TASTE ACCEPTANCE IN SQUIRREL MONKEYS (SAIMIRI SCIUREUS)†

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Abstract. Six squirrel monkeys were presented with solutions representing the four primary tastes. The solutions included various concentrations of glucose or sodium saccharine (sweet), sodium chloride (salty), citric acid (sour), and quinine sulfate or sucrose octaacetate (bitter). A 24 hr two-bottle choice technique was employed. Amount of food, water, and solution consumed every 24 hr was recorded. The results showed that the maximum intake for glucose solution was with the 5.0% concentration, although maximum caloric intake was with the 1.25% concentration where there was a potentiation of food intake. Water was preferred over sodium saccharine at three of the four concentrations which were tested, and water was preferred over or equally to the concentrations of sodium chloride and citric acid that were used. However, quinine sulfate and sucrose octaacetate were preferred over or equally to water at most of the concentrations which were tested.

1. Introduction

During recent years the squirrel monkey (Saimiri Sciureus) has become a favourite experimental subject for neuroanatomical (Gergen and MacLean, 1962; Emmers and Akert, 1963), neurophysiological (MacLean *et al.*, 1963; Dua and MacLean, 1965; Snell, 1965), pharmacological (Cook and Kelleher, 1961, 1962), and primate communication and social behaviour (Ploog and Melnechuk, 1969) experiments. This small South American primate's popularity has to some extent been attributed to its small body and large brain (Carmichael and MacLean, 1961), and its safe and easy handling (Kelleher *et al.*, 1963). Brodie and Marshall (1963) feel that the squirrel monkey might prove to be the most useful primate for gastrointestinal, physiological and pharmacological studies because of its higher spontaneous gastric acid secretions.

In their natural environment these monkeys are known to eat buds, fruits, nuts and a wide variety of insect matter (Thorington, 1968). Under captive conditions they are maintained on different proportions of commercial monkey chow, peanuts, fruits like bananas, apples and grapes, and at times on a mixture of milk, eggs and cereals (DuMond, 1968). Some laboratories also feed them insects and meal worms (personal observations). While the squirrel monkey has been used in the laboratory for the last two decades, few systematic studies have been done on its food and water intake, and taste preferences.

† In conducting the research described in this report, the investigators adhered to the 'Guide for Laboratory Animal Facilities and Care', as promulgated by the Committee on the guide for Laboratory Animal Resources, National Academy of Sciences – National Research Council.

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The present report concerns the squirrel monkey's acceptance of solutions representing the four basic tastes in man; viz., sweet, sour, salty, and bitter.

2. Method

Six male squirrel monkeys (Saimiri Sciureus), weighing between 474 and 556 g at the beginning of the experiment and between 575 and 657 g at the end of the experiment, were housed in individual cages and kept on Purina monkey chow (25% protein) *ad libitum.* In addition to the Purina pellets, a thin slice of apple or banana was given twice a week. On two occasions oranges were also tried but the monkeys did not seem to like them. As it was planned to present the monkeys with a 2-bottle preference situation at a later date, *ad lib* water was also provided through 2 inverted bottles fixed to one of the side walls of the cage. Each morning at 8:30 a.m. fluid intake and food intake for the previous 24 hr were determined. The room temperature and humidity were maintained at 21–24 °C and 60–65%, respectively. The animals were kept in an artificially lighted room and the light–dark cycle was rotated at 12 hr, light being available from 8:00 a.m. to 8:00 p.m. During the initial one and a half month's period when these monkeys were quarantined and became acclimatized to the new surroundings, it was realized that the walls and floor of the cages were not suitable for the measurement of daily food intake because the monkeys threw food pellets onto the floor through the walls and bottom of the cages. The cages were subsequently modified so that all the walls and floor were reinforced with small mesh. After this initial period of 1½ months, systematic recording of food and water intake was done.

