

ABSOLUTE BEHAVIORAL TASTE THRESHOLDS IN THE RAT¹

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The behavioral taste threshold of the rat has been a topic of lively interest since Richter (1939) pointed out that the rat's preference taste threshold for sodium chloride decreases markedly after adrenalectomy. He suggested that the internal environment may act directly on the taste receptors to decrease the absolute taste threshold. Subsequent work by Pfaffmann and Bare (1950), using electrophysiological recording from the *chorda tympani* nerve, indicated, however, that the taste threshold for NaCl was unchanged following adrenalectomy. This seems to mean that adrenalectomy changes the rat's motivation and preference for salt rather than its ability to taste it. To test this interpretation, Carr (1952) and, independently, Harriman and MacLeod (1953) employed a method of forced taste discrimination in which thirsty rats were punished by electric shock if they drank the incorrect solution. Their data showed no difference between the taste capacity of normal and adrenalectomized rats, but Harriman and MacLeod obtained thresholds considerably lower than those reported by Carr. Our purpose, therefore, was to attempt to devise a more reliable method of detecting the rat's absolute behavioral taste threshold for NaCl, and using this method, to determine the taste thresholds for sweet, sour, and bitter substances as well.

METHOD

Three main problems needed to be solved: (a) To motivate the animal to drink large quantities of fluid so that many pairs of solutions could be tasted in each experimental session. (b) To train the rat to sample the fluid in both tubes when presented, but to continue licking only the correct one. (c) To present pairs of taste stimuli in such a way that a reliable estimate of the rat's taste capacity could be made for each experimental session.

Two methods of motivating the rat to drink were

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used. The first, which has been described in detail in previous publications (Teitelbaum & Derks, 1958; Williams & Teitelbaum, 1956), consists in training the animal to avoid electric shock by licking a tube of fluid a minimum number of times. The second method, which has not been described previously, is exactly analogous to the first in that a hungry rat is trained that it will receive a pellet of food for licking the fluid.

In what follows, we will use the food-reward method as our prototype, but everything applies equally to the first method in which the rat drinks to avoid shock. Thus, whenever we say a hungry rat receives a pellet of food, it is understood that the rat working to avoid shock receives a 30-sec. reprieve until the next trial. And when a hungry rat misses a pellet, the rat being shocked receives no postponement of shock during the 30 sec. between trials. Once an animal has been trained to lick for food, and is licking readily for each pellet, it must be taught to lick only the appropriate taste solution freely. Since rats usually display marked position preferences when two tubes are offered, they must be taught to seek a single tube in either of two positions. After that is accomplished, two tubes are presented simultaneously, one containing the taste solution and the other, distilled water. The taste solutions are arranged randomly but equally often in the right and left position. The rat now receives a pellet of food only if it licks the taste solution 10 times in succession prior to 8 licks of the distilled water; otherwise it receives no pellet. In either event, the trial is terminated. If the difference between the solutions is highly discriminable, say distilled water versus 1% NaCl, a rat soon learns to lick the salt solution continuously, even when the position is randomly changed from right to left. When its performance has become so skilled that it makes practically no errors, it is time to narrow down the difference between the two solutions. A modified psychophysical "tracking" method was employed which is similar to that used by von Bekesy (1947) in determining human auditory thresholds and also to that used by Blough (1958) for visual brightness thresholds in pigeons. Each time the animal chooses correctly, the taste solution of the next pair is reduced in concentration. So long as the rat continues to make correct choices, it is forced to ever more difficult discriminations and ultimately makes an error. When this happens, not only does it fail to get a pellet, but in the next presentation the concentration is two steps higher in the series. Provided the steps between the concentrations are appropriately chosen, there is a concentration that it almost always gets right and the next one below it that it usually gets wrong. The solution between them is taken to be the threshold solution for the session. Once the animal was fluctuating in this way around the threshold, it was then returned to the strong end of the series of concentrations. If the rat was performing reliably, it would return via a series of correct choices to the same threshold concentration. Four or five de-

terminations of the threshold were performed in each experimental session, and their average was chosen as an estimate of the threshold for that session.

