Saline intake in gerbils (*Meriones unguiculatus*)

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Experiment 1 assessed the NaCl preference-aversion function of gerbils on the two-bottle test. The results indicated that gerbils do not show the strong preference for 0.9% NaCl that rats do. There was also no significant difference between the gerbils' intake of 0.9% and 2.0% NaCl. However, there was a significant decrease in the gerbils' saline consumption when the solution was 4.0% by weight. Experiments 2 and 3 demonstrated that the interposition of a single bottle of hypertonic saline prior to the two-bottle test with isotonic saline and water can decrease the gerbils' preference for isotonic saline relative to a control group. This effect depended upon the tonicity of the interposed solution. Although rats show a marked reduction in saline preference following exposure to a single bottle of 2.0% NaCl for 24 h, gerbils do not react similarly. However, when the interposed solution is 4.0% NaCl, gerbils show a subsequent reduction in isotonic saline intake. These results suggest parametric differences between the variables affecting fluid regulation of mesophytic and xerophytic adapted animals which reflect species differences in renal handling of osmotic loads.

The Mongolian gerbil (*Meriones unguiculatus*) is a remarkable rodent whose ability to conserve water reflects the animal's physiological adaptation to natural selection pressures of a dry, xerophytic, desert environment. This rodent can manufacture all its water requirements from its solid food diet and can utilize higher concentrations of NaCl solution than can rats (Winkelman & Getz, 1962). Because most of our knowledge about fluid ingestion in rodents has been derived from the rat, it is possible that our models about the regulation of consumption are appropriate only to animals adapted to a mesophytic habitat. We must come to grips with species-specific components of the regulatory mechanism as well as general principles of such regulation. The gerbil was evolved from a xerophytic niche and undoubtedly, its mode of adaptation to water requirements is very different from that of the rat. Thus we would expect some interesting differences in the way the gerbil responds to various experimental conditions.

Until recently, there have been few well-controlled experimental studies on the water and saline consumption of gerbils. Grimsley (1973) sought to determine the gerbil's intake of salt solutions of varying concentration. Numerous studies have shown that rats show greater preference for isotonic saline than any other concentration of the solution or of water (see the review by Young, 1966). In attempting to derive the NaCl preference-aversion function among gerbils, Grimsley used the single-stimulus method

developed in the classic study on rats by Weiner and Stellar (1951). This method involves the presentation of only one solution at a time, and thus choice behavior is not directly assessed with this method. Grimsley's gerbils were water-deprived for 19 h before the 1-h tests, and one of five test solutions of varying concentration was used each day. The results indicated that the maximum intake of NaCl occurred at the 0.9% (isotonic) level. Concentrations of saline above and below this level produced much lower intakes.

In view of the discussion of ecological and physiological differences between rats and gerbils, it is surprising that the preference-aversion function of gerbils was found to be so similar to the curve for rats. Although Grimsley (1973) argued that the concentration maximally preferred through the single-stimulus method correlates well with preference measures, it is nonetheless paramount that the gerbil's preference should be studied in a direct choice situation. I believe that a distinction must be drawn between preference and intake. Young (1966) had pointed out that the single-stimulus method is not a true preference method because it excludes the possibility of choice.

There is another aspect of Grimsley's (1973) procedure that makes an interpretation of his results problematic. Throughout his experiment, the gerbils were fed a salt-deficient diet and were water-deprived 19 h before each test session. It should be noted that all of the studies indicating maximum preference for 0.9% NaCl solution among rats involved animals tested under normal, nondeprived conditions. For this reason, it is impossible to compare Grimsley's findings among gerbils with preference for isotonic saline among rats. If anything, sodium-deprived

This research was supported by a grant from the National Research Council of Canada, 67-0247. I thank Beverly Clark for her help in gathering and analyzing the data.

rats prefer hypertonic saline over solutions of lower tonicity. Thus, I feel that data on the preference-aversion function in gerbils should be gathered among animals fed a normal balanced diet.

