual inspection under 30 x magnification. While this method of controlling volume was found to be reliable following sufficient practice, it was felt that a less time consuming method of controlling volume might be obtainable by mechanical means. This attempt to obtain greater ease of control over droplet volume led to testing of three other types of stimulators.

The first such stimulator consisted of a variable speed infusion-pump (Model No. 795 Harvard Apparatus, Millis, Massachusetts) in series with an electronic timer (Model No. 1116 Hunter Apparatus, Iowa City, Iowa). With 1 cc glass tuberculin syringes positioned in the pump, droplet volume could be controlled by the duration that the pump-drive was activated. Using 30 gauge (0.006" inner diameter) stainless steel tubing and needles, in conjunction with PE-10 (0.011" inner diameter) polyethelene tubing, a solution droplet could be formed at the tip of the polyethelene tubing. By threading this tubing through a 1 cc plastic syringe barrel (plunger removed) and the shaft of a 20-gauge stainless

steel needle attached to the syringe, a handy holder for placement of the droplet was made. This type of delivery system is similar to that previously used by McCutcheon and Saunders (1972).

Although this type of delivery system also provided accurate placement of the droplet on a papilla and a minimum of tactile interference, the variability in droplet volume was found to be no less than that obtained by visual inspection of manually controlled volume. In addition, the complexity of preparing a large number of syringes and tubing, as well as the task of cleaning the delivery system after each session, outweighed any savings in time afforded by the mechanical control of the droplet volume.

In order to avoid the complexity of the infusion pump stimulator, but to still attempt greater ease of control over droplet size, an ultra-prevision micrometer syringe (Model No. 53100, Gilmont Instruments, Great Neck, New York) was tested. By manually turning the micrometer screw through a preset angle, a constant volume droplet could be formed at the needle tip.

Repeated testing using this apparatus showed no greater reliability in droplet volume than that provided by visual inspection of manually controlled volume. In addition the bulk of the instrument decreased the ease and accuracy of placing the droplet on a papilla and offset any time advantage gained by mechanical control of the volume.

Insofar as neither the infusion-pump apparatus nor the micrometer syringe provided any better control over droplet volume than simple visual inspection under a microscope, it was hypothesized that the

variability in droplet volume for each of these stimulating systems was limited by the fact that the solution droplet was in continuous fluid-contact with the solution reservoir. Thus, touching the droplet to a surface caused a variable and undetermined amount of fluid to be drawn from the needle shaft, as a result of cohesive forces in the fluid.

In order to eliminate the possible source of variability in droplet volume hypothesized above, two automatic micropipettes (Finnpipette, Code No. 10, Markson Scientific Apparatus, Del Mar, California; and Oxford, Model No. 21-199, Fisher Scientific Apparatus, Medford, Massachusetts) were tested. Since a micropipette is loaded with only as much fluid as is to be dispensed, there is no possibility of excess or variable amounts of fluid being released through contact with a fluid reservoir. However, as was readily determined by testing, most commercially available micropipettes do not provide very precise control of volume for droplets on the order of .05 μl, as is the case in these experiments. In addition, the bulk of these instruments requires the use of both the hands to operate them, thereby preventing focusing of the tongue during presentation of the droplet.

In considering the three criteria established for adoption of an adequate stimulator and the performance of the five stimulators tested, it was concluded that the manually-operated syringe stimulator was the best stimulator for use in these experiments. Such a stimulator is extremely simple to operate. Its small size and pencil-like shape enable quick and accurate placement of the droplet on a single papilla, and the 33-gauge needle tip is small enough to allow stimulation of

papillae as small as 0.01" in diameter. As numerous test solutions were employed during any one session in these experiments, the low cost of the stimulator allowed for a separate stimulator to be used for each. solution. In addition, the ease of cleaning and rinsing the stimulators after each session was an added practical advantage.

As the plunger of the syringe stimulator is operated manually, a period of practice is needed in order to be able to deliver constant volume droplets repeatedly. Such expertise is best acquired by visual inspection of the needle tip under 30 x magnification (the same magnification used during experimental placement). Holding the barrel of the syringe as one would hold a pencil, and with the forefinger placed on the top of the plunger, very slight pressure of the forefinger on the plunger will produce a bulge of the fluid from the tip of the needle. Slightly greater pressure will cause a fine droplet to be formed at the tip, and still further pressure will increase the size and volume of the droplet to any desired magnitude. By relieving pressure on the plunger the volume of the droplet can be correspondingly decreased. That such a manual method enables as high reliability in the production of constant volume droplets as do any of the mechanical methods, is an indication to the extremely fine control and flexibility of the human hand when compared to expensive and sophisticated mechanical apparatus.

Appendix B

Instructions for Experiments II and IV

Your task in this experiment is to judge the taste and intensity of minute droplets of solution placed on your tongue.