Apparatus

An automatic apparatus was constructed to program the above procedure and to record the choices.⁴ To detect the number of licks accurately, a drinkometer (Stellar & Hill, 1952) was connected to each tube when the pair of tubes was in position facing the animal. The licks were counted with stepping relays. When the animal had made a prescribed number of licks on the correct or incorrect tube, a relay control panel programmed the presentation of the next pair. The 10 pairs of tubes were mounted on a 10-sided disk, 43 cm. in diameter, that was located in front of the experimental cage, and they were rotated into position by a motor. An aluminum plate (14 by 24.5 cm.) was mounted on each side of the disk, and two drinking tubes were attached to each plate. Each tube consisted of an inverted glass culture tube, capable of holding 70 ml. of fluid, capped with a screw-on polyethylene cap. A 9-mm. hole was drilled in the center of each cap so that 10-mm. glass tubing could be inserted snugly into the culture tube. The lower end of the glass tubing was bent to form a 30° angle with the vertical cage front, and the tip was flame-polished down to a 3-mm. aperture. In the front wall of the cage, 62 mm. above the cage floor and 70 mm. apart, were two 11-mm. holes. The tips of the drinking tubes were on a level with these holes, 4 mm. outside the cage front. Thus, it was possible for a standing rat to lick either tube through the holes in the cage wall, and each lick was recorded by the corresponding drinkometer.

A correct choice of the taste solution drove the disk to the next lower taste concentration; an incorrect choice sent it to the position presenting the taste concentration two steps higher in the series. After each choice, the disk rotated to the next position and the drinkometers were inactivated for 30 sec. During this time, the animal ate if it was in the food-reward group and had made a correct choice or continued to be shocked if it was in that group and had made an incorrect choice; it could not do anything during this period to alter the consequences of its previous choice. The sequence of positions of the rotating disk was recorded on an Esterline-Angus recording milliammeter; this furnished an exact record of the animal's performance and, thus, of its threshold during the session.

Subjects

Eight adult female albino rats, ranging from 7 to 14 months of age, were used. One group of four was trained to lick to avoid shock and the other group, to lick to get a pellet of food. They were housed individually and were weighed daily. The animals attempting to avoid shock were allowed ad libitum access to food and water. The animals working to get food were supplied with food in their home cage, if necessary, to keep their

weight at 80% to 90% of ad libitum feeding weight; most of their intake was obtained in the experiment. Each animal was deprived of water during the hour immediately before being tested.

Procedure

Preparation of taste solutions. All taste solutions were prepared in terms of the number of grams of solute dissolved in 100 ml. of solution. This method yields the percentage concentration, as used by earlier workers, or by a simple conversion, the actual molar concentration (Pfaffmann, Young, Dethier, Richter, & Stellar, 1954). All chemicals used were of reagent quality.

Concentration steps chosen between taste solutions. Two main considerations guided our selection of concentration steps. First, both the concentration range and the steps within that range should be different from day to day so that no animal could possibly discriminate a solution on the basis of its position in a fixed sequence. Second, the series should contain one or two easily discriminable solutions, a number of solutions spaced in small steps around the probable threshold value so its determination would be accurate, and some between the two extremes to make the transition between the discrimination of strong and weak solutions as smooth as possible. With these criteria in mind, we chose ranges of two, three, or four log units, depending on the taste substance being used, and subdivided each log unit into several arbitrarily spaced steps. Figure 1 illustrates the series of concentrations used in a typical threshold determination of NaCl and of quinine. The total ranges explored were: .0000042 M to .1 M for NaCl; .00028 M to .3 M for sucrose; .0000015 M to .0002 M for quinine hydrochloride; and .00011 M to .016 M for HCl. Pictorial records of each threshold determination, showing the exact series of solutions used during every experimental session, are available (Koh, 1958).

