

Taste Mechanisms in Preference Behavior

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I SHOULD like to preface my remarks with some general considerations on the chemical senses. Sensory psychologists and physiologists classically refer to these as "lower senses." Compared to the "higher senses" of vision and hearing, they are relatively primitive and yield much less detailed information concerning the stimuli that activate them. None the less, much of the research on the chemical senses has been moulded after the pattern of studies of vision and hearing. Witness the attempts of von Skramlik and others to derive taste-mixture equations in a manner analogous to those for color mixture.¹ The concern with such classic problems of sense function has resulted in a neglect of the other features that give the lower senses their special significance and importance for adjustive behavior. They merit study in their own right with particular regard to their role in preference and aversion behavior.

Such behavior appears to be relatively "stimulus bound." Thus the direct relevance of sensory stimulation for behavior is more obvious than in the case of the higher senses. This is not to say that the behavioral consequences of taste or olfactory stimulation are fixed and unchanging. The interaction of physiologic processes, environmental factors and learning can all be demonstrated. The classic work of Dr. Richter, our chairman, is a well known example. Other participants in this session will undoubtedly provide other examples.

The chemical senses and the behavior they control present a kind of model "stimulus-

response" system of behavior, sometimes designated as "motivated behavior." Since all behavior is motivated, this designation implies that the motivational aspects here are more directly amenable to manipulation and direct observation. Thus, the study of the lower senses and the behavior they instigate is of significance for understanding behavior processes in general.

For want of time and because our laboratory has concentrated on the study of taste mechanisms, I shall restrict my discussion to that sense.† Our basic method, which has been described elsewhere,² is to record the afferent nerve impulses in the chorda tympani nerve of anesthetized animals. Rats, cats, rabbits and hamsters have been employed. Significant species differences have been found which appear to bear some relation to behavioral differences in the preference situation^{2,3,4} However, for today's purposes we shall concentrate on the data from the rat and hamster.

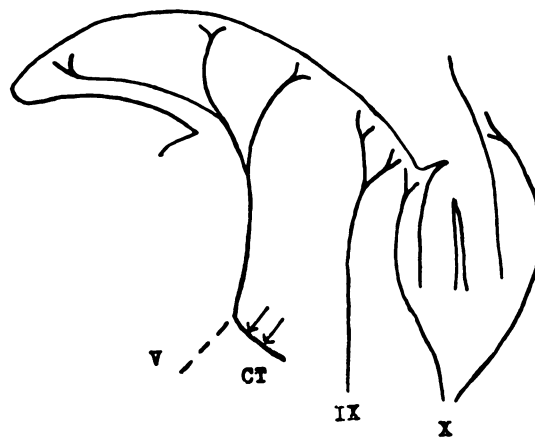


Fig. 1. Diagram of peripheral nerve supply to the tongue. V, trigeminal nerve; IX, glossopharyngeal n.; X, vagus n.; C. T., chorda tympani n. Arrows show the placement of recording electrodes.

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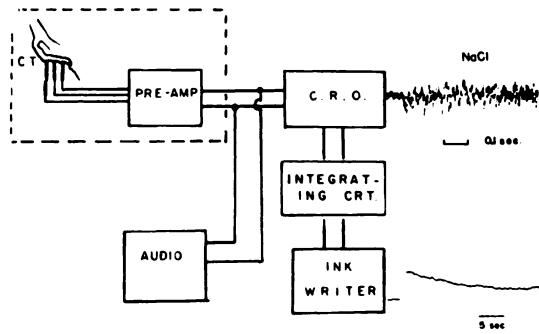


Fig. 2. Diagram of recording method. The two tracings on the right are sample records. C. R. O., cathode ray oscillograph.

METHODS

Figure 1 reviews the anatomic relations of the chorda tympani to the total nerve supply to the tongue. Most of the taste fibers leave the lingual nerve to pass centrally via the chorda tympani. The concentration of taste fibers here makes it especially suitable for electrophysiologic study. The method is illustrated in Figure 2 which shows the various features of the recording circuit. The usual amplifier oscillograph unit is supplemented by a summing or integrating circuit adjusted to give a running average of the impulse traffic up the nerve. The deflection of the summator recorder is proportional to both the frequency of discharge and number of fibers active. When the discharge drops to zero, the deflection of the summator likewise falls to zero. This circuit yields a quantitative measure of the typically asynchronous multifiber discharge.