At the start of the experiment position your head in the chin-restraint in front of you. Using the turn-bolt on the front of the restraint, adjust the height of the restraint to a level that is comfortable for you. Then adjust your seat, so that your entire body is as comfortable as possible, and rest your hands on the table in front of you.

When you are positioned comfortably, the experimenter will tell you to extend your tongue and rest it on your lower lip. Throughout the entire experiment it will be very important for you to keep your tongue as motionless as possible. In order to best achieve this, be sure that your tongue rests comfortably on your lower lip and keep your eyes closed until it is time for you to make a response.

After a predetermined time period has elapsed, the experimenter will place a droplet of solution on your tongue. As soon as the droplet has been presented, he will tell you that you may give your judgment of its taste. Do not retract your tongue until after you have made your judgment, and be sure to give your judgment as quickly as possible after the experimenter indicates that you should do so. In addition, since some of the taste sensations may be very weak, be sure to pay careful attention after each droplet is presented.

To make your judgment of the taste of the solution, use the labels printed on the sides of the cube in front of you. If the taste of the solution is either "salty," "sweet," "sour," or "bitter," place one of the so-labelled sides of the cube face-up on the table. If you taste something, but it is so weak that you cannot discriminate it as being one of the above tastes, then place the side labelled "indistinct or vague taste" face-up. If you taste nothing at all, then place the side labelled "no taste" face-up on the table. Lastly, if the solution has a strong taste, but you think that some label other than those available to you is more appropriate, then write "complicated taste" on the pad of paper provided you and follow it with a one- or two-word description of the taste. When you have finished writing your description, place the labelled side of the cube which is closest to the "complicated taste" face-up on the table.

Note: When the droplet is initially placed on your tongue you may feel a slight "touch" or a "metallic sensation" caused by the metal tip of the solution dispenser. Ignore these sensations, as they are not true taste sensations.

After describing the taste of the solution, you must also judge its intensity. Do this by assigning a number to it and writing this number on the pad of paper in front of you. You may assign any number you wish to this first solution; however, once you assign a number to it, be sure to make all your subsequent intensity judgments proportional to this first one. For example, if you happen to assign the number "100" to the intensity of the first solution, and on the next trial you are presented

a solution that tastes twice as intense, then you should call the intensity of the second solution "200." Likewise, if the second solution tastes one-half as intense as the first, then you should call it "50," and so forth. You may use whole numbers, decimals, fractions, or anything else you may wish in making your judgments.

After you have made your judgment, but with your tongue still extended, position your tongue over the sink and rinse it with a flow of water from the plastic squeeze bottle at your left. Spit any excess water into the sink after you have finished rinsing. You may then retract your tongue, reposition your head in the restraint and wait for the next trial to begin.

Appendix C

Frequencies of responses given to electrical stimulation of single papillae by individual Ss

Subject	Sensation	Current Off		Current On	
SC (34v, 110 Hz)	Gustatory	Salty,tingly	1	Sour	1
		Sweet	1	Salty	7
				Salty, sharp	5
				Salty, vibration	1
				Salty, strong	1
				Sweet	5
				Sweet, cool	1
				Sweet, strong	1
				Sweet, tingly	1
				Sweet, buzz	1
				Sweet, metallic	1
	Tactile	Tingly	9	Vibration	5
		Buzz	8	Buzz	3
		Vibration	6	Vibration, strong	2
		Metallic	3	Buzz, strong	2
				Tingly, strong	1
				Burning	1
	Thermal	Cool	9	Cold, buzz	1
				Cool, tingly	1
	No Sensation	--	13	--	8
MS (22v, 110 Hz)	Gustatory	Salty	1	Sour	2
		Sweet	1	Salty	29
				Sweet	3
				Sweet-salty	1

Appendix C - Continued

Subject	Sensation	Current Off		Current On	
MS (continued)	Tactile	Brassy	26	Brassy	3
				Vibration	3
				Indistinct, vague	2
	Thermal	Cold	16	Cold	4
	No Sensation	--	6	--	3
DP (26v, 110 Hz)	Gustatory	Sour	10	Sour	5
		Sour, buzz	4	Sour, buzz	5
		Sweet	1	Bitter, buzz	2
		Bitter	1		
	Tactile	Buzz	15	Buzz	18
		Shock	3	Shock	5
	Thermal	--		--	
	No Sensation	--	16	--	8
EG (55v, 110 Hz)	Gustatory	Sour, metallic	1	Sour	11
				Sour-salty	1
				Salty	4
				Salty, vibration	1
				Bitter, peculiar	1
	Tactile	Metallic	49	Metallic	13
				Metallic, strong	12
				Vibration	7
	Thermal	--		--	
	No Sensation	--	0	--	0