

TASTE PREFERENCES IN THE HISPID COTTON
RAT FOR FIVE SUGARS, THREE SALTS
AND TWO ACIDS

BY

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CHAPTER I

INTRODUCTION

Beach (1960) proposes two desiderata for building a truly comparative science of behavior. First, the behavior studied should be "natural" or species-specific. Second, the kinds of behavior chosen for analysis should be as widely distributed as possible. Beach felt this would increase the opportunity for interspecific comparisons and improve the probability of arriving at valid and broad principles of a comparative science of behavior.

In response to Beach's first condition, it is noted in the behavioral sciences, that an overabundance of studies have focused on the habits of the laboratory rat. The excessive, and often exclusive, use of the domesticated Norway rat for laboratory research in physiology and behavior has been criticized by Richter (1954). More recently, Lockard (1968) questioned the use of this species in preference to other species of animal subjects. The notion that the albino rat provides an adequate model for comparison of species-typical behavior between levels of the phylogenetic scale is apparently based on opinion rather than fact. The albino rat has become a highly artificial breed. It has been long since removed from the influences of natural selection, and specific traits have been bred into the species all the way from docile behavior patterns to increased gastrointestinal capacity.

Taste preferences seem to be worthy of study, in regard to Beach's

second condition for a comparative science of behavior, Wenzel (1974) states that it seems likely that the earliest animal forms received messages from their environment by means of chemical stimuli alone. As a means of communication, it is undoubtedly as venerable as any, if not the most venerable of all. Consequently, every form of modern animal probably possesses some sort of chemoreceptor, but relatively few of these organs have ever been studied in detail.

The present paper deals with species-specific comparisons of taste preferences within the rodent family. In this respect, the study differs from the studies on taste which have reported findings from work with the laboratory rat. Specifically, the paper reports taste preference by the cotton rat (Sigmodon hispidus).

Hilgard (1948) feels that Homo sapiens is in some ways, a truly unique species. Hebb and Thompson (1954) say that man is the only animal capable of "syntactic" behavior. Although some primates and other life found may demonstrate a crude means of communication, it is important to note that in human behavior language serves as more than a means of communication. A great deal of human problem solving and thinking is done in terms of language symbols. Man is also able to anticipate possible or inevitable future events using language symbols.

Because of man's apparent uniqueness as a species Beach (1960) suggests that man be removed from his central point in the comparative science of behavior. This may prove to be the very best way of reaching a better understanding of his place in nature. In this manner, science could better arrive at characteristics that man shares with other animals as well as those which he possesses alone or which are in him developed to a unique degree.

In a study of taste preference behavior in laboratory and wild Norway rats, Shuemake, Thompson and Caudill (1971) found domestication does not lead to substantial changes in genetically determined taste preference behavior. Some minor quantitative differences, however, were noted. If man is to be removed from a central point in comparative psychology, other cross-species comparisons assume a greater importance than before. It seems that at some point in time, behavioral researchers will have to search for alternate, more vigorous and less studied species, than the laboratory rat, or comparative research may find itself in a retarded state with many isolated facts about a single artificial species.

It would appear to be quite valuable to engage in cross-species comparisons at the behavioral level, as illustrated by the research of Carpenter (1956), much in the same way that the biological sciences engage in cross-species comparisons at the electrophysiological level. It is only by this practice that the behavioral sciences may prevent the paradox of sterility to follow closely on the heels of prolonged study of a single species in the laboratory environment.

It would seem that one cannot engage in research in taste preferences without becoming at least secondarily concerned with the application of results to the area of chemicals as incentives or their function as motivating agents. Harlow (1953) stated that this was an area only superficially explored and which should be systematically attacked by rodentologists and primatologists alike. While the data gathered in the present study will be for the purpose of cross-species comparison primarily, application of the findings to the area of food incentives may prove of some heuristic value.

Historical Review

There seem to have emerged two basic approaches to the study of comparative taste preferences: Electrophysiological and behavioral. In electrophysiological studies on the sense of taste, the comparative approach has been recognized and used effectively for quite some time (Beidler, Fishman and Hardiman, 1955; Pfaffmann, 1953; 1955).

Pfaffmann (1953) studied the sense of taste in three species (the rat, rabbit and cat) by recording sensory nerve impulses from the tongue. In three species, hydrochloric acid and sodium chloride produced significantly more neural activity than did quinine HCl or sucrose. The response to hydrochloric acid in the three species was strikingly similar. Sucrose chloride was also much more effective than potassium chloride in eliciting response from the rat. The relation was reversed for rabbits.

Later research of an electrophysiological nature included the work of Beidler, Fishman and Hardiman (1955). Beidler recorded a large spontaneous discharge in the chorda tympani which is also present when the tongue is rinsed with distilled dilute sodium chloride solutions after an initial rapid stimulation. Frank (1973) determined sensitivities to moderately intense stimuli representing the four taste qualities of man for seventy-nine hamster chorda tympani fibers. Some fibers were very sensitive to sucrose, sodium chloride, or hydrochloric acid, but none were very sensitive to quinine. These sensitivities were not randomly distributed among fibers. Specifically, sucrose sensitivity was separated from, and negatively correlated with, the other sensitivities which were associated and positively correlated with each other.

In the behavioral studies on the sense of taste, the comparative approach has been utilized relatively infrequently. A majority of these studies have been concerned with determining drinking preferences of various species (e. g., Carpenter, 1956; Kare and Ficken, 1963).

Richter (1936) pioneered the study of drinking preferences in animals which has become a standardized method in establishment of taste discrimination. In Richter's procedure, various concentrations of a test solution are paired separately with distilled water and presented ad libitum to each animal for a period of 24 hours. A variety of behavioral measures have been used to assess taste in animals. The two-choice preference test (Richter, 1942), originally used with the rat, has been subsequently used with other animals.

A According to Carpenter (1956), Richter's was the first comparative investigation of taste preference at the behavioral level of analysis. The approach used the two-bottle Richter test to assess the taste preferences, of rabbits, hamsters, and cats for the compounds NaCl, KCl, sucrose, saccharin, and QHCl at various concentrations. Carpenter reported that KCl and QHCl produced similar responses in the three species. A compound was classified as "preferred", "avoided" or "not discriminated" on the basis of the compound/tap water consumption ratio. Carpenter found that hamsters preferred sucrose and sodium saccharin but avoided QHCl, HCl, and KCl. Rabbits preferred sucrose, sodium saccharin, and NaCl, but avoided QHCl. For rabbits, cats, and hamsters, the preference for NaCl was greatest from .10-.20 M concentration. For hamsters, the preference for KCl peaked at .2 M, but hamsters showed no NaCl preference.

Cagan and Maller (1974) assessed the differences in taste preferences in rats using a brief exposure single-stimulus testing procedure and a two-bottle choice, 24 hour testing procedure. The animals, (naive male Fischer rats), were trained to sample the test solution immediately upon presentation in the brief exposure single-stimulus test. Intake was measured periodically for 10 minutes using fructose, glucose, or sucrose as a stimulus and water as a control. Relative "sweetness" was predicted from the data to be sucrose, fructose, and glucose. The two-choice, 24 hour preference test.