When the activity in the chorda tympani nerve is so recorded, the application of quinine, hydrochloric acid, sodium chloride or sucrose solutions leads to a nerve response which first appears at some threshold concentration. The magnitude of the nerve response then increases approximately as a sigmoid function of the logarithm of the stimulus concentration. The response thus tends to level off or saturate at some high concentration value. The responses for the four typical taste stimuli enumerated above arrange themselves in the rat in the following order of thresholds from low to high: quinine, hydrochloric acid and sodium chloride

at the same concentration, and sucrose, (lower graph of Figure 3). Note, however, that the magnitude of response in terms of voltage differs from substance to substance. Whereas NaCl and HCl yield substantial voltages and hence maximal deflections of the recorder, quinine and sucrose yield relatively small responses. This is one respect in which the species show significant differences. In the hamster, for example, sucrose, NaCl and HCl all yield large and approximately equal responses which, however, lie in different regions of the concentration scale. Only the quinine response is small. Differences of this sort among the species presumably reflect a difference in the number of nerve fibers mediating

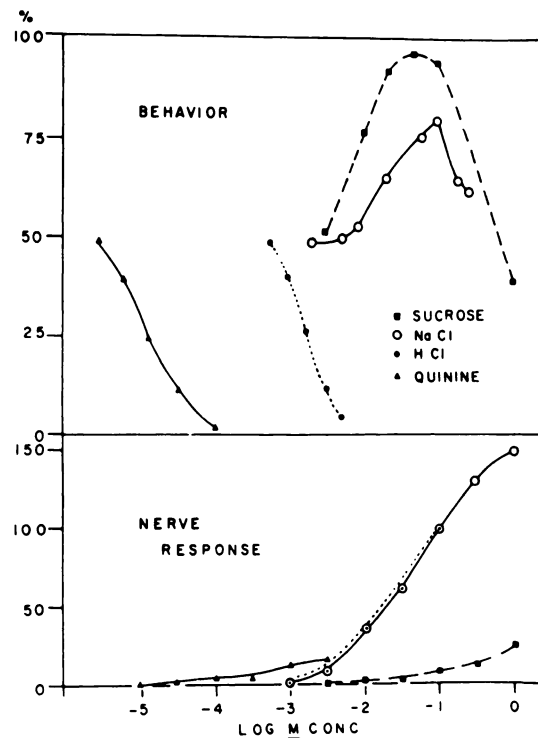


Fig. 3. Composite graph of behavioral and afferent neural responses. Upper figure shows preference-aversion responses. Lower figure shows neural responses (see text).

sensitivity to the different stimuli. A graph such as this summarizes the taste sensitivity in the average animal. The responses from animal to animal are remarkably constant.

THE PREFERENCE SITUATION

The upper part of Figure 3 represents responses by the intact normally behaving animal toward these same taste stimuli when presented in the typical two-bottle preference situation. This provides the animal with a choice of two calibrated containers, one of which contains water, the other taste solution. In the case of preferred substances, the animal will drink mostly from the container with that substance. If the solution is avoided he will drink mostly from the water container. When different concentrations of the same solution are presented in an ascending order, it is possible to determine a preference or aversion threshold value. Aversion threshold may be defined as that concentration where the animal first begins to take more water and less solution. The response to solutions above this value (suprathreshold solutions) bears a systematic relation to concentration. This is conveniently measured by the volumes of water and taste solution ingested during a 24-hour *ad libitum* period. A percentage preference (or aversion) may be computed by dividing the volume of taste solution ingested by the total fluid ingested (i.e., water plus taste solution). Where the animal takes equal amounts of water and solution, the percentage equals 50 per cent. Values below 50 per cent indicate aversion, those above a preference. The upper part of Figure 3 shows that two substances, quinine and hydrochloride acid, are avoided and that the percentage aversion increases systematically with increase in concentration up to a complete avoidance. Two substances, sodium chloride and sucrose, are preferred. They both show the typical preference aversion function in which the intake or preference first rises to a maximum value and then falls off. With higher concentrations, these response curves will fall below the 50 per cent point when the stronger concentrations are avoided.

These curves show that the concentration ranges of the four stimuli correspond roughly on both the physiologic and behavioral response scales. The behavioral values shown are averages. The quinine hydrochloride values on 113 animals were compiled by Dr. R. M.