Standard "tasteless" solutions. Ideally, an absolute taste threshold determination should be based upon choices between the appropriate concentration of taste solute dissolved in distilled water versus distilled water. However, to use the drinkometer to detect the licks, it is necessary that both fluids be electrolytes so that they will pass the minute amount of grid current needed for the vacuum tube to operate the plate relay. Therefore, as the standard "water" stimulus in the present experiment, we used a concentration of the taste substance far weaker than the lowest concentration detectable by the animal. The "water" stimulus for NaCl was .0000021 M NaCl; and for HCl, it was .00000027 M HCl. Since sucrose is not an electrolyte and quinine hydrochloride is a relatively poor one, the apparently undetectable .0000021 M NaCl was used as the standard "water" stimulus for comparison with these substances. For the same reason, the .0000021 M NaCl solution was also used as the "water" solvent for the series of sucrose taste stimuli. To check the validity of this assumption that weakly concentrated standard stimuli did not appreciably bias the thresholds obtained, and also to be sure that the drinkometer itself did not affect them, control experiments were run for sucrose and HCl after 10 threshold determinations had been obtained on each

⁴ We wish to thank Byron A. Campbell, Bartley G. Hoebel, and Mark E. Molliver for their help in the design and construction of this apparatus.

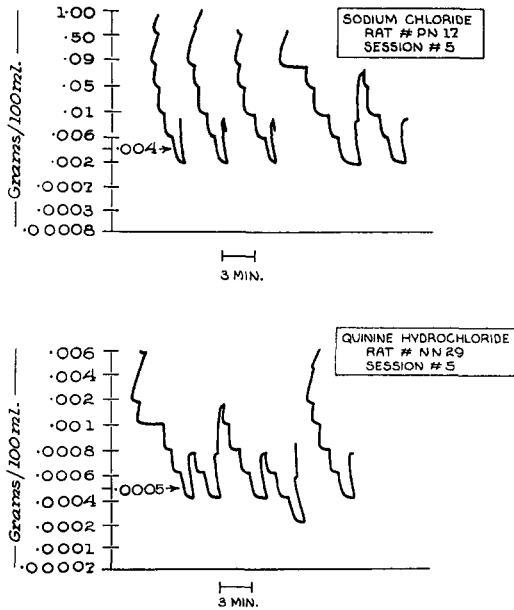


FIG. 1. Typical records obtained during a taste threshold determination session. Top: rat tasting NaCl to get food. Bottom: rat tasting quinine to avoid shock.

animal. With distilled water as the standard stimulus and as the solvent for sucrose and HCl, the drinkometers were disconnected and the *E* counted the licks. Otherwise, the procedure was unchanged.

Sequence of experiments. The threshold determinations were done in the following order: NaCl, sucrose, sucrose control, quinine hydrochloride, HCl, and HCl control. The pilot phase of the experiment was done with NaCl and shock avoidance. Many conditioning schedules were tried out until the procedure described above was settled on as a satisfactory one. Three rats, NH 7, NH 35, and NN 44, were used in the pilot study; they were also used in the final threshold measurements for all substances. These rats had received about five months of varied training before the final procedure was adopted. An additional rat was then added to the shock-avoidance group, and four rats were trained to make taste discriminations to get food.

Choice of correct solution. In the experiment to determine the taste threshold for NaCl, half the rats in each group were rewarded for licking the NaCl solution and half were rewarded for licking the standard "water" solution. As will be seen, this did not seem appreciably to affect the threshold value attained, but did seem to increase the variability in performance, especially where a marked preference might lead a rat to continue licking NaCl even if this did not lead to food reward or shock avoidance. Therefore, in the subsequent determinations that substance which was more preferred or less aversive was rewarded. This seemed both to enhance the performance of the animal and to prevent reluctance to drink from becoming an important factor in the threshold estimate. This is especially important toward the end of an experimental session. Thus, sucrose

was correct versus H₂O, and water was correct versus both quinine and HCl.

Criteria for determining the adequacy of the threshold. In determining the taste threshold for each taste substance, the animals were trained for approximately 1 hr. each day, and threshold determinations were made in each session. As the obtained thresholds became more reliable, in that they were less variable within each session and more consistent around the approximate threshold point, series of taste solutions with finer steps around the threshold value were used until the reliability and accuracy of threshold determination were judged to be adequate. With the final training procedure, 15 to 30 days of training seemed to be adequate to yield stable taste thresholds. Then the final series of 10 threshold-determination sessions were run on each animal.