Young and Green (1952) reported similar results when comparing brief exposure methods to 24 and 48 hour tests. It was speculated that in preferred compounds, in which the range of discrimination is close to the concentration of body fluids, there is probably a balance between taste discrimination and limiting postingestional factors. The intake of those compounds that range of discrimination concentrations is too low to affect fluid balance, depends primarily on the response to intensity of stimulation in the mouth. If post-ingestional factors can be experimentally ruled out, as in brief exposure tests, the optimal concentration for sugars is greater than that found in most prolonged ingestion tests.

According to Kare (1961) and Kare and Ficken (1963), each species lives in an "isolated taste world". There exists differences within the species and certain absolute differences among species. Kare and Ficken report that smaller magnitudes of differential preferences of individuals support the idea of differences of degree in taste preference behavior among individuals of the same species. Wenzel (1973) argues that, while certain innate factors do seem to exist, such

tendencies can be modified by factors such as rate of ingestion, amount ingested, nutritional status, and preceding stimuli.

Duncan (1962) supports the concept of absolute differences in taste preferences between species with data describing the responses of pigeons and rats to NaCl solutions. Both pigeons and rats showed a different overall pattern of response to NaCl. For pigeons, one maximum mean preference point was observed at .04 M, and another was found occurring at .08 M. Solutions of about .14 M or stronger were "rejected" when consumption was compared with that of water. Rats tested by the method of single stimuli showed a maximum preference of .14 M NaCl. Stimulative efficiency of the cations K^+ , Na^+ , NH_4^+ , and Ca^{++} were assessed for both pigeons and rats. Rats showed a pattern of stimulative efficiency which may be represented $NH_4^+ \searrow Ca^{++} \searrow K^+$, while pigeons presented a pattern of $Na^+ \searrow NH_4^+ \searrow K^+ \searrow Ca^{++}$. Harriman (1968) provided evidence for limitation of the generality of the assumption that taste sensibility differ sharply from one animal form to another. The order of acceptance for six cations as chlorides were determined in two-bottle tests with squirrel monkeys (samiri sciurcus), Mongolian gerbils (Meriones unguiculatus), Sprague-Dawley strain white rats, Starlings (Sturmus v. vulgaris), and Japanese quail (Coturnix coturnix japonica) was $Na^+ \searrow K^+ \searrow NH_4^+ \searrow Ca^{++} \searrow Mg^{++} \searrow Sr^{++}$.

Krecek (1972) offers support for the hypothesis of differences in degree in taste preference among individuals of the same species. In his study, free selection between water and 3 percent saline intake was investigated in the rat as a function of sex. Administration of 1 mg testosterone propionate to rats aged 2 days seems to suppress the pretest sex differences in saline intake. The same dose of this

hormone injected at 12 days, however, did not differentially affect the sexes in regard to saline intake. The females continued to ingest more saline solution than did males.

Richter (1942) reported that, although various studies using sugars as taste stimuli differ widely in the details of the experimental procedures, a common response pattern has been found. The volume of sugar solution consumed increases with increasing concentrations up to a maximum. Further increases in concentration lead to decreased intake, and sometimes more water than test solution is ingested.

Fisher, Pfaffmann and Brown (1965) have stated that the mechanisms regulating taste preferences may also be mechanisms regulating reinforcement in the conditioning situation. Preferences for dulcin and sodium saccharin in four male squirrel monkeys (Saimiri sciurus) were studied and compared to data obtained from five male albino rats. The Richter two-bottle preference test was used to assess the taste function of the animals. Squirrel monkeys demonstrated an aversion to sodium saccharin (set at 25 percent, or less of the total fluid intake). The aversion threshold for sodium saccharin was about .005 M. Dulcin, on the other hand, was preferred by these animals with a preference threshold (set at 75 percent or more of the total intake) at about .001 M. Rats showed a clear preference for sodium saccharin beginning at about .0003 M and only a suggestion of a dulcin preference at the concentration of .003 M.

In a more recent study Harriman (1970) investigated the drinking preference, as measured in 48-hour, Richter-type drinking test, by Mongolian gerbils (Meriones unguiculatus). Test solutions were prepared from four sugars (D-fructose, D-glucose, maltose and sucrose),

two acids (hydrochloric acid and citric acid), and three salts (potassium chloride, dried magnesium sulfate, and sodium chloride). Eleven female gerbils were assigned to each of nine groups. Each group was tested with a different solution at five concentrations in the range .005 M - 1.0 M (sugars and salts) or 2.3 pH - 1.5 pH (acids). Percentages of drinking preferences were maximal for fructose and sucrose at 0.5 M and for glucose and maltose at 1.0 M. Hydrochloric acid and citric acid were strongly rejected at all concentrations (rejection being greater for citric acid than for hydrochloride acid at equal pH). The salts were consumed at the same rate as water at concentrations below 0.1 M. At higher concentrations, rejection increased with increases in molarity.

Stockton and Whitney (1974) studied the drinking preferences of each of 5 genotypes of house mouse measured by the 48-hour Richter drinking test with 5 concentrations (.005, .05, .15, .50, 1.0 M) of glucose and sucrose. The solutions were presented in ascending order from lowest to highest molarity. Results indicated that significant differences in sugar preferences exist between individuals of a single species of mouse. The x strain in the study exhibited a pattern of taste response unique to the other genotype but similar to the preferences of Mongolian gerbils (Harriman, 1970) in preferring a .50 M concentration of sucrose. The results obtained by Stockton and Whitney seem to support the statement of Kare (1961) concerning the differences of degree in taste preferences within a species and, at the same time, oppose the notion of certain absolute differences among species (concerning sucrose taste preferences).

Bloom, Rogers and Maller (1973) investigated taste responses of

the North American porcupine (Erethizon dorsatum). The two-bottle choice method developed by Richter was used to assess taste responses to sodium chloride, hydrochloric acid, quinine sulfate, and sucrose at varied concentrations. Sucrose, glucose, fructose, xylose, and the noncarbohydrate sodium saccharin were examined. A peak response to sucrose was noted at .30 - .60 M. This preference level corresponds to previously cited studies (Harriman, 1970; Stockton and Whitney, 1974) which reported taste preferences of other rodents. Porcupines did not display a preference for the other sugars tested over water. Hydrochloric acid evoked aversive responses at higher concentrations which began approximately $0.2 - 0.4 \times 10^{-2}$ M.