Benjamin in our laboratory.⁵ There is evidence of a definite behavioral response to concentrations at least one log unit below the point where the neural response is just detectable. The neural response threshold, of course, is limited by the "noise" level of the preparation, especially where the response magnitude is small. In addition, it must be remembered that our neural records sample only activity in the chorda tympani nerve. Until the contribution of the IXth nerve has been examined, our information on the total sensory input from the taste field will be incomplete. This qualification, of course, applies to all attempted correlations between behavior and chorda tympani records.

The response to HCl, obtained in a smaller group of 27 animals, is shown in the dotted curve. Here the neural response is substantial, beginning at around -3 (log M conc.). In both quinine and acid, the suprathreshold neural activity is related to strong and almost complete avoidance.

Sodium chloride is of interest because there is a clear and definite neural discharge very similar to that for acid. The behavior here indicates a preference rather than aversion. The afferent message, therefore, must contain information beyond mere *magnitude* of discharge which permits differential response. We have studied this problem by means of recordings from the single elements in the chorda tympani. These results have been reported elsewhere² and are not germane to the present discussion. Note here that the electrophysiologic response appears and reaches a significant value before the preference becomes evident. This is contrary to the relation seen for the two aversive stimuli. Furthermore, we note a systematic rise to a maximum with a falling off in the range where the neural response is steadily rising.

Consider now the response to sugar. Here the neural response is small and the behavioral effect is a strong preference with the typical rising, maximal and falling phases. There is approximate agreement in the concentration range where the two effects occur. It should be noted that all data presented here reflect the behavior and physiologic response of nor-

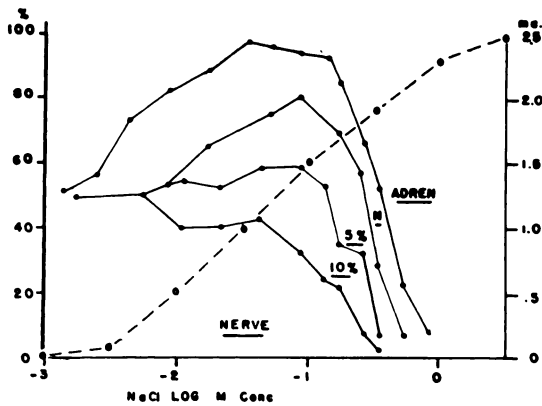


Fig. 4. Composite graph of neural response (broken line) and preference-aversion curves (solid lines) to sodium chloride solutions. Preference ordinate to the left, neural response ordinate to the right.

mal Wistar descendant rats maintained on an *ad libitum* diet.

That these relations are not fortuitous is indicated by the effect of denervating the tongue. Although the interference with taste sensitivity is not as great as originally believed⁶ there is clear evidence of impairment in preference behavior following bilateral chorda tympani and IXth nerve removal.⁷ Taste stimulation thus appears to be an initial sensory instigator of such behavior. Post-ingestion effects may modulate the behavior further.^{8,9}

SODIUM CHLORIDE

Figure 4 shows an expanded scale for the NaCl response only. The neural response to NaCl (open circles, broken line) is similar to that shown in Figure 3. Four sets of data from preference studies carried out at various times in our laboratory are shown by the solid lines and dots. Each point is an average value. Curve N (normal) shows the full extent of the preference-aversion function with a peak preference at about 0.1 M (log -1). The 5 per cent and 10 per cent curves show the preference-aversion functions for two groups, one in which the diet was supplemented and mixed with additional NaCl to make a total salt content of 5 per cent. The lower curve shows the same data for the animal fed on a diet containing 10 per cent NaCl. Note the systematic shift in the

preference curve as a function of the added salt. These figures do not show changes in the absolute volumes of fluid ingested, for under these conditions the fluid intake is much increased. The point here is that the relative intake of salt and water are shifted systematically from the normal, especially if we pay attention to the suprathreshold portions of the curve.

