SPECIES DIFFERENCES IN TASTE PREFERENCES[1]

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Comparative studies are conducted for two reasons: (*a*) common features of different species are emphasized, and these may be basic to an understanding of the general theoretical problem, and (*b*) specific characteristics of a particular species allow single features to be studied as though magnified.

In the field of taste, a comparative study is composed of three main variables—the stimulus, the species, and the method of studying the problem—two of which must be held constant in order to make comparisons within the third variable. In the past, failure to maintain strict control of two variables (particularly methods) while the third was studied has nullified most of the findings so far as comparative purposes are concerned.

Recent work has stressed species differences in hunger and thirst mechanisms (1), and in the electrophysiological response of the taste nerve (2, 11). The differential effect of method has received some attention (13). However, there are no comparative studies at the behavioral level.

In this experiment the responses of three species to five stimulus compounds were obtained, using a standard method of stimulus presentation. Comparisons of species and stimuli are then possible because methodological differences have been eliminated.

METHOD

Subjects

Rabbits, cats, and hamsters served as *S*s for this experiment. Of the rabbits, one group consisted of five litter-mate Dutch rabbits, four females and one male, six months old at the beginning of the experiment. Five series of stimulus solutions were employed. A second group of Dutch rabbits was used for a single series (QHCl). This group consisted of four males and one female, not litter mates, also six months old at the beginning of the experiment.

Originally five cats were used. The number was later increased, as cats became available, to eight. Of the eight used at one time or another, only one was a male. One of the original cats died and was replaced during the experiment.

The group of hamsters consisted of nine males, approximately 150 days old at the beginning of the experiment.

Cats and hamsters were fed dry Purina Rat Chow (.5 per cent NaCl), and the rabbits dry Purina Rabbit Chow (.5 per cent NaCl), ad libitum.

Apparatus

The rabbits and cats were housed in a bank of ten metal cages. When the cages were used for cats, metal pans filled with sawdust were used to collect urine and feces. The hamsters were also housed in individual cages.

Each rabbit and cat cage was fitted with two plastic drinking units which supplied the animal with fluid from two 32-oz. rectangular bottles. A pressed-wood panel and shelf was fitted to each cage to hold the drinking units and bottles. The whole assembly—panel, two drinking units, and two bottles—could be tilted several degrees to drain the fluid from the bottles and drinking units.

The drinking apparatus used with the hamsters consisted of drinking tubes attached to burettes. The drinking tubes were made from number 8 glass tubing with the mouth end closed down to 2.1 mm. Fifty-milliliter burettes calibrated to 0.1 ml. served as reservoirs for the solutions.

Solutions

All animals received the following compounds in solution: NaCl, KCl, sucrose, saccharin (sodium saccharin) and QHCl (quinine hydrochloride). All compounds except sucrose (ordinary table sugar) were reagent quality. Solutions were made with tap water. The different solutions of NaCl, KCl, saccharin, and QHCl were mixed in highly concentrated stock solutions from which the various concentrations in each series were made every two days. To avoid fermentation, fresh sucrose was mixed each day from the dry compound.

Procedure

An identical procedure was used for the rabbits, cats, and hamsters. This was the standard two-bottle procedure, used with an ascending order of concentrations. In summary of this method: (*a*) solution in one bottle and water in the other were presented to each of the animals. (*b*) A given concentration remained on the cages for 48 hr., but the position of the solution was varied so that it was once on the *left* and once on the *right*, 24 hr. in each position. (*c*) The concentration

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then increased ⅓ log molar step and was placed in the *right* position for the first 24 hr., and in the *left* for the next 24 hr. This formed an LRRL series. (*d*) The beginning concentration in a series was chosen on the assumption that it would not be discriminated by the animals. The following beginning concentrations were used: NaCl, KCl, and sucrose for all species, .005 mol.; saccharin for rabbits, .00005, for cats and hamsters, .0002; QHCl for all species, .000002. The series ended when the animals avoided the solution.