Occasionally, even after an animal seemed to be well trained, it would appear to be discriminating very poorly in a session. This was immediately apparent, because with the tracking method used, consistent failure to discriminate resulted in the presentation of the strongest solutions that ordinarily were discriminated without error. When an animal showed this lack of discrimination by failing to discriminate better than the three strongest concentrations in the series for 10 to 20 consecutive trials, the data for that day were discarded. Marked variability in the threshold was sometimes also seen. That is, the animal's threshold would fluctuate around one concentration for a few trials, and then around a much higher one for the next few trials. If the threshold seemed to vary over a range of 5 of the 10 steps in the taste-concentration series, the data for that session were considered too variable and were also discarded. Measurements were continued on succeeding days until 10 days of threshold determinations had been obtained. The discarded data constituted approximately 10% of the data for the food-rewarded group and approximately 30% of the data for the shock-avoidance group.

Spuriously low taste thresholds may be obtained if a rat can discriminate the solutions by their smell. This was a problem with HCl. The rats were seen to be sniffing repeatedly at the solutions. Whenever this was observed, we attempted to overcome it by using fresh solutions even within a session and by using an electric fan to blow a stream of air across the drinking tubes. This seemed to help, in that the sniffing behavior tended to disappear.

RESULTS

Figure 1 illustrates representative threshold determinations for two rats. The top curve is a threshold determination for NaCl, and the bottom is a determination for quinine hydrochloride. In the NaCl determination, the rat reliably and repeatedly made a series of correct discriminations down to .002% NaCl, at which point it is consistently unable to make the correct choice. This is so despite the fact that after an incorrect choice the series was

TABLE 1
ABSOLUTE TASTE THRESHOLDS FOR NaCl
(Grams per 100 ml. of Solution)

| Session | Food Group ($N = 4$) | | | | Shock Group ($N = 4$) | | | |
|------------------------------|---|-------|--------------|-------|--------------------------|-------|--------------|-------|
| | H ₂ O Correct | | NaCl Correct | | H ₂ O Correct | | NaCl Correct | |
| | PH16 | PH18 | PN17 | PN22 | NH7 | NH35 | NN29 | NN44 |
| 1 | .0045 | .0045 | .0040 | .0024 | .0030 | .0013 | .0080 | .0020 |
| 2 | .0020 | .0045 | .0045 | .0035 | .0035 | .0050 | .0080 | .0020 |
| 3 | .0065 | .0065 | .0019 | .0016 | .0065 | .0030 | .0075 | .0008 |
| 4 | .0035 | .0030 | .0060 | .0030 | .0030 | .0030 | .0075 | .0020 |
| 5 | .0030 | .0065 | .0065 | .0030 | .0020 | .0030 | .0075 | .0008 |
| 6 | .0070 | .0035 | .0030 | .0035 | .0030 | .0065 | .0075 | .0030 |
| 7 | .0035 | .0070 | .0040 | .0008 | .0040 | .0050 | .0090 | .0030 |
| 8 | .0008 | .0070 | .0060 | .0030 | .0060 | .0060 | .0070 | .0030 |
| 9 | .0019 | .0055 | .0040 | .0045 | .0040 | .0060 | — | .0045 |
| 10 | .0060 | .0060 | .0040 | .0040 | .0019 | .0050 | — | .0040 |
| <i>M</i> | .0039 | .0054 | .0044 | .0029 | .0037 | .0044 | .0078 | .0025 |
| Molar conc. $\times 10^{-4}$ | 6.6 | 9.2 | 7.4 | 5.0 | 6.3 | 7.4 | 13.2 | 4.3 |
| | Combined $M = .0044$ Gm. per 100 ML. Combined $M = 7.4 \times 10^{-4}$ Moles | | | | | | | |

begun again at a high, but random, concentration. Since .002% NaCl was rather consistently incorrect and .006% NaCl was consistently correct, the threshold was estimated to be .004% for that session. In the bottom curve for quinine, the rat was allowed to fluctuate around the threshold point a bit more before *E* reset the drum to different points at the high end of the series. This rat was unable to discriminate a solution of .0004% quinine four out of five times but was always able to discriminate correctly a solution of .0006% quinine; therefore, the threshold was estimated as .0005% quinine for that session.