The top curve is the preference response shown by a group of adrenalectomized animals. Note that the entire preference-aversion function of the normal animal is enhanced. The salt-needy animal not only takes relatively more of the stronger solutions, he does so at all concentrations so that his preferential response becomes apparent at a lower concentration level. This observation, of course, is merely a repetition in our laboratory of Richter's classic experiments on salt need and self selection. The additional point here, however, is that the behavior toward the stimulus might be described as an exaggeration of that seen in the normal non-deprived animal.¹⁰⁻¹³

Young¹⁴ speaks of two factors underlying the intake of NaCl solutions, (a) the properties of the stimulus (e.g. concentration of the solution) and (b) intra-organic factors (e.g. need produced by deprivation, etc.). We might say that the behavior is "stimulus bound" but modulated by variations in physiologic state.

THE NEURAL RESPONSE CURVE

So far I have said little about the neural response curve. The graph reproduces the points obtained from a number of normal animals. It was not obtained under any of the experimental conditions outlined. The only exception to this is for the threshold point which Dr. Bare and I reported on a number of years ago.¹⁵ We found that the electrophysiologic thresholds for adrenalectomized and normal animals were essentially the same. We could find no evidence of an enhancement of sensitivity of the receptor as a result of adrenal insufficiency, which leads to such dramatic increases in the intake of salt solution. We have not determined the suprathreshold neural response under adrenalectomy. However, the confirmation of our finding of no difference in

sensitivity between normal and adrenalectomized animals by several workers utilizing the conditioned reflex method^{16,17} appears to establish the fact that the receptor sensitivity curve is a relatively stable function. It is our belief that the function outlined by the broken line defines the basic operating limits of the taste receptor mechanism for the rat. Further, this appears to be a stable property of the receptor and is not influenced by changes in physiologic state of the internal environment bathing the taste cells.

From the form of the behavioral and neural response curves it appears that the normal animal can taste the salt solution, but is not motivated to ingest it. This is the only case where the neural response appears at a point lower on the concentration scale than does the preference effect. Both our data and that of Richter show the preference response to begin at a concentration value of around -2 on our scale. The preference behavior in the adrenalectomized animal is variously reported to appear from -2.5 to -3.2 , which is in the range where the neural response first becomes obvious. Although Young and Chaplin¹⁸ found no enhancement of preference behavior in adrenalectomy, Young¹⁴ reported preference thresholds and/or evidence for discrimination of NaCl solutions by normal animals in the range -3 to -2.5 . Only the data obtained by Harriman and MacLeod¹⁷ by a conditioned shock avoidance method show discrimination of salt solutions at values far below these concentrations. They report values as low as -5 on our scale. This is lower than that obtained by Carr¹⁶ using a similar method. Harriman and MacLeod took special precautions to lower the concentrations by small steps and to subject the animal to prolonged training. Discrepancies of nearly this magnitude between neural and behavior responses were noted above in our data in the case of quinine where the nerve responses were especially limited by the signal to noise ratio. The NaCl thresholds of single nerve fiber preparations which do not suffer from this limitation were found to lie at or above the

* This value is lower by approximately $1/4$ of a log step than that first reported by Pfaffmann and Bare.¹⁹

-3 level.* Fibers sensitive to lower concentrations must be very few in number. Further work in the threshold range by both behavioral and physiologic methods seems warranted.

SUGAR

We have one further recent observation to report, this time utilizing the sensitivity to sucrose.¹⁹ As is well known, again from the work of Dr. Richter and others, the preference for sugar solutions can be markedly increased by a number of procedures, hunger and injection of insulin being two well known examples. It has been reported that human sensory thresholds were altered during hypoglycemia.²⁰ There is evidence that the taste receptors for sugar might be stimulated by a different kind of chemical mechanism than are the salt receptors. Thus, it seemed desirable to test the generality of our conclusion that the taste sensitivity at the periphery is unchanged by changes in the constituents of blood stream (short of excessive changes which might produce a generalized impairment).

As noted above, the hamster is one species in which there is a strong and readily observed response to sugar. Mr. Hagstrom and I examined the response in the chorda tympani of the hamster after the blood sugar was severely lowered by the injection of insulin. As a preliminary test to insure that differential suppression of the sugar receptors could occur, we determined the effect of the local action of Gymnemic acid, a drug which differentially suppresses sweet sensitivity in man, yet leaves salt sensitivity unimpaired. A 10-minute application of Gymnemic acid to the tongue surface reduced the response to sugar but had no effect on that to salt. We then recorded for a much longer period before and after the intraperitoneal administration of insulin. Blood sugar determinations were carried out after the administration of insulin, to insure its effectiveness. Five units of insulin were injected intraperitoneally. Prior to administration blood sugar values ranged from 40 to 70 mg/per 100 ml. After administration the values ranged from 7 to 23 mg/per 100 ml. No evidence was found of a differential enhancement or suppression of sensitivity to

sugar compared with that to NaCl. Lowering the blood sugar did not appear to affect sensitivity of the peripheral gustatory receptors.