In a recent study comparing the consumatory behavior of voles and gerbils, Laughlin, Donovan, and Burright (1975) tested the animals' intake of solutions including 0.9% and 3.2% NaCl. With the single-stimulus method, the nondeprived gerbils' consumption of both isotonic and hypertonic saline solution was about equivalent to that of water. When tested with the double-stimulus method, the gerbils ingested more water than either isotonic or hypertonic saline. Certainly these results are different from those obtained by Grimsley (1973) and are challenging. It is partly for this reason that the present experiment was conducted.

EXPERIMENT 1

Method

The subjects were 15 male gerbils (*Meriones unguiculatus*) ranging in weight from 50 to 70 g at the beginning of the experiment. They were housed in plastic mouse cages (Carworth) measuring 12 × 17 × 27 cm with Sanicell bedding and Purina Lab Chow on the floor.

I tested the two-bottle preferences of gerbils by placing a bottle of water and one of saline through the wire cage lids. The left-right position of the bottles was alternated from day to day, and the daily intake from each bottle was recorded at the same time (0900 h). The animals were first tested for 8 days with a bottle of water and one of 2.0% NaCl solution. Then they were given water only for the subsequent 8 days before being tested with a bottle of water and one of 0.9% NaCl. Following another 8 days where water was the only source of fluid, the gerbils were then given a choice between water and 4.0% NaCl for another 8 days.

Results and Discussion

Data from the two-bottle test were first analyzed in terms of a preference score consisting of (saline intake/saline + water intake) × 100. This score minimizes the error due to individual variation in total fluid consumption within and between subjects. The saline preference of the gerbils over the 8 test days for each NaCl concentration is shown in Figure 1. An examination of the data indicated that, unlike rats, gerbils do not show a strong preference for 0.9% NaCl solution. In contrast to the rats' tendency to show a saline preference of about 70% (Davenport, 1973; Wong, 1977), the gerbils showed about 53% preference for isotonic saline. When the gerbils were tested with 2.0% NaCl solution, they showed about 46% saline preference. There was no significant difference between the gerbils' intake of 0.9% and 2.0% NaCl ($p > .05$).

When the gerbils were tested with 4.0% NaCl, their saline preference dropped to 31%. The t-test of the difference scores indicated that the gerbils significantly reduced their saline intake when the solution was 4.0%. Comparisons between their

Figure 1. Percent saline intake of gerbils on the two-bottle test.

intakes of 0.9% and 4.0% NaCl ($t = 4.36, p < .001$) and of 2.0% and 4.0% NaCl ($t = 6.10, p < .001$) demonstrated this point.

The data on the gerbils' absolute intake of water and saline were also analyzed. Their mean intake of 0.9% NaCl during the 8 test days was 7.5 ml, in contrast to their intake of 5.1 ml of water. When tested with 2.0% NaCl and water, the gerbils drank 8.6 ml of saline and 8.9 ml of water. However, when offered a choice between 4.0% NaCl and water, the animals' mean intake of saline was 4.2 ml and that of water was 8.5 ml. The matched-group t test was used to compare the animals' intake of water and 0.9%, 2.0%, and 4.0% NaCl. The only significant comparison was that between 4.0% NaCl and water ($t = 2.90, p < .05$). These findings corroborate the outcome of the analysis of the saline preference scores.

The finding that gerbils showed about a chance-level preference for 2.0% NaCl is particularly interesting. Observations on the low (8%) preference of rats for 2.0% NaCl indicate that they find this solution aversive (Wong & Krontz, 1977). The fact that gerbils show about 46% preference for 2.0% NaCl suggests that this solution does not have the same negative effects on their intake as it does with rats.

Although gerbils do not prefer 4.0% NaCl to water, they nevertheless show a higher preference for this solution than do rats for 2.0% NaCl. I did not test the rats' preference scores for 4.0% NaCl, but it is likely that they would not drink more of it than of a 2.0% NaCl solution. I also did not test the gerbils' preference for hypotonic saline solution. Because their preference for isotonic saline was at a chance level, it is unlikely that they would drink less saline relative to water as the tonicity decreases and the substances of the two bottles becomes more similar.