RESULTS

The main results are presented in Figures 1 to 5. Each figure compares the three species on a single stimulus compound. The number in parentheses after "cats" indicates the number of cats used for that compound. The total intake for all animals of each species is plotted as a function of the logarithm of the molar con-

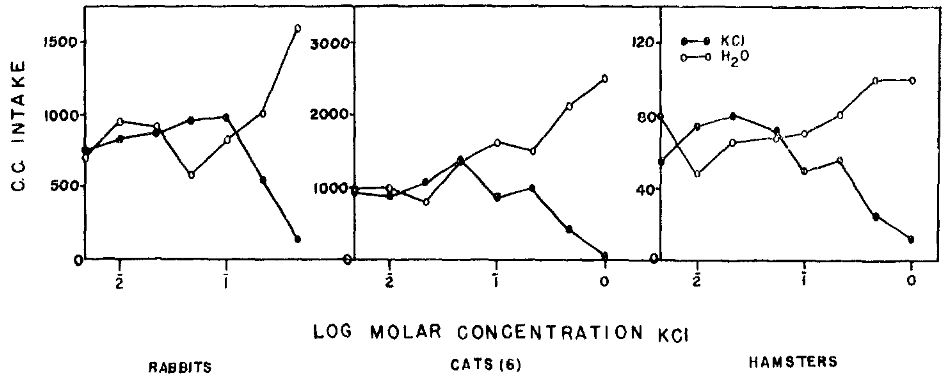

FIG. 1. Intake curves for potassium chloride.

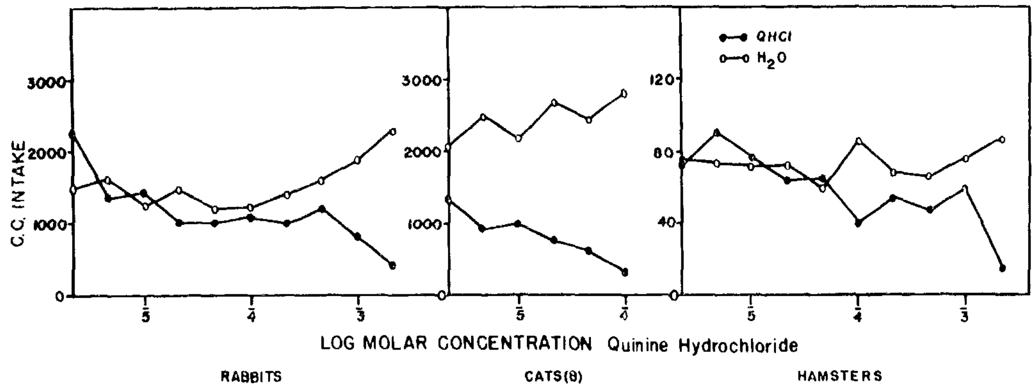

FIG. 2. Intake curves for quinine hydrochloride.

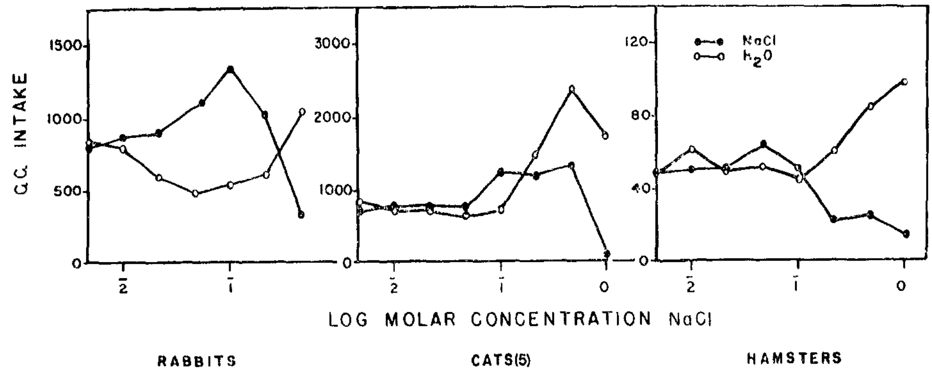

FIG. 3. Intake curves for sodium chloride.