SUMMARY

We have presented certain electrophysiologic observations on taste sensitivity and the correlation with behavioral responses to the same stimuli. An approximate agreement between the concentration ranges for the two responses was noted for the mean response curves, especially for suprathreshold effects.

Receptor function was studied under conditions that modify the physiologic state of the organism and with which pronounced changes in preference behavior have been reported. Under these circumstances no change in the gustatory response was noted. It is concluded that changes in behavior under these conditions reflect not a change in the peripheral afferent neural message but changes in its significance for central neural processes.

REFERENCES

1. VON SKRAMLIK.: *Handbuch der Physiologie der niederen Sinne*. Bd. 1, Thieme; Leipzig, 1925, pp. 454-462.
2. PFAFFMANN, C.: Gustatory nerve impulses in rat, cat, and rabbit. *J. Neurophysiol.* 18: 429, 1955.
3. BEIDLER, L. M., FISHMAN, I. Y., and HARDIMAN, C. W.: Species differences in taste responses. *Am. J. Physiol.* 181: 235, 1955.
4. CARPENTER, J. A.: Species differences in taste preferences. *J. Comp. & Physiol. Psychol.* 49: 139, 1956.
5. BENJAMIN, R. M.: *Cerebral mechanisms in gustatory discrimination*. Ph.D. Thesis, Brown University 1951.
6. RICHTER, C. P.: Transmission of taste sensation in animals. *Tr. Am. Neurol. A.* 65: 49, 1939.
7. PFAFFMANN, C.: Taste preference and aversion following lingual denervation. *J. Comp. & Physiol. Psychol.* 45: 393, 1952.
8. STELLAR, E., HYMAN, R., and SAMET, S.: Gastric factors controlling water and salt solution drinking. *J. Comp. & Physiol. Psychol.* 47: 47, 1954.
9. LE MAGNEN, J.: Immediate regulation of spontaneous intake of water and salt in the white rat in imposed states of hydromineral imbalance. *Compt. rend. Soc. Biol.* 147.1: 619, 1953.
10. BARE, J. K.: The specific hunger for sodium chloride in normal and adrenalectomized white rats. *J. Comp. & Physiol. Psychol.*, 42: 242, 1949.
11. RICHTER, C. P.: Increased salt appetite in adrenalectomized rats. *Am. J. Physiol.* 115: 155, 1936.
12. RICHTER, C. P.: Salt taste thresholds of normal and adrenalectomized rats. *Endocrinology* 24: 367, 1939.
13. RICHTER, C. P.: Self-regulatory functions. *Harvey Lecture* 38: 63, 1942.
14. YOUNG, P. T.: Palatability versus appetite as determinants of the critical concentrations of sucrose and sodium chloride. *Comp. Psychol. Monog.* 19: 1, 1949.
15. PFAFFMANN, C., and BARE, J. K.: Gustatory nerve discharges in normal and adrenalectomized rats. *J. Comp. & Physiol. Psychol.* 43: 320, 1950.
16. CARR, W. J.: The effect of adrenalectomy upon the NaCl taste threshold in rat. *J. Comp. & Physiol. Psychol.* 45: 377, 1952.
17. HARRIMAN, A. E., and MACLEOD, R. B.: Discriminative thresholds of salt for normal and adrenalectomized rats. *Am. J. Psychol.* 66: 465, 1953.
18. YOUNG, P. T., and CHAPLIN, J. P.: Preferences of adrenalectomized rats for salt solutions of different concentrations. *Comp. Psychol. Monog.* 19: 44, 1949.
19. PFAFFMANN, C., and HAGSTROM, E. C.: Factors influencing taste sensitivity to sugar. *Am. J. Physiol.*, 183: 651, 1955.
20. MAYER-GROSS, W., and WALKER, J. W.: Taste and taste selection of food in hypoglycemia. *Brit. J. Exp. Path.* 27: 297, 1946.