Tables 1 through 4 summarize the threshold measurements for all the rats for NaCl, sucrose, quinine hydrochloride, and HCl, respectively. The control measurements on sucrose and HCl, made without using the drinkometer and with distilled water as the standard stimulus, show no appreciable difference from the experimental thresholds. Therefore, the drinkometer coupled with a weak electrolyte "tasteless" solution apparently did not affect the obtained thresholds. These tables also indicate clearly that the discrimination shown by the food-motivated rats was usually better than that shown by rats motivated to avoid shock. Shock seemed to disrupt the rat's behavior during the act of discriminating.

DISCUSSION

Figure 2 compares our findings with those obtained by earlier investigators using a variety of methods.⁵ First, it is clear that the increasing order of effectiveness of the stimulating substances is: sucrose, .0099 M; NaCl, .00074 M; HCl, .00046 M; and quinine hydrochloride, .000012 M.

Second, the thresholds we have obtained are in very close agreement for all substances with the findings of previous investigators, but ours are generally slightly lower than those previously reported. For each substance, the average threshold for each rat is indicated by the hatched and filled triangles. The filled triangles represent our measurements on rats avoiding shock, and the hatched triangles, those rewarded by food. The food-motivated rats do significantly better in their taste discriminations than those avoiding shock ($p < .002$). But the difference between the mean thresholds

⁵ Many of these earlier studies presented findings in terms of percentage concentrations. It is a reasonable assumption that these were weight-volume ratios, and therefore we felt justified in transforming them into molar concentrations.

We are indebted to R. M. Benjamin for allowing us to cite the preference thresholds for quinine and hydrochloric acid obtained in his unpublished PhD thesis. We are also grateful to Carl Pfaffmann for his helpful suggestions concerning Figure 2.

TABLE 2
TASTE THRESHOLDS FOR SUCROSE
Grams per 100 ML.

| Session | Food Group (N = 4) | | | | Shock Group (N = 4) | | | |
|--|--------------------|------|------|------|---------------------|------|------|------|
| | PH16 | PH18 | PN17 | PN22 | NH7 | NH35 | NN15 | NN29 |
| Absolute Taste Thresholds | | | | | | | | |
| 1 | .09 | .30 | .40 | .09 | .50 | .90 | .40 | .10 |
| 2 | .25 | .20 | .10 | .40 | .30 | .70 | .50 | .40 |
| 3 | .09 | .40 | .20 | .10 | .20 | .60 | .40 | .40 |
| 4 | .30 | .20 | .10 | .30 | .50 | .60 | .50 | .20 |
| 5 | .10 | .20 | .09 | .10 | .70 | .60 | .20 | .40 |
| 6 | .20 | .60 | .20 | .10 | .70 | .80 | .40 | .60 |
| 7 | .09 | .20 | .20 | .40 | .60 | .60 | .50 | .20 |
| 8 | .20 | .10 | .07 | .30 | .60 | .60 | .40 | .40 |
| 9 | .20 | .20 | .30 | .40 | .20 | .60 | .40 | .30 |
| 10 | .10 | .20 | .08 | .40 | .40 | .50 | .30 | .40 |
| M | .16 | .26 | .17 | .26 | .47 | .65 | .40 | .34 |
| Molar conc. $\times 10^{-3}$ | 4.7 | 7.6 | 5.1 | 7.6 | 13.7 | 19.0 | 11.7 | 9.9 |
| Combined $M = 9.9 \times 10^{-3}$ Moles | | | | | | | | |
| Control Thresholds (without Drinkometer) | | | | | | | | |
| 1 | .10 | .20 | .20 | .20 | .20 | .90 | .30 | .40 |
| 2 | .30 | .08 | .20 | .40 | .20 | .70 | .20 | .30 |
| 3 | .20 | .20 | .20 | .40 | .40 | .50 | .20 | .60 |
| 4 | .10 | .20 | .20 | .20 | .70 | .80 | .40 | .40 |
| 5 | .40 | .20 | .50 | .30 | .20 | .60 | .20 | .60 |
| M | .22 | .18 | .26 | .30 | .34 | .70 | .26 | .46 |
| Molar conc. $\times 10^{-3}$ | 6.4 | 5.1 | 7.6 | 8.8 | 9.9 | 20.5 | 7.6 | 13.5 |
| Combined $M = 9.9 \times 10^{-3}$ Moles | | | | | | | | |

is quite small, and there is a considerable overlap between them. Since the obtained thresholds are relatively independent of the motivation used to get the animals to make the discriminations, our numbers may represent the actual taste capacity of these animals.