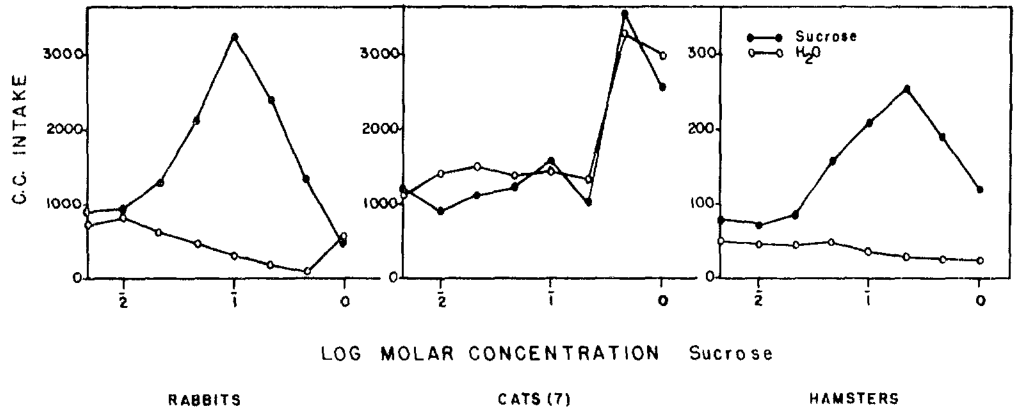

Fig. 4. Intake curves for sucrose.

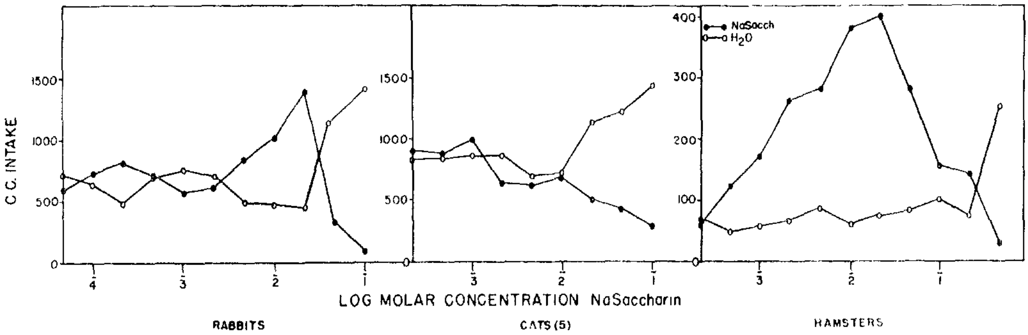

Fig. 5. Intake curves for saccharin.

centration. Thus each point of the curves represents the total intake during the 48 hr. that a given concentration was available to the animals.

In Figure 3, both curves for cats up to and including .5 mol. are based on the data for 48-hr. periods at each concentration for 7 cats. But the values at 1.0 mol. are estimates based on a single day for 6 cats (intakes of water and sucrose times 2). Therefore, the values at 1.0 are probably underestimates. The experiment was concluded on the first day of the 1.0 concentration in order to preserve the health of the animals. The cats were ill (vomiting, diarrhea) at the .5 molar concentration. Two of the animals were found prostrate in their cages after the first day on 1.0 molar concentration. One of these died shortly after being found. The remaining cats received .2 molar NaCl and water for two days following the termination of the sucrose series and recovered from the symptoms. A relatively healthy animal's data were not recorded in the emergency concerned with treating the other cats.

Compounds are classified as preferred, not-discriminated, and avoided compounds depending upon the responses made to them. "Preferred compounds" are those for which the solution intake at some concentration is significantly greater than the water intake. When the intakes of the solution and water are equal, the compounds are classified as "not-discriminated." "Avoided compounds" are those the intakes of which at lower concentrations are equal to water intake and then drop proportionately to the increase in concentration. Table 1 presents a classification of compounds according to the responses of the different species.