Carpenter (1956) suggests that discrepancies between neurophysiological and behavioral data may be due to the fact that neural data are from a restricted sample of fibers. The population of fibers may differ topographically with respect to specific taste sensitivities. The behavioral method, however, allows all receptors an equal chance of contributing to taste data. Carpenter noted that sucrose preference in hamsters peaked at the 0.2 M concentration. Frank (1973) analyzed the peak response of the chorda tympani of the hamster to various concentrations of sucrose and found that the greatest response was shown at the 0.6 M concentration. It may be noted that the chorda tympani represents only the anterior third of the population of taste receptors in the hamster tongue and, thus, might offer a possible explanation for the observed discrepancy. It is due to the lack of comparative studies on taste at the behavioral level of analysis (Kare, 1963) that this paper proposes cross-species comparisons of taste preferences utilizing behavioral data.

It is suggested that the very lack of research in the area of taste preference at the behavioral level may be a secondary cause of the lack of agreement between behavioral and physiological studies in comparative taste preferences. Several variables not mentioned previously render it often times difficult to evaluate data of any sort dealing with taste preferences. Pfaffmann (1965) notes that salt-deprived animals exhibit a lowered NaCl preference threshold and have been observed to respond positively to weak saline solutions towards which normals were indifferent. It was suggested that lowered preference thresholds reflected increased sensitivity of the taste receptors. Whether taste preferences are actually reflecting those typically found in a species or artificially produced preferences due to deprivation of various substances not in the animals laboratory diet can only be resolved through research in the area of food and water requirements as typified by the work of Harriman (1969, 1973).

Taste preferences seemingly may be altered by prior experience with aversive stimulation. These and other phenomena may account for Kare and Ficken (1963) reporting differences in degree of taste preferences within species. It is quite likely that organic factors as well as learning in the individual could distort taste preferences characteristic of a species.

Harriman and MacLeod (1953) using shock avoidance to salt showed no differences between normal and adrenalectomized animals at threshold. Normal animals actually exhibited an enhancement of taste discrimination due to the pairing of salt to electrical shock.

Cappell and Blanc (1973) in a conditioned taste aversion paradigm, demonstrated that doses of d-amphetamine which are intravenously self

administered by rats may inhibit saccharin drinking. The aversion was not antagonized by chlorpromazine. Drug-induced saccharin aversion was reversed by chlordiazepoxide however.

Braun and Synder (1973) reported that rats injected with methyl mercuric chloride (5 mg/kg), following exposure to the taste of saccharin, rejected saccharin on subsequent days to a significantly greater extent than did either rats poisoned following plain water or rats injected with normal saline following saccharin exposure.

Johnson and Fisher (1973) studied water-deprived and cholinergically stimulated Wistar rats using the two-bottle sucrose-water preference test. The results indicated that animals under good condition of testing show a similar pattern of sucrose solution and water ingestion when the intake is carefully monitored over the course of an exposure session. Thirsty animals did not show a specific preference as a function of the manipulation used to induce that thirst. They did, however, show an ingestion pattern or profile which reflected the relative strength of the drive induced by a given manipulation.

Due to the possible confounding of the previously mentioned variables and the differences in methodology between and within behavioral and electrophysiological studies, it may be premature at this time to propose statements or offer generalizations. A primary reason for this investigation is to provide more information upon which to base generalizations about taste preference behavior across species.

Statement of the Problem

The review of literature has demonstrated that the behavioral data on the rodent preference for salt are divergent. Several Old World

rodents such as hamsters (Carpenter, 1956) and gerbils (Harriman, 1970) seem to demonstrate no distinct NaCl preference. Other New World criceid rodents such as grasshopper mice (Harriman, 1970) and laboratory rats (Duncan, 1962) have demonstrated a specific measurable preference for salt.

The studies on rodent response to "sweetness" are somewhat less contradictory but still in apparent disagreement. All rodents seem to demonstrate a common response pattern, reported by Richter (1942), to the sugar sucrose. The literature remains contradictory as to the maximum concentrations of sucrose test solution (over water) consumed by various species of rodents. Many researchers studying a wide variety of species have noted a maximum concentration of sucrose consumption from 0.2 to 0.6 M (Carpenter, 1956; Harriman, 1970; Stockton and Whitney, 1974; Bloom, Rogers and Maller, 1973).

In the current study, the cotton rat (Sigmodon hispidus), preferences for various concentrations of various sapid solutions were compared with taste preference of other rodents previously mentioned. According to Meyer and Meyer (1944), cotton rats feed largely on stems, foliage and seeds of plants, grasses and meadow growths and cultivated crops in the wild state. Large insects, they note, also form a part of their diet. Stoddard (1931) noted that captive cotton rats usually eat meat readily and the fondness of certain individuals for quail eggs makes them obnoxious upon the quail preserve.

This study was performed to investigate the taste preference behavior of cotton rats (Sigmodon hispidus) when given a free choice in the two-bottle test (test solution or distilled water) for five sugars (fructose, glucose, lactose, maltose, sucrose) and for three salts

(magnesium sulfate, potassium chloride, sodium chloride) at five levels of molar concentration. Two acids (hydrochloric and citric) were also paired with water at six levels of pH. The investigation was also concerned with any cross-species comparisons of sweetness or salt preferences that might be due to differential preference of Sigmodon hispidus for the various concentrations of sucrose or NaCl.

CHAPTER II

METHOD

Subjects

Ten male and ten female cotton rats (Sigmodon hispidus) bred and reared in a psychological laboratory at Oklahoma State University were used as subjects. The cotton rats ranged in weight from 22g to 175g and had a mean weight of 107.6g and a standard error of 8.7g.

A species that was fairly similar on the phylogenetic scale with the northern grasshopper mouse (Onychomys leucogaster) and the mongolian gerbils (Meriones unguiculatus) was chosen for investigation. These two species had been previously investigated by Harriman (1970, 1976) under identical laboratory conditions. A secondary objective of this paper is a replication of research conducted previously by Harriman (1976).

The hispid cotton rat according to Ellerman (1941) is located phylogenetically under the order Rodentia, family Muridae as is the mongolian gerbil and the northern grasshopper mouse. The cotton rat and the northern grasshopper mouse in addition share a common subfamily Cricetinae. The mongolian gerbil belongs to the subfamily Gerbillinae. All members of the subfamily Cricetinae are anatomically similar and are classified by taxonomists primarily on the basis of dental differences. While the species Meriones unguiculatus demonstrates more variation in physical appearance from the subfamily Cricetinae than do

species within the subfamily, a similarity in geographic origin with Sigmodon is noted. A fossil species or closely allied genus is noted in Eastern Asia. The same region (Longolia north to Siberia) is presently occupied by the Mongolian gerbil (Meriones unguiculatus). Thus, while the cotton rat seems to be more closely related to the northern grasshopper mouse on the phylogenetic tree and presently occupies the same geographical regions as the grasshopper mouse, ancestors of the species once occupied regions that the Mongolian gerbil now occupies.