EXPERIMENT 2

Although rats offered a choice between water and isotonic saline solution prefer saline, they show a decrease in this preference following the interposition of a single bottle of either isotonic or hypertonic saline prior to the two-bottle retest (Devenport, 1973). Recently, I have shown that this effect occurs only among rats that had been reared on water prior to the test sessions (Wong, 1977). Rats that had been reared on isotonic saline from weaning until testing time do not exhibit the Devenport effect. These results were interpreted in terms of Devenport's hypothesis that the ability of saline to expand the intracellular and extracellular space is poor compared with that of water. Thus these are mildly aversive consequences from the ingestion of saline. I had predicted that rats adapted to isotonic saline would not experience the degree of aversive postingestional effects from saline consumption that normally reared rats do, and the results appear to support this prediction.

Up to the time of the present experiment, there has not been any published evidence on the existence of the Devenport effect with species other than rats. In order to assess the generality of the Devenport phenomenon as well as to test the validity of his proposed mechanism underlying this effect, I tested gerbils using the Devenport paradigm. The results of this experiment would be particularly interesting because of the gerbils' unique ability to utilize hypertonic saline. Although the results of Experiment 1 suggest that gerbils do not necessarily prefer isotonic saline over water, it is nevertheless possible that the interposition of hypertonic saline could decrease their level of saline preference to below chance or 50%.

The present experiment consisted of exposing a new group of gerbils to water and isotonic saline for 3 days before half of the group was given exclusive access to 2.0% NaCl and the other half access to water for 24 h. The aim of this experiment was to determine whether the interposition of 2.0% NaCl would decrease the gerbils' subsequent preference for isotonic saline in the two-bottle test relative to those receiving the interposition of water.

Method

The subjects were 16 male gerbils (*Meriones unguiculatus*) that were housed in 12 × 17 × 2 cm plastic mouse cages. The floor was covered with Sanicell bedding and Purina Lab Chow was available ad lib. The gerbils were tested with the two-bottle procedure in a manner similar to that of Experiment 1. This procedure was followed for 3 days.

After their baseline level of saline and water intake was assessed, the gerbils were split into two groups. One group received a bottle of 2.0% NaCl solution for 24 h and the other group received water during this period. Following this period of single-bottle exposure, the gerbils were tested for another 5 days in the two-bottle situation. All two-bottle measures were obtained during a 24-h continuous access period.

Results and Discussion

Data from the two-bottle test were first analyzed in terms of the saline preference ratio used in Experiment 1. The results indicated no significant difference between the experimental and control groups during the critical two-bottle test sessions ($p < .05$). The group receiving the interposition of 2.0% NaCl for 24 h showed a preference of 50% for isotonic saline during the two-bottle test, while the group receiving the interposition of water showed 52% preference for isotonic saline.

The effects of the interposition of a single bottle of 2.0% NaCl on the gerbils' absolute intake of 0.9% NaCl in the two-bottle test was also assessed. The mean saline intake of the experimental group was 8.1 ml, while that of the control group was 8.4 ml. These results are consistent with those derived from the saline preference analysis.

It is apparent that the interposition of 2.0% NaCl did not decrease the gerbils' subsequent preference for 0.9% NaCl during the two-bottle test. In contrast, Devenport's (1973) rats showed a dramatic shift in saline preference as a result of this experimental procedure. This interexperimental difference is due in part to the fact that gerbils do not find the ingestion of 2.0% NaCl solution as aversive as rats do. This finding suggests that the hypertonicity of the interposed solution per se is not the controlling mechanism underlying the Devenport effect. In Devenport's experiments, the effect was evident when either isotonic or 2.0% saline was interposed between the baseline and test sessions.

On the basis of the results of the present experiment, I feel that the Devenport effect is manifested only when the interposed solution is of a concentration that an animal finds aversive (i.e., accepts at a level lower than that of isotonic saline). The data of Experiment 1 indicate that 4.0% NaCl is relatively aversive to gerbils and that the Devenport effect may be observed if I were to use a solution of this tonicity during the interposition phase of the experiment.

EXPERIMENT 3

Method

The subjects were 16 male gerbils (*Meriones unguiculatus*) that were housed and reared under the same conditions of those in Experiments 1 and 2. These animals were about 6 months old and had not been used in any previous experiments. They were assessed for 3 days in the two-bottle situation for their baseline intake of 0.9% NaCl and water. Then eight gerbils were assigned to the experimental condition where they received a single bottle of 4.0% NaCl for 24 h. The other eight gerbils were assigned to the control condition, where they received a single bottle of water for 24 h. Following this period of single-bottle exposure, the gerbils' intake of isotonic saline and of water in the two-bottle situation was assessed for another 5 days.