Table 2 contains the results of the *t* test for related measures. For both preferred and avoided compounds, *t*'s were calculated, at given concentrations for each species, between the intakes of water and solution. The *t*'s were calculated at the optimal concentrations for

TABLE 1

Classification of Compounds for Species

Species	Preferred	Avoided	Not Discriminated
Cat	NaCl	QHCl Saccharin KCl	Sucrose
Hamster	Sucrose Saccharin	QHCl NaCl KCl	
Rabbit	Sucrose Saccharin NaCl	QHCl KCl	

TABLE 2

Tests of Significance Between Water and Solution Intakes

Compound	Species	Concentration (mol.)	p
NaCl	Rabbit	.1	.05
	Cat	.1	.05
	Hamster	.2	.01
KCl	Rabbit	.5	.01
	Cat	.5	.01
	Hamster	.2	.05
Sucrose	Rabbit	.1	.01
	Cat		–
	Hamster	.2	.01
Saccharin	Rabbit	.02	.05
	Cat		
	Hamster	.02	.01
QHCl	Rabbit	.002	.02
	Cat	.000005	.01
	Hamster	.002	.01

preferred compounds. The "optimal concentration" is that concentration at which greatest consumption of solution occurred and which is significantly greater than water consumed during the same period. For avoided compounds, t's were calculated at increasing concentrations until significance was obtained.

DISCUSSION

Behavioral Relations

Table 1 shows that the response to the five test solutions is different in the three species. Only KCl and QHCl are classified in the same category, as avoided substances, for the three. Two points should be emphasized in the evaluation of this result: (*a*) The KCl curve (Fig. 1) for the rabbits shows a trend similar to the curves found for the preferred compounds. It is possible that by employing smaller increments of concentration, a significant optimal concentration would have been obtained. (*b*) In the response of the rabbits and hamsters to QHCl (Fig. 2), the difference between the intake of water and solution is relatively small compared with the magnitude of the difference in the cats. Thus, it might be better to characterize this substance as a high-threshold avoided substance for these species, since the intensities at which clear-cut avoidance occurred were at least 2⅓ log units above the first concentration discriminated by the cats. It should be noted that this is the only compound in which the effective concentration range is not the same for all species. For the rabbits and hamsters concentrations as high as .002 mol. were required before a significant avoidance was obtained.

It is interesting that NaCl (Fig. 3) does not evoke the same response in the three species, considering the importance that this compound has for the physiology of water balance. It is a preferred compound for the rabbits and cats, the effective range of concentrations in the cat being small due to truncation of the preference limb of the curve. The hamsters showed only an avoidance response, which occurred at a lower concentration than avoidance did for the rabbits or cats. If the present results can be supported, they single out the hamster for special study.

It is difficult to separate the control exercised by mouth and postingestion factors (specifically, osmotic pressure of the extracellular fluids [8]) in experiments where both may be thought to operate. Gilman (5), Heyer (7), McCleary (8), and Stellar, *et al.* (12) have shown that hypertonicity induced artificially in the body fluids or stomach results in compensatory drinking (increased intake of water or hypotonic solutions, decreased intake of hypertonic solutions), presumably to restore the normal state. Compensatory drinking implies that the animals can discriminate solutions by taste. Failure to discriminate coupled with changes in fluid intake suggest that postingestion factors are operative, as in the cats' response to sucrose (Fig. 4). In this experiment, cats were unable to discriminate between sucrose and water (contrary to the findings of

Frings [3]), and all the animals showed marked disturbances of fluid balance. The dramatic rise in the intake of both sucrose and water at between .2 and .5 mol. would be expected under the circumstances. The osmolar concentration of the extracellular fluids lies at approximately .31 (4) to .34 (6) mol. Similarly, it is the water intake which is adjusted to the rise in voluntary NaCl consumption in the cats; a preferential increase in NaCl consumption at high concentrations above .1 mol. results in compensating water increases. Postingestion factors may determine when to drink and how much, but what to drink seems to be determined in the mouth.

Saccharin (Fig. 5) was avoided by the cats, in contrast with the rabbits and hamsters, which preferred it. Since the responses to saccharin and sucrose are so different for the cats, it can only mean that these are qualitatively different stimuli for this species. A similar result has been obtained in rats (9), which accepted saccharin and avoided sucaryl. The saccharin curve resembles the QHCl curve very closely and suggests that there are similar features which determine the cats' response to these two compounds.

McCleary (8) has suggested that postingestion factors do not operate for saccharin. It is likely that other compounds exist whose intake is governed solely by the mouth. A likely candidate is QHCl. Data from Pfaffmann (10) and Benjamin[3] support this contention. Pfaffmann reports that water-deprived rats drink less NaCl solution. Benjamin, on the other hand, observed that rats drank more QHCl under water deprivation. Thus, the intake of QHCl, as contrasted with that of NaCl, seems to be controlled by taste, at least at concentrations which animals will ordinarily consume.