The hispid cotton rat is a common field mammal of the southern United States and Mexico. The parents of the experimental subjects utilized in the study were trapped wild in central Oklahoma. Sigmodon hispidus is both a unique and worthy species to study. The animal is found in relative abundance near Stillwater, Oklahoma, is not difficult to trap and is comparatively gentle while being handled. For those reasons, over and above phylogenetic similarity to Onychomys leucogaster and Meriones unguiculatus, Sigmodon hispidus has been chosen as a subject of the present research project.

Apparatus

After weaning, the subjects were individually housed within an environmental chamber in Wahmann L C 75/A cages. Ambient temperature in the chamber was 24.5 degrees C., the relative humidity was 50.0 percent, and the chamber was lighted from 8:00 A. M. to 8:00 P. M. daily. Drinking fluids and food (Rockland Mouse/Rat Diet) were available ad libitum throughout the study. The fluids were contained in a pair of 140-ml graduated Wahmann drinkers attached to the face of each cage. The glass tube at the bottom which was the only part of the

drinker to extend into the cage, protruded about two inches from the bottom of the cage. Thus, the opening in the drinker was positioned immediately left of center, and the other drinker was positioned immediately right of center at the front of the cage.

Procedure

At the outset of the study, the animals were given a 10-day pre-test during which distilled water was offered in each drinker. At 24-hour intervals, the drinkers in each pair were switched in position. Also, every 48 hours, the drinkers were replaced with clean containers holding fresh fluids. Following pretesting, the animals were entered into a series of 52-consecutive 48-hour, Richter-type drinking tests. On the day prior to each test in the series, a slip identifying both the compound and the concentration at which the item was to be offered was selected by lot. After preparation, the solution was stored at room temperature or, in the case of the sugars, refrigerated and then returned to room temperature by the start of the test. Compounds used in the tests were as follows: (Sugars) D (-) fructose, D (+) glucose, D (+) lactose, D (+) maltose, and D (+) sucrose; (Salts) dried magnesium sulfate, potassium chloride, and sodium chloride; and (Acids) citric acid and hydrochloric acid. Each of the sugars and salts was tested at five different concentrations (.005, .05, .10, .50, and 1.0 M, and the acids were tested at six different levels of pH. The salts and acids were reagent grade, and the sugars were of the highest purity commercially available. Clean drinkers were used in each test. Also, control drinkers were used to correct for evaporative losses. Percentages of preferences for each of the three classes of chemicals were

treated by the technique of analysis of variance for a multifactor experiment having repeated measures on the same elements and by tests for trends (Weiner, 1971).

CHAPTER III

RESULTS

Sugars

In a treatments-by-treatments-by-subject analysis of variance of total fluid intake, with concentrations collapsed for all sugars, a significantly different amount of fluid intake was noted between the various sugars ($F=5.37$; 4, 76 df, $p < .001$), between amounts of test solution and distilled water consumed within all sugar categories ($F=14.79$; 1, 19 df, $p < .005$) and a significant interaction of these two main effects ($F=9.55$; 1, 19 df, $p < .001$). A two-factor mixed analysis of variance with repeated measures on one factor revealed a significant difference in consumption of sucrose at different molarities ($F=21.73$; 4, 72 df, $p < .001$). A significant sex difference was noted in consumption of sucrose over all concentrations ($F=6.289$; 1, 18 df, $p < .025$); however, the interaction of sex and concentration was not significant. A trend analysis for concentration effects on male animals yielded a significant linear component ($F=5.40$; 1, 80 df, $p < .025$) and a significant quadratic component ($F=7.45$; 1, 80 df, $p < .01$). A similar analysis for female subjects attained significance ($F=11.86$; 1, 80 df, $p < .005$) for linear and quadratic ($F=11.76$; 1, 80 df, $p < .005$) components.

A two-factor mixed analysis of variance with repeated measures on one factor for differential intake of fructose of different molarities

suggested a significant difference ($F=6.91$; 4, 72 df, $p < .001$). No main effects due to sex differences were noted; however, the interaction of main effects was significant ($F=5.16$; 4, 72 df, $p < .005$). Trend analysis for concentration effects yielded a significant linear ($F=15.28$; 1, 80 df, $p < .001$) trend and cubic trend ($F=5.88$; 1, 80 df, $p < .025$) for females only.

Differences in fluid consumption over concentrations were significant for lactose ($F=3.43$; 4, 72 df, $p < .025$). No significant main effect due to sex differences or interaction effect was observed. An overall trend analysis a significant quadratic trend ($F=4.97$; 1, 80 df, $p < .05$).

Differences in intake of glucose were noted to be significant ($F=6.01$; 4, 72 df, $p < .001$). No significant differences were noted due to sex, and the sex x concentration interaction was also significant. An overall trend analysis revealed a significant linear trend ($F=8.20$; 1, 80 df, $p < .005$) over concentrations of glucose. Other trends were significant.

Differential consumption of maltose yielded a significant concentration difference ($F=12.08$; 4, 72 df, $p < .001$). No significance due to sex of subject or sex x concentration interaction was observed. A significant linear ($F=5.18$; 4, 72 df, $p < .005$) and quadratic trend ($F=13.58$; 1, 80 df, $p < .001$) were noted in the concentration main effect.

Percentage intake was calculated for all subjects by dividing the amount of test solution by the total amount of fluid (both test solution and distilled water) consumed. The numerator and denominator of this ratio were first divided by the weight of the subject in grams.

Preference percentages were expressed as amount consumed per forty-eight hours per 100 g of body weight. The mean percentage intake peaks for sugars were as follows: Sucrose 85.97%, fructose 87.22%, glucose 85.21%, lactose 71.60%, and maltose 78.05% all at the concentration .10 M.

Salts

A treatments-by-treatments-by-subject analysis of variance examining total intake of salt solutions, with concentrations collapsed, revealed no significance between different salts, test solutions and distilled water consumed within all salt categories and no interaction effect.

A two-factor mixed analysis of variance with repeated measures on one factor revealed a significant difference in $MgSO_4$ intake ($F=5.86$; 4, 72 df, $p < .001$). No significant sex difference or interaction effect was observed. A trend analysis for concentration suggested a significant linear ($F=12.04$; 1, 80 df, $p < .001$) and cubic trend ($F=4.07$; 1, 80 df, $p < .05$).

A significant difference for concentration effects in NaCl ($F=3.71$; 4, 72 df, $p < .01$) was noted. A significant sex difference, in addition, was noted ($F=6.00$; 1, 18 df, $p < .025$). The interaction of the main effects was also significant ($F=5.18$; 4, 72 df, $p < .005$). A trend analysis for female subjects revealed a significant linear ($F=13.47$; 1, 80 df, $p < .001$) and cubic ($F=5.01$; 1, 80 df, $p < .05$). No significant trend was noted for male subjects.

A two-factor mixed analysis of variance with repeated measures on one factor for concentration effects in consumption of KCl was signifi-

cant ($F=4.07$; 4, 72 df, $p < .05$). No sex differences or interaction effects were observed. A trend analysis revealed a significant linear trend ($F=5.60$; 1, 80 df, $p < .025$). The mean percentage intake peaks were as follows: $MgSO_4$ 61.94% at .05 M, NaCl 48.63% and KCl 52.96% at .005 M.