There are a number of interesting comparisons that may be made with the findings of earlier investigators for NaCl. Our result, .00074 M, agrees closely with results obtained by Carr (1952) using a forced behavioral taste-discrimination method, with Pfaffmann and Bare (1950) using an electrophysiological method, and with Richter (1939) using a preference method with adrenalectomized rats. It is clearly different from the threshold for NaCl obtained by investigators using a preference method in normal rats.

Therefore, behavioral taste thresholds for NaCl may be obtained from the normal rat that are as low as those obtained from the adrenalectomized animal. This supports the hypothesis that the difference in the NaCl preference threshold between normal and adrenalectomized rats is due to a difference in their motivation to obtain NaCl.

It can also be seen in Figure 2 that Harriman and MacLeod (1953), using a forced taste-discrimination method, obtained NaCl taste thresholds in normal and adrenalectomized animals that are appreciably lower than those reported by other investigators (Carr, 1952; Pfaffmann & Bare, 1950). Ours are not as low

TABLE 3
ABSOLUTE TASTE THRESHOLDS FOR QUININE HYDROCHLORIDE
(Grams per 100 ML. of Solution)

| Session | Food Group (N = 24) | | | | Shock Group (N = 4) | | | |
|--|---------------------|-------|-------|-------|---------------------|-------|-------|-------|
| | PH16 | PH18 | PN17 | PN22 | NH7 | NH35 | NN15 | NN29 |
| 1 | .0008 | .0004 | .0004 | .0002 | .0006 | .0003 | .0006 | .0009 |
| 2 | .0004 | .0008 | .0007 | .0004 | .0005 | .0006 | .0002 | .0006 |
| 3 | .0009 | .0004 | .0001 | .0004 | .0007 | .0007 | .0004 | .0008 |
| 4 | .0002 | .0004 | .0002 | .0004 | .0008 | .0009 | .0004 | .0007 |
| 5 | .0004 | .0007 | .0002 | .0004 | .0007 | .0007 | .0004 | .0005 |
| 6 | .0003 | .0007 | .0007 | .0003 | .0005 | .0009 | .0007 | .0005 |
| 7 | .0003 | .0005 | .0002 | .0004 | .0005 | .0007 | .0007 | .0008 |
| 8 | .0003 | .0003 | .0002 | .0004 | .0009 | .0003 | .0004 | .0006 |
| 9 | .0005 | .0006 | .0003 | .0005 | .0003 | .0004 | .0008 | .0003 |
| 10 | .0003 | .0003 | .0003 | .0002 | .0005 | .0005 | .0004 | .0004 |
| M | .0004 | .0005 | .0003 | .0004 | .0006 | .0006 | .0005 | .0006 |
| Combined $M = .0005$ | | | | | | | | |
| Molar conc. $\times 10^{-6}$ | 10.1 | 12.6 | 7.6 | 10.1 | 15.1 | 15.1 | 12.6 | 15.1 |
| Combined $M = 12.6 \times 10^{-6}$ Moles | | | | | | | | |

TABLE 4
TASTE THRESHOLDS FOR HCL
Grams Per 100 ML.