Both saccharin and QHCl are voluntarily ingested by the species used here, and by the rat, at concentrations far below the osmolar level of the extracellular fluids. Thus, in order to obtain compensatory drinking responses following stomach loads of saccharin, concentrations at levels comparable to the total osmotic level of the body fluids should have been chosen. Similar conditions should obtain for QHCl. If this speculation were supported, it would imply that compounds ingested at very low concentrations are consumed on the basis of taste alone.

Something should be said about the cogency of the preferred, avoided, and not-discriminated classification categories. These categories are useful descriptive terms when the relationship between solution and water intake is unequivocal. However, since the behavior may be better represented on a continuum, intermediate responses are arbitrarily forced into one of the three categories. This is especially true for the ascending order of stimulus presentation, in which the series is terminated when the solution is avoided.

However, the classification categories are not without their usefulness. Compounds that are not discriminated point directly to postingestion factors in the acceptance of fluids. For 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 postingestion factors (see 12). The intake of those compounds whose range of discriminated concentrations is too low to affect fluid balance, depends on the response to intensity of stimulation in the mouth. Thus, if postingestion factors can be experimentally ruled out, as in brief exposure tests (14), the optimal concentration for sucrose should be higher than that found in most prolonged ingestion tests in the rat. No such effect should be seen for saccharin. The avoidance compounds show no competition between taste and postingestion factors if avoidance begins at concentrations lower than the osmolar level. This again represents the response of mouth factors to intensity of stimulation.

Neural-Behavioral Relations

On the three species studied, electrophysiological data (2, 11) show that the response to sugar is strong in the hamster and rabbit but poor in the cat. This agrees in general with the behavioral responses; namely, that the rabbit and hamster show preference behavior both to sucrose and saccharin, whereas the cat shows no discrimination of sucrose and only slight aversion to saccharin. Of all the species studied electrophysiologically, only the cat gave a strong response to QHCl. The cat

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[3] R. M. Benjamin. Personal communication, 1954.

shows a stronger behavioral response than does the hamster or the rabbit to this substance. On the other hand, the behavior toward electrolytes does not correspond to the physiological data. Whereas NaCl is a strong stimulus for the hamster but relatively ineffective for the rabbit and cat, NaCl instigates a strong preference response in the rabbit but only a slight one in the cat, and no preference in the hamster. KCl, which is strikingly more effective in the rabbit and cat than in the hamster, leads to about the same behavior, aversion, in all three species.

These discrepancies between neurophysiological and behavioral data may result from several factors: (*a*) The chorda tympani represents the anterior third of the receptor field. Thus the neural data are from a restricted sample of fibers, the population of which may be topographically differentiated with respect to specific sensitivity. Presumably the behavioral method allows all receptors an equal chance of contributing to behavior.[4] (*b*) The data of this experiment were obtained from a single behavioral method, one of many possibilities, as were the neural data. Since the contribution of method to results has received little systematic attention, it is not surprising that the relationship between one behavioral method and one neurophysiological method is complex.

As pointed out earlier, there are preference and avoidance compounds with an effective range of concentrations that does not disturb fluid balance. Responses to these substances would relate more directly to the neural activity. On the other hand, the response to those compounds that disturb fluid balance would be more influenced by processes of the central nervous system, and thus a more complicated relationship would exist between neural and behavioral data.

SUMMARY AND CONCLUSIONS

Taste preference-avoidance behavior in three species, rabbit, hamster, and cat, was studied under standard conditions with the same stimuli and by the same method of presentation. Significant species differences were noted in the response to NaCl, sucrose, and saccharin. KCl and QHCl gave the same responses in the three species except for quantitative differences.

It was suggested that the intake of fluids is the result of the interaction of taste and osmotic effect exerted by compounds ingested at approximately isotonic levels. The intake of solutions at very low concentrations may be controlled by taste alone.

A partial relationship was shown between the behavioral data of this experiment and the neurophysiological data of other workers. Factors which might account for the observed discrepancies were discussed.

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[4] C. Pfaffmann. Personal communication, 1955.