Acids

A treatment-by-treatment-by-subject analysis of variance for total fluid intake in acids, with concentrations collapsed, yielded a significant difference between HCl and citric acid intake ($F=16.42$; 1, 19 df, $p < .001$). No differences in amount of distilled water and test solution consumed was noted over different sugars, but no significant interactions were noted.

A two-factor mixed analysis of variance with repeated measures on one factor for concentration effects in HCl was significant ($F=3.76$; 5, 80 df, $p < .005$). No significant sex or interaction differences were noted. A trend analysis for concentration revealed a significant linear relationship ($F=5.30$; 1, 100 df, $p < .025$) and quadratic relationship ($F=4.31$; 1, 100 df, $p < .05$).

A significant difference in intake over concentrations of citric acid was observed ($F=5.85$; 5, 80 df, $p < .001$). No significant sex differences or interaction effect was noted. A trend analysis yielded a significant linear ($F=15.88$; 1, 100 df, $p < .001$) component over concentrations. Mean percentage intake peaks were 38.48% for HCl at .005 M and 52.90% for citric acid at the same concentration.

TABLE I
 MEAN AND STANDARD ERROR FOR PERCENTAGES INTAKE OF
 TEST SOLUTION: SUGARS AND SALTS

Molarity	.005		.05		.10		.50		1.0	
	M	SE	M	SE	M	SE	M	SE	M	SE
Sucrose	30.04	6.71	81.90	4.59	85.97	4.74	89.43	3.21	75.21	5.15
Fructose	49.67	7.40	81.91	5.29	87.22	3.65	79.41	4.98	82.84	5.54
Glucose	50.09	7.71	73.83	5.71	85.21	3.48	81.45	2.21	85.42	5.26
Lactose	52.83	7.73	51.22	7.49	71.60	6.25	48.35	5.63	42.31	4.67
Maltose	64.58	7.56	92.99	2.61	78.05	6.08	74.65	5.16	76.52	5.88
MgSO ₄	54.62	8.12	61.94	6.93	46.10	5.06	11.14	3.09	11.96	3.82
NaCl	48.63	7.24	28.30	6.91	39.99	8.74	13.80	2.74	18.73	3.28
KCl	52.96	7.91	35.33	8.79	44.82	6.30	21.30	5.68	13.21	3.82

TABLE II
 MEAN AND STANDARD ERROR FOR PERCENTAGES INTAKE OF
 TEST SOLUTION: ACIDS

pH	4.0		2.3		2.0		1.8		1.6		1.5	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
HCl	38.4	6.8	31.5	7.8	16.2	3.6	15.5	4.8	9.2	5.0	8.0	4.0
Citric Acid	52.9	7.9	15.3	5.2	8.8	3.1	4.8	1.7	3.2	1.8	3.3	1.0

CHAPTER IV

DISCUSSION

It is quite likely that taste responses for all concentrations of the chemicals were a function of many interacting variables, including innate taste sensitivities palatability and acquired feeding habits, to name just a few. Young (1959) made an interesting distinction between factors influencing various aspects of performance. The aspects of performance were examined: Rats running back and forth on the experimental apparatus for a single food and discriminating preferentially between two foods. Both aspects of performance were found to depend upon a group of interrelated factors: Familiarity with the experimental apparatus, palatability of the food reward, previous conditioning to one of the test-foods, state of health of the animals, diet, and state of hunger/satiety.

Nachman (1959) suggests that for saccharin consumption, a strong genetic component influences the behavior of rats. Albino rats which preferred 0.25% saccharin solution to water, and animals which preferred water to 0.25% saccharin were selectively bred. Significant differences were noted in the F1 generation between the two genetic groups in their amount of 0.25% saccharin preference. Differences between the two groups were found to be maximal in the intermediate concentration range of saccharin solutions (.25%, .50% and 1.0%). For weaker (.05% and .10%), and for stronger concentrations levels (2.0%),

the two genetic groups were similar.

It has been often cited that in rodents, salt preference or specific appetite for sodium chloride is, in part, hormonally regulated (Epstein and Stellar, 1955; Fregly, 1958; Rubin and Krick, 1933). Hormonal control of NaCl intake has been verified in other families as well (Denton and Sabine, 1961). Epstein and Stellar (1955) noted that post-operative experience with salt solution is not a necessary condition for the adrenalectomized rat's specific hunger for the sodium ion. Moreover, the appetite of adrenalectomized rats appears to be enhanced for a number of substances that contain sodium ions in great quantities among these were sodium chloride, sodium nitrate, sodium sulfate, sodium acetate and sodium iodide (Nachman, 1962). Thus, as with the earlier findings (Richter, 1939), it may be noted that specific appetite for sodium is enhanced by alteration of hormone levels in the general physiology of the rodent. Although one specific hormone has never been thought responsible for enhanced sodium appetite, several such delineated chemical complexes have been often cited as the probable components responsible for the alteration in behavior (Bare, 1949; Blair-West et. al., 1963; Fregly, 1961).

It was noted in analysis of both sucrose and NaCl intake over concentrations, that females demonstrated definite trends (both linear and quadratic). In contrast male subjects either demonstrated much weaker trends or no significant trends. While these findings indicate that the female members of the species S. hispidus might be more sensitive or differentially sensitive to variations in concentration, one can only speculate as to the possible causation of such sex differences. In light of the previous evidence presented concerning hormonal regulation

of sodium appetite in rodents, a hormonal explanation might be in order and would certainly merit further investigation.

As it has been previously stated, it is quite likely that taste responses for all chemicals at all concentrations is partially a function of previous history of the subject or prior taste experiences. Benjamin (1959) subjected rats to varying amounts of preoperative practice on a simple taste discrimination before ablation of the cortical taste area. With moderate amounts of practice, the lesion produced a seven to eleven-fold increase in threshold. However, if the animals were naive or overtrained, the operation had no effect. A concept that the sensory neocortex plays a static role, unaltered by the effects of experience, in taste discrimination behavior would not account for the previous results.

Not only would previously acquired taste patterns, present in the natural environment, have some bearing on interpretation of the present results, but also experiential factors during the experiment itself must be considered. Beebe-Center, Rogers, Atkinson and O'Connell (1959) measured the sweetness and saltiness of twenty-five compound solutions of sucrose and NaCl in terms of the concentration of equi-sweet simple solutions of sucrose and equi-salt simple solution of NaCl. The compound solutions were sampled in steps of one half log units covering almost the entire range of concentrations from threshold to solubility limit for sucrose and NaCl. Some enhancement of sweetness was found in the case of weak solutions. The principle effect, however, was one of mutual masking.