| Session | Food Group (N = 4) | | | | Shock Group (N = 3) | | |
|--|--------------------|-------|-------|-------|---------------------|-------|-------|
| | PH16 | PH18 | PN17 | PN22 | NH7 | NN15 | NN29 |
| Absolute Taste Thresholds | | | | | | | |
| 1 | .0015 | .0030 | .0008 | .0006 | .0035 | .0010 | .0030 |
| 2 | .0008 | .0009 | .0015 | .0009 | .0020 | .0030 | .0030 |
| 3 | .0015 | .0010 | .0009 | .0009 | .0010 | .0030 | .0015 |
| 4 | .0030 | .0020 | .0009 | .0020 | .0030 | .0030 | .0020 |
| 5 | .0015 | .0015 | .0005 | .0009 | .0020 | .0015 | .0015 |
| 6 | .0020 | .0015 | .0009 | .0015 | .0010 | .0010 | .0009 |
| 7 | .0007 | .0015 | .0008 | .0007 | .0015 | .0030 | .0030 |
| 8 | .0009 | .0020 | .0015 | .0006 | .0020 | .0030 | .0030 |
| 9 | .0009 | .0009 | .0009 | .0007 | .0009 | .0030 | .0030 |
| 10 | .0020 | .0030 | .0008 | .0009 | .0020 | .0030 | .0020 |
| M | .0015 | .0017 | .0010 | .0010 | .0019 | .0025 | .0023 |
| Combined M = .0017 Gm. per 100 ML. | | | | | | | |
| Molar Conc. × 10 ⁻⁵ | 40.7 | 47.5 | 26.1 | 26.6 | 51.9 | 67.4 | 63.0 |
| Combined M = 46.2 × 10 ⁻⁵ Moles | | | | | | | |
| Control Thresholds (without Drinkometer) | | | | | | | |
| 1 | .0010 | .0010 | .0009 | .0030 | | | |
| 2 | .0020 | .0030 | .0010 | .0005 | | | |
| 3 | .0009 | .0020 | .0009 | .0007 | | | |
| 4 | .0010 | .0030 | .0007 | .0009 | | | |
| 5 | .0020 | .0030 | .0007 | .0015 | | | |
| 6 | .0015 | .0030 | .0008 | .0015 | | | |
| 7 | .0009 | .0015 | .0010 | .0015 | | | |
| 8 | .0020 | .0020 | .0010 | .0008 | | | |
| 9 | .0030 | .0030 | .0007 | .0010 | | | |
| 10 | .0040 | .0030 | .0008 | .0009 | | | |
| M | .0018 | .0025 | .0009 | .0012 | | | |
| Combined M = .0016 Gm. per 100 ML. | | | | | | | |
| Molar conc. × 10 ⁻⁵ | 50.3 | 67.4 | 23.3 | 33.8 | | | |
| Combined M = 43.7 × 10 ⁻⁵ Moles | | | | | | | |

as those of Harriman and MacLeod; we do not know how to account for the difference. One possibility is that our use of the weak NaCl solution as the standard "water" stimulus prevented the rats from discriminating NaCl solutions in the range reported by Harriman and MacLeod.

Turning to sucrose and quinine, we see in Figure 2 that there is a rather narrow spread in the threshold values obtained by different methods. For sucrose, the preference thresholds obtained by Richter and Campbell (1940) agree quite closely with those obtained by Hagstrom and Pfaffmann using an electrophysiological technique (1959), and also with the present findings using a behavioral taste method with

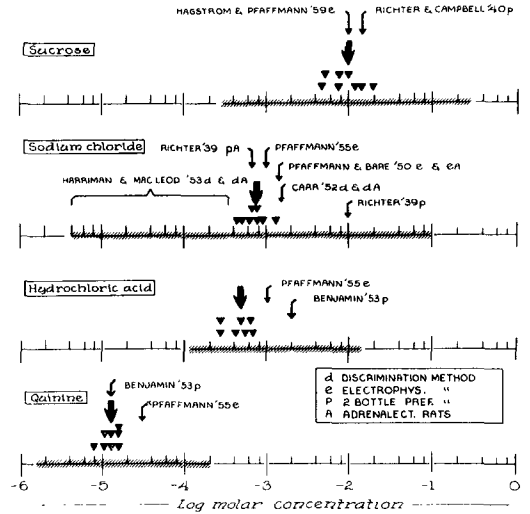


FIG. 2. Comparison of taste thresholds for the rat obtained by different methods. The heavy arrows indicate the mean thresholds obtained for each substance in the present experiment. The hatched bar on each scale indicates the range of taste concentrations used for that substance. (See text.)

high motivation. This may mean that for some substances, the motivation to obtain or to avoid the substance itself is sufficient to cause the animal to make a very fine discrimination. Campbell (1958) has pointed out that motivation level can clearly affect the preference threshold for sucrose. His preference thresholds for sucrose in very hungry rats are quite comparable to our discrimination taste thresholds. This supports the idea that sucrose is highly reinforcing for the rat, and means that Richter's preference threshold measure may, for appropriate substances, be a simple and highly accurate method of determining the taste threshold. However, wherever one doubts that the motivation level is high enough to produce optimal discrimination, a comparison with the threshold obtained under another motivation, such as food rewards for correct discrimination, should be made.