Total 24 hr intake was recorded by weighing the food, water, and test solution to the nearest gram. On two days where only water and food were available, intake was recorded every 12 hr. The taste preference experiments were conducted using the two-bottle choice technique. One bottle always had water and the other the test solution. Monkeys had access to both of the bottles for 24 hr, after which the positions of the bottles were reversed and the monkeys were given access to the same solutions for another 24 hr. Thus, each test solution was presented twice in any test trial. After the 2 day test trial, the monkeys were maintained on only water for another two days. Such a procedure should have minimized any possibility of carry-over effects from the previous test solution. The test solutions were offered in an ascending series of concentrations. The various test solutions used were: Glucose (1.25, 2.5, 5.0, 10.0, 20.0, 30.0, 40.0 and 50.0 g%), sodium saccharine (0.001, 0.01, 0.05 and 0.1 g%), sodium chloride (0.9, 1.8 and 3.6 g%), quinine sulphate (0.001, 0.002, 0.004, 0.008, 0.016, 0.032, 0.064 g%), sucrose octaacetate (0.001, 0.002, 0.004, 0.008, 0.016, 0.032, 0.064 and 0.128 g%), and citric acid (0.00625, 0.0125 and 0.025 *M*). The solutions were made weight by volume with tap water.

3. Results

On a typical day the average food intake across animals was 37 g with 31.5 g or 85% of

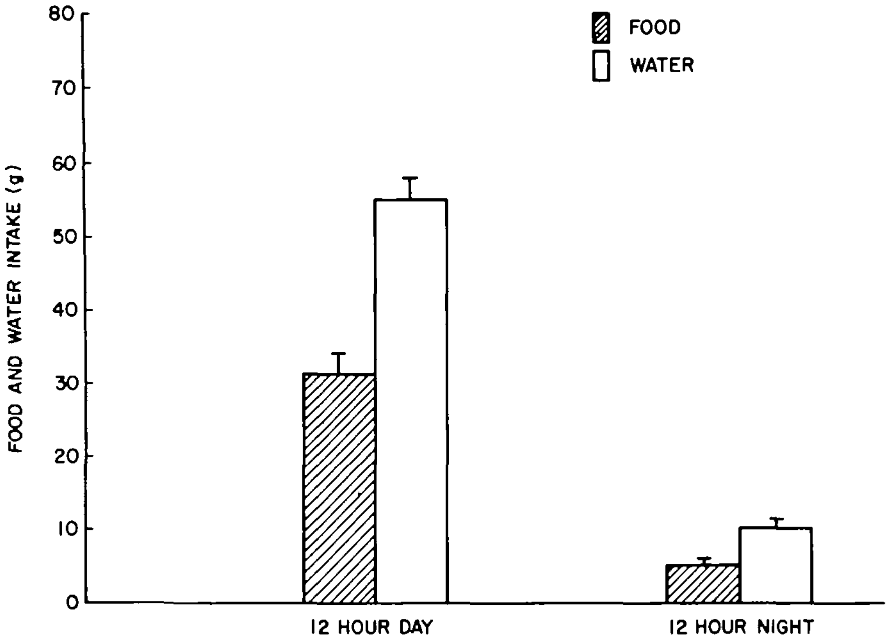

Fig. 1. Average water and food intake during 12 hr of light (day) and 12 hr of dark (night). (Horizontal bars represent standard error of the mean).

this being consumed during the 12 hr light period (Figure 1). The average water intake for this day was 66 g with 55 g or 83% being consumed during the 12 hr of light.

3.1 Glucose

Figure 2 represents 24 hr intake of glucose solution, food, water, and calories. It can be seen that the intake of glucose solution increased as a function of concentration up to the 5% and 10% concentrations, after which further increases in concentration were accompanied by decreases in consumption of the solution. There was a decrease in 24 hr food and water intake at all concentrations of glucose except for 1.25% and 2.5% glucose solutions. At the 1.25% concentration the food intake showed a 36% increase over the control value ($t = 3.80$, $p < 0.05$). The series was later repeated for 1.25% glucose solution and consistent results, showing increase in food intake, were again observed. Although there was a depression in food intake for the other concentrations of glucose, the total 24 hr intake increased 7–16% with concentrations varying from 2.5% to 30% glucose. On the days of 1.25% glucose, the 36% increase in food intake was accompanied by a 39% increase in caloric intake. With the 40% and 50% concentrations the total caloric intake was somewhat lower than on control day. Thus, in most test trials of glucose intake, the animals showed enhanced total caloric intake irrespective of decreased caloric intake through food, the extra calories coming from glucose.