Results and Discussion

An analysis of the saline preference scores of the gerbils indicated no significant difference between

the experimental and control animals during the 3-day baseline period ($p > .05$). However, following the 24-h interposition of either 4.0% saline or water, there was a significant difference between the groups, $F(1,14) = 5.56$, $p < .05$. These data are plotted in Figure 2, and it can clearly be seen that the experimental animals showed a lower saline preference than the controls during the initial sessions. Multiple comparisons between the groups indicated that the suppression of saline intake among the experimental animals occurred during the first 2 test days ($p < .05$). No differences were obtained during the subsequent test sessions. It can be seen that by the fifth test session, the saline preference of the experimental animals had recovered to the level that the control animals maintained throughout the session. An analysis of the absolute saline intake of gerbils in the experimental and control conditions revealed results similar to those obtained from the saline preference scores.

The results of the present experiment appear to support the hypothesis that the Devenport effect can be induced in gerbils if the interpolated solution is sufficiently concentrated so that it is below the animal's acceptance level. Although Devenport was able to induce the suppression of saline intake in rats with the interposition of isotonic or hypertonic (2.0%) saline, I was not able to produce this effect in gerbils unless I used a more hypertonic (4.0%) saline solution. Despite differences in the rat and the gerbil's baseline isotonic saline preference and the tonicity of the interposed solution, there appear to be parallel processes underlying the effect with these species. In the present experiment, the suppression effect was evident for only 2 days after the interposition of hypertonic saline. After two sessions, the experimental animals showed a gradual recovery to

the baseline saline preference. This phenomenon also was observed with rats by Wong (1977).

GENERAL DISCUSSION

It is clear that there are a number of unique features of the gerbil's reactions to saline solution. Gerbils do not show a greater preference for isotonic saline than for any other concentration of the solution or of water. In contrast, comparable two-bottle comparisons with rats indicate that 0.9% NaCl is preferred over water as well as 2.0% NaCl (Young, 1966). However, when gerbils are tested with a highly hypertonic solution such as 4.0% NaCl, they show a decreased tendency to ingest such a solution. This behavioral finding is interesting because of the fact that the renal concentrating capacity of the *M. unguiculatus* probably exceeds the 600-700 mEq Na per liter found in 4.0% NaCl solution. Detailed data on the renal concentrating capacity of *M. unguiculatus* has not been documented, but such information is available for the related genus, *Gerbillus*. Burns (1956) found that when fed salted barley, gerbils from North Africa produced urine that was 1300 mEq Na per liter (equivalent to about 7.6% NaCl). The present results indicate that although the renal system of *M. unguiculatus* can process 4.0% NaCl, these animals will not ingest much of it if water is also available. Behaviorally speaking, the gerbils found 4.0% NaCl relatively aversive but not the 2.0% and 0.9% NaCl solutions.

The results of Experiments 2 and 3 are consistent with those from Almli and Weiss' (1975) series of experiments on the reactions of rats, gerbils and guinea pigs to various dipsogenic challenges. They found that these animals differed quantitatively rather than qualitatively in their responses to cellular stimuli for thirst. The rats' drinking following water deprivation and subcutaneous NaCl injections is more closely attuned to osmolality change than is the cue for gerbils and guinea pigs. These experimenters had also shown that the differential responses to osmotic stimuli were due to species differences in renal handling of osmotic loads. These differences, in turn, are related to renal functional capacity that has evolved to suit the species to its natural habitat. Our results suggest that, although the parameters are different, a model about the regulation of fluid ingestion of mesophytic adapted animals has some validity for the analysis of fluid consumption of xerophilous animals.

Figure 2. Percent saline intake of gerbils on the two-bottle test with water and 0.9% NaCl following the interposition of 4.8% NaCl (O—O) or water (O— —O) for 24 h.

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(Received for publication December 20, 1976;
revision accepted February 4, 1977.)