By the same logic, the present design, which was a factorial one with repeated measures, is useful when one has a large number of treat-

ment permutations to administer and a limited number of subjects. However, the basic disadvantage of presenting all treatments to all subjects randomly is the possibility of carryover effects from one treatment to the following treatment. Thus, in consideration of the present results, ideally, one would strive to keep the order of presentations of treatments in mind during the evaluation process, or, in the future, utilize a design that would evaluate the effects of order of presentations.

Morrison (1974) noted in hooded rats, prior drinking a distinctly flavored fluid (quinine or saccharin) lowers the subsequent palatability of that flavor. In a two-bottle choice situation, preference will shift away from the flavor previously tasted. In a single bottle test, the animal will drink more if two equally palatable flavors are alternated than if one is presented. The noted effect is short lasting, with recovery occurring within thirty minutes.

The consumption of test fluids in the present study may have also been dependent upon still another environmental variable—that of conditioned taste aversions which conceivably could occur in the native habitat. Bartoshuk, et. al. (1975) reported that cats reject saccharin and cyclamate and are indifferent to dulcin, although they, like other animals, prefer sucrose (Carpenter, 1956). The rejection threshold for saccharin was determined to be at .001 M. Saccharin was presumed to be aversive to the cat because it stimulates receptor sites sensitive to substances perceived as bitter by man as well as those sensitive to sugars. In addition, it was thought that saccharin may not be an effective stimulus for all sugar-sensitive sites.

Nachman and Hartley (1975) tested the effects of several toxic agents in producing taste aversions. After a 10-minute sucrose drink-

ing trial, groups of rats were injected intraperitoneally with lithium chloride or with a strong, near lethal dose of rodenticide. Strong sucrose aversion, was acquired by groups injected with lithium chloride, copper sulfate, sodium fluoracetate, or red squill, and very weak or no aversions were learned by groups injected with thallium, warfarin, cyanide, or strychnine. It was indicated that the effectiveness of a substance to produce a learned aversion depends upon the unconditioned stimulus it is paired with and upon the type of symptoms associated with the specific poisoning.

Frumkin (1975) attempted to condition taste aversions to the object of two mineral specific hungers. Both the innate preference of adrenalectomized rats for sodium and the learned preference of parathyroidectomized rats for calcium were studied. None of the sodium-deficient rats poisoned after drinking sodium chloride (NaCl) reached a taste-avoidance criterion, even after nine pairings of salt ingestion with aversive lithium chloride injections. Six of the eleven calcium-deficient rats did not meet the salt-avoidance criterion after ten pairings. Nondeficient control subjects learned to avoid these salt solutions.

Kalat (1974) noted that rats form stronger aversions to solutions that are either more concentrated or more novel and noted that in most instances the novelty factor overshadows the concentration factor. Thus, in the list of environmental factors that possibly could be operating in the data (Palatability, acquired feeding habits, specific hungers due to deficiencies or hormone imbalance, sequency of fluid consumption), the possibility of conditioned taste aversions must be added for fuller consideration.

Harlow (1953) stressed the need for research to focus upon such topics as incentive value of reinforcers and to include motivation in the consideration of experimental results in animal as well as human studies. Guttman (1954) investigated the relative reinforcing values of sucrose and glucose solutions for rats in the aperiodically reinforced barpressing situation to note whether the results were consistent with the relative sweetness of various concentrations of sucrose and glucose for human observations. In four 50-minute tests on each of seven sucrose and seven glucose concentrations, plus two tests with water reinforcement, rate of barpressing was found to be an increasing function of concentration of both substances, with the rate for sucrose always above that of glucose at a given concentration.

It appears likely that certain concentrations of sugars that rodents demonstrate the greatest preference for, possibly in the range of .20 to .60 M for sucrose (Harriman, 1970; Bloom, Rigers and Maller, 1973; Carpenter, 1956), would also be the same concentrations to which maximal responding in an operant situation would occur.

Koh and Teitelbaum (1961) obtained absolute behavioral taste thresholds in rats for sweet substances. Rats were trained to taste solutions to avoid shock. A threshold for sucrose was found at .0099 M. There was noted close agreement between the thresholds obtained using motivation to avoid shock and taste thresholds reported by earlier investigators using preference or electrophysiological methods (Cambell, 1958; Hagstrom and Pfaffmann, 1959). Possibly, the most preferred sugars used in the present study (sucrose, fructose and glucose) would serve as reinforcers of high incentive values for members of this species.

The results of the present study indicate that hispid cotton rats

exhibit differing degree of preference for all concentrations of sugars, salts, and acids. The possible factors that might have contributed to the ultimate results of the experiment have been briefly discussed. The present findings and review of the literature would seem to support the notion (Kare, 1961; Kare and Ficken, 1963) that different species live in an "isolated taste world".

As a final comment, although in the past taste research has been dominated by both behavioral and electrophysiological measures of gustation, it seems feasible to this writer that in future investigations electrophysiological research involving cortical mapping of receptive fields of the tongue (Frank and Pfaffmann, 1969) and electric coding of taste signals from the chorda tympani and nucleus tractus solitarius (Doetsch et al., 1969) have produced most significant contributions to the study of taste in man and lower animals during the past decade.