The total fluid intake at all concentrations of glucose was higher than water intake

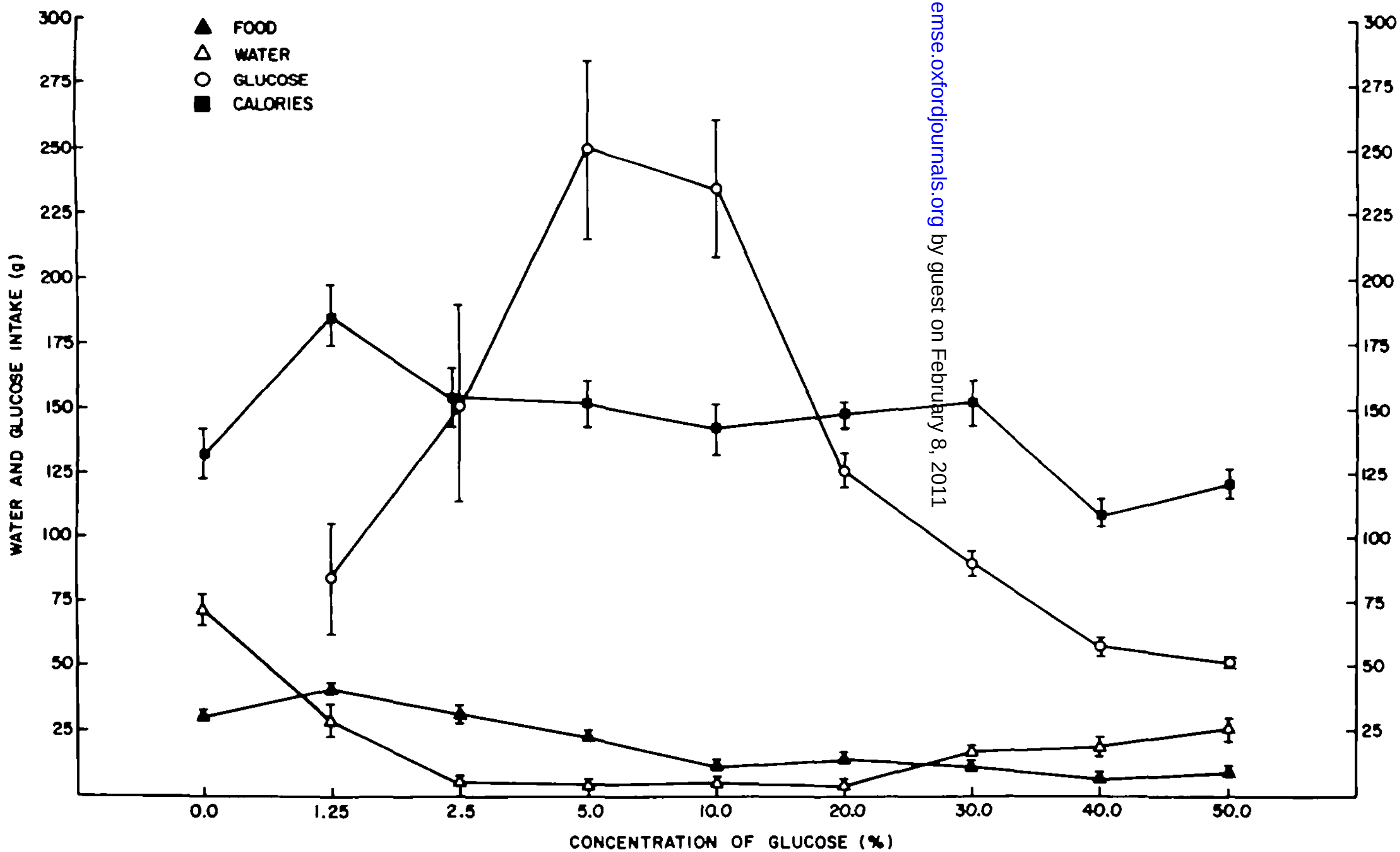

Fig. 2. Average 24 hr intake of various glucose concentrations. Water, food and caloric intake are also shown. (Horizontal bars represent standard error of the mean).