The method described here seems potentially valuable for studies investigating the sensory physiology of taste in the rat. Thus, after cortical ablation, where preference taste thresholds seem to be more easily affected by motivation and by the particular method of stimulus presentation (Benjamin, 1955), it may be valuable to use a discrimination method motivated by food reward or shock avoidance. Also,

rapid assessment of the threshold is important in testing the changes in taste capacity where recovery is a factor, as in the short-term effects of drugs upon the taste threshold.

SUMMARY

Absolute behavioral taste thresholds for salt, sour, sweet, and bitter substances were obtained in rats. Four rats were trained to taste solutions to avoid shock and four hungry rats tasted to obtain food. By using a psychophysical tracking method, it was possible to obtain an estimate of the threshold within a few minutes.

The increasing order of effectiveness of the stimulating substances is: sucrose, .0099 M; NaCl, .00074 M; HCl, .00046 M; and quinine hydrochloride, .000012 M. There was close agreement between the thresholds obtained using motivation to avoid shock or to obtain food, and generally very good agreement with the taste thresholds reported by earlier investigators using preference or electrophysiological methods.

REFERENCES

- BENJAMIN, R. M. Cerebral mechanisms in gustatory discrimination. Unpublished doctoral dissertation, Brown University, 1953.
- BENJAMIN, R. M. Cortical taste mechanisms studied by two different test procedures. *J. comp. physiol. Psychol.*, 1955, **48**, 119-122.
- BLOUGH, D. S. A method for obtaining psychophysical thresholds from the pigeon. *J. exp. Anal. Behav.*, 1958, **1**, 31-43.
- CAMPBELL, B. A. Absolute and relative sucrose preference thresholds for hungry and satiated rats. *J. comp. physiol. Psychol.*, 1958, **51**, 795-800.
- CARR, W. J. The effect of adrenalectomy upon the NaCl taste threshold in rat. *J. comp. physiol. Psychol.*, 1952, **45**, 377-380.
- HAGSTROM, E. C., & PFAFFMANN, C. The relative taste effectiveness of different sugars for the rat. *J. comp. physiol. Psychol.*, 1959, **52**, 259-262.
- HARRIMAN, A. E., & MACLEOD, R. B. Discriminative thresholds of salt for normal and adrenalectomized rats. *Amer. J. Psychol.*, 1953, **66**, 465-471.
- KOH, S. D. Absolute taste thresholds of rats obtained by a psychophysical method. Unpublished doctoral dissertation, Harvard University, 1958.
- PFAFFMANN, C. Gustatory nerve impulses in rat, cat, and rabbit. *J. Neurophysiol.*, 1955, **18**, 429-440.
- PFAFFMANN, C., & BARE, J. K. Gustatory nerve discharges in normal and adrenalectomized rats. *J. comp. physiol. Psychol.*, 1950, **43**, 320-324.
- PFAFFMANN, C., YOUNG, P. T., DETHIER, V. G., RICHTER, C. P., & STELLAR, E. The preparation of solutions for research in chemoreception and food acceptance. *J. comp. physiol. Psychol.*, 1954, **47**, 93-96.
- RICHTER, C. P. Salt taste threshold of normal and adrenalectomized rats. *Endocrinology*, 1939, **24**, 367-371.
- RICHTER, C. P., & CAMPBELL, K. H. Sucrose taste thresholds of rats and humans. *Amer. J. Physiol.*, 1940, **128**, 291-297.
- STELLAR, E., & HILL, J. H. The rat's rate of drinking as a function of water deprivation. *J. comp. physiol. Psychol.*, 1952, **45**, 96-107.
- TEITELBAUM, P., & DERKS, P. The effect of amphetamine on forced drinking in the rat. *J. comp. physiol. Psychol.*, 1958, **51**, 801-810.
- VON BEKESY, G. A new audiometer. *Acta otolaryng., Stockh.*, 1947, **35**, 411-422.
- WILLIAMS, D. R., & TEITELBAUM, P. Control of drinking behavior by means of an operant conditioning technique. *Science*, 1956, **124**, 1294-1296.

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