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APPENDIX

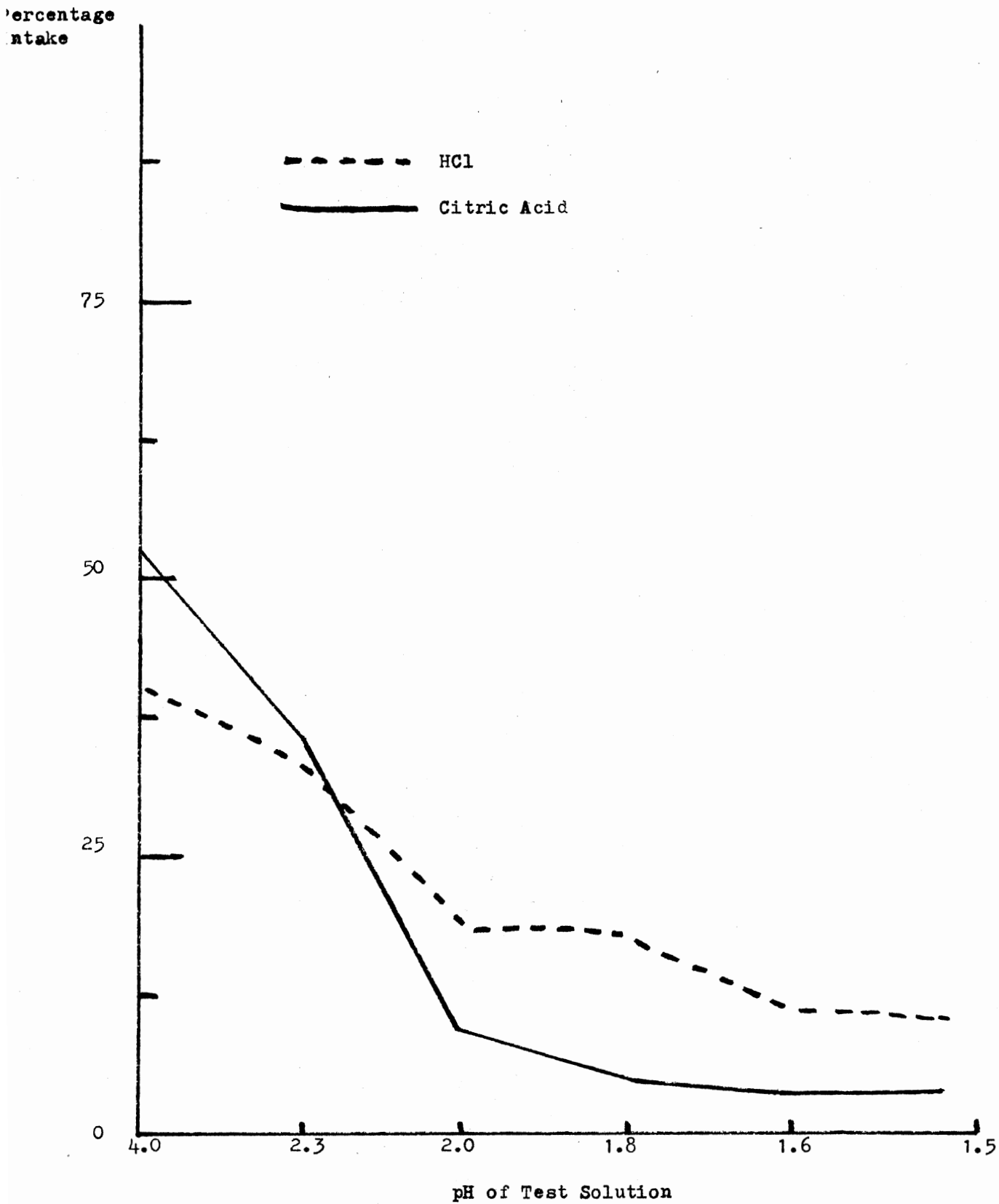


Figure 1. Mean Percent Intake for Acids

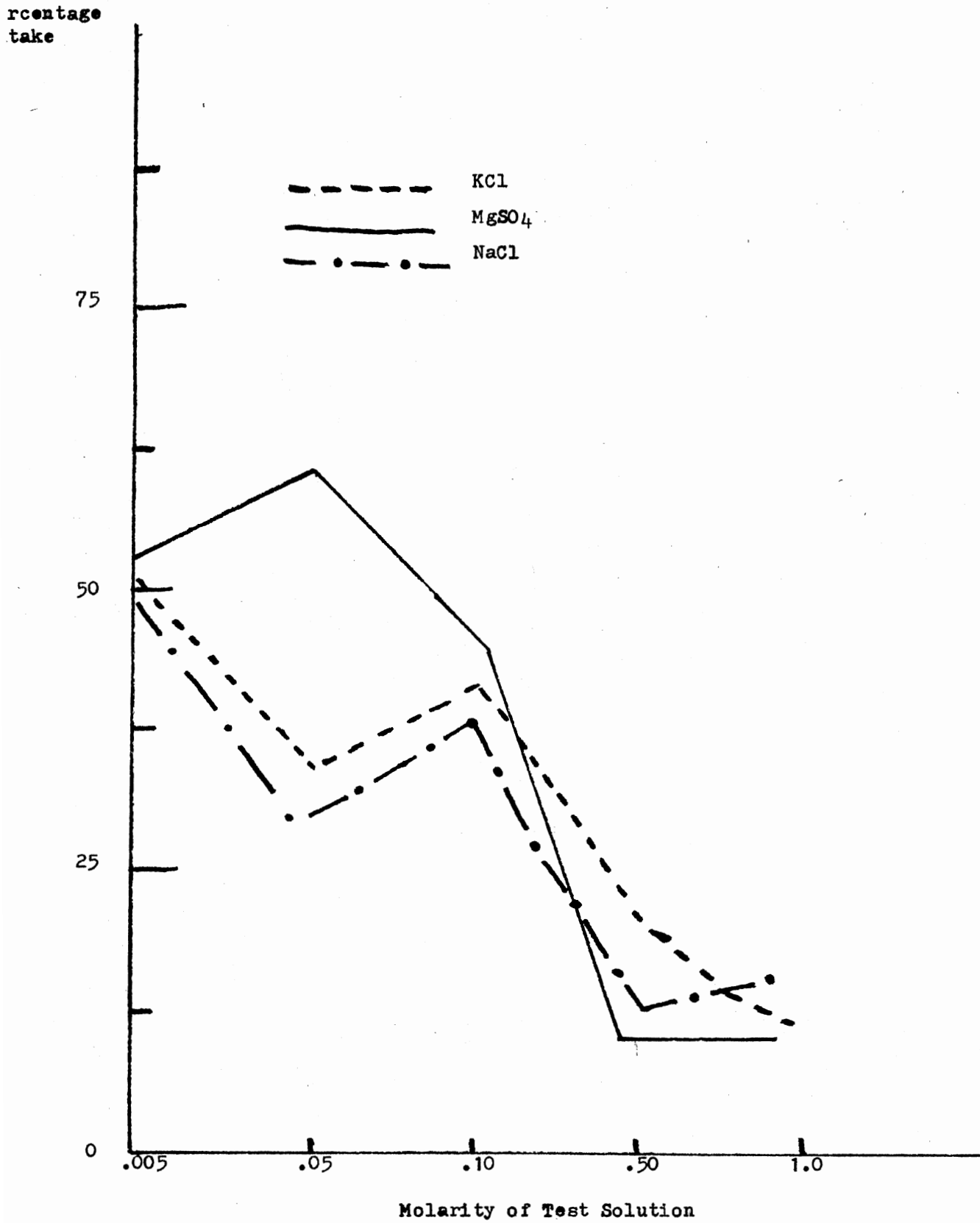


Figure 2. Mean Percent Intake for Salts

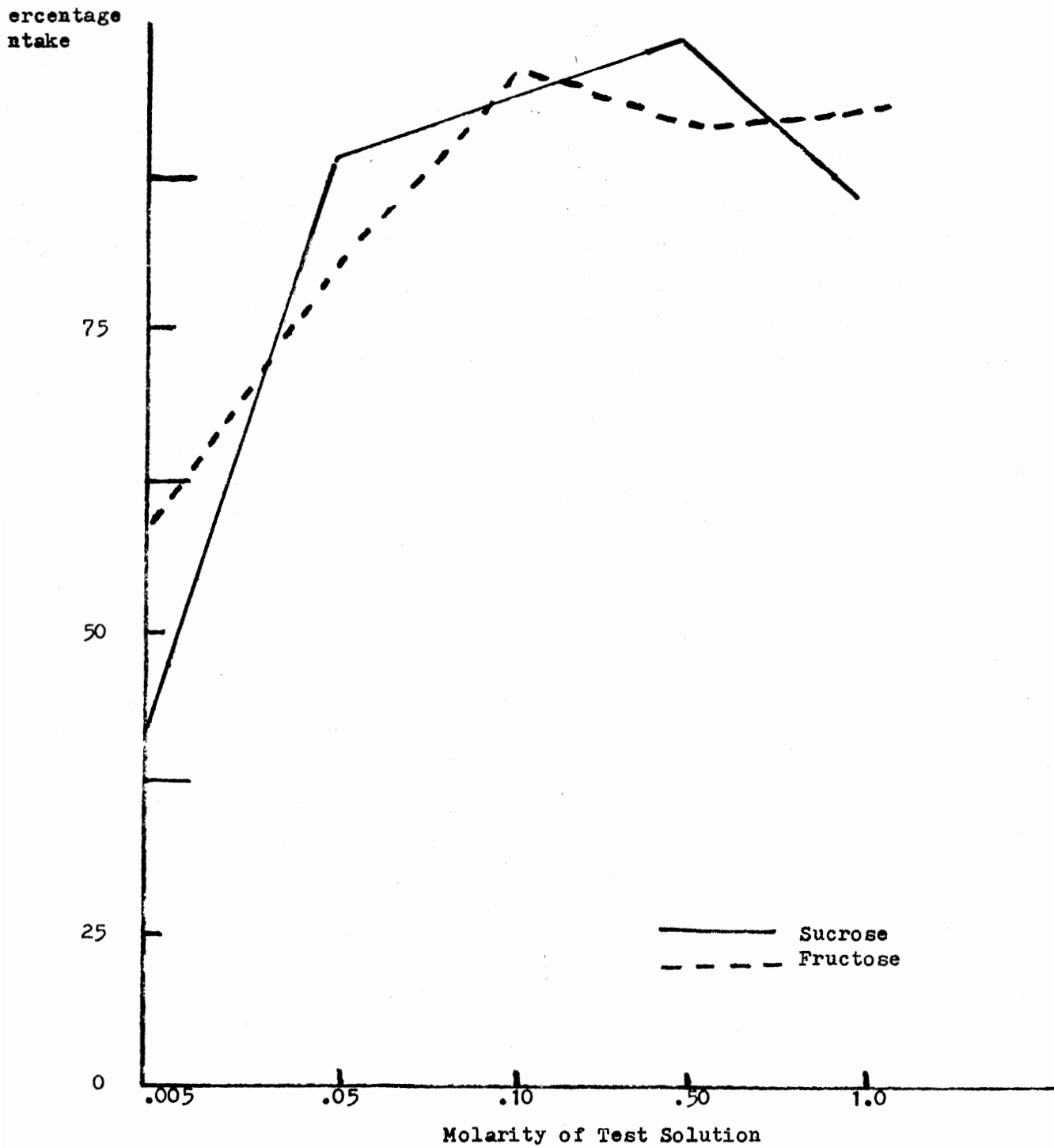


Figure 3. Mean Percent Intake for Sucrose and Fructose

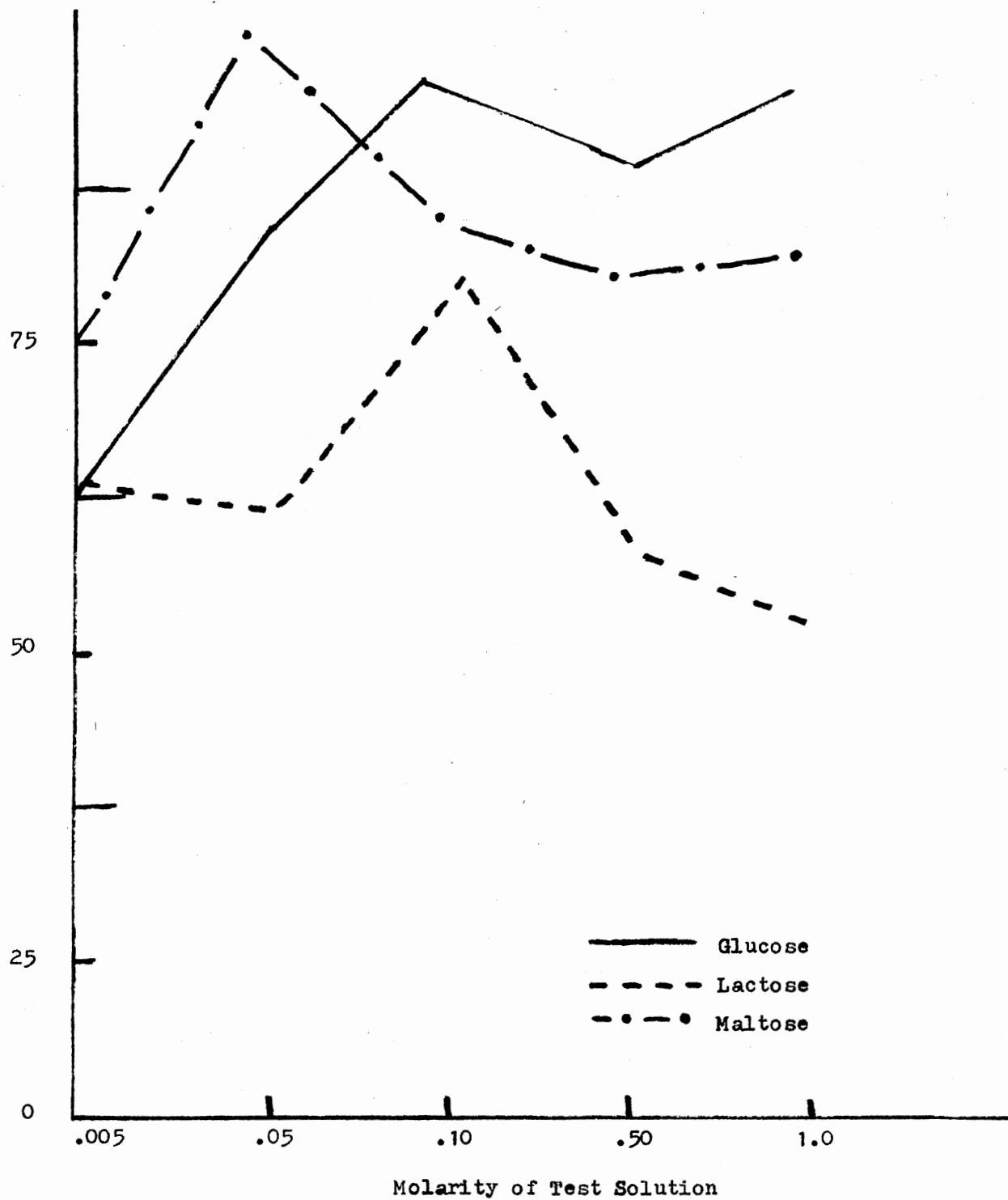
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Figure 4. Mean Percent Intake for Glucose, Lactose and Maltose

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