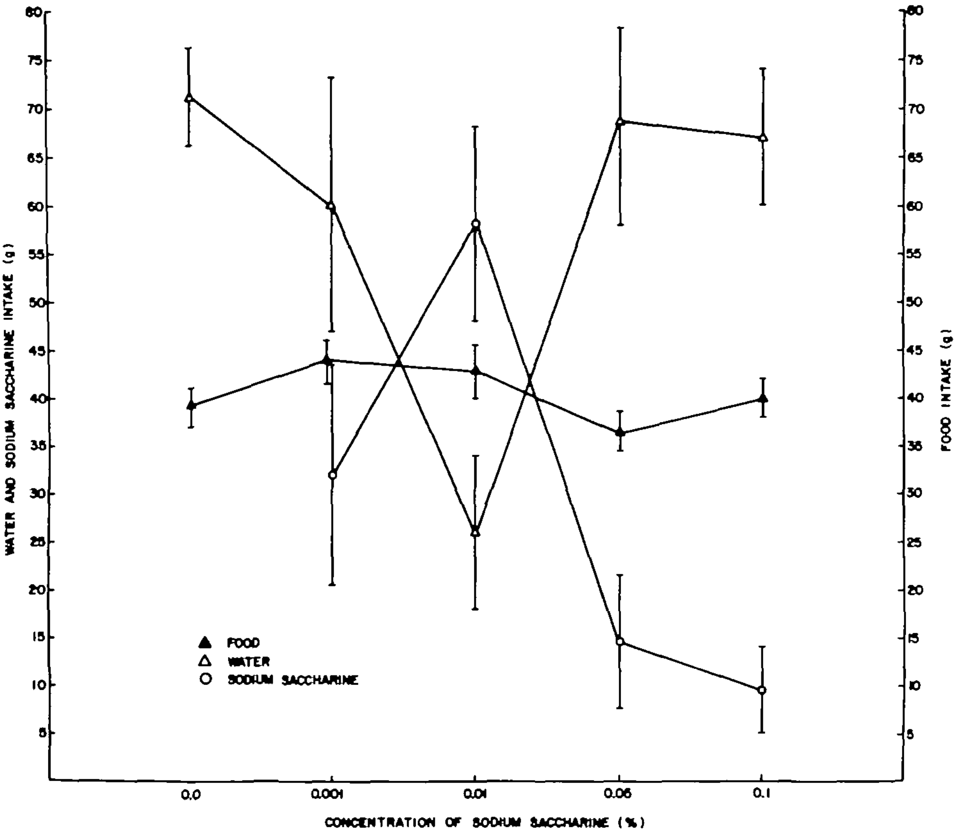

Fig. 3. Average 24 hr intake of various sodium saccharine concentrations. Water and food intake are also shown. (Horizontal bars represent standard error of the mean).

when only water was available in spite of the fact that water intake was depressed at all of the glucose concentrations. The depression of water intake was very conspicuous between 2.5 to 20% glucose. At higher concentrations of glucose, water intake did increase somewhat but was still less than the volume of glucose solution taken even at the 50% concentration.

3.2 Saccharine

Two of the monkeys were very erratic in their response to sodium saccharine. The graph presented in Figure 3 is the average of 4 monkeys only. Sodium saccharine was preferred over water only in the concentration of 0.01%. There was a sharp drop in its intake at concentrations of 0.05% and 0.1%. The food intake and total fluid intake did not show any change with any strength of sodiûm saccharine solution.

To make sure that it was not the acidic pH of the solution which may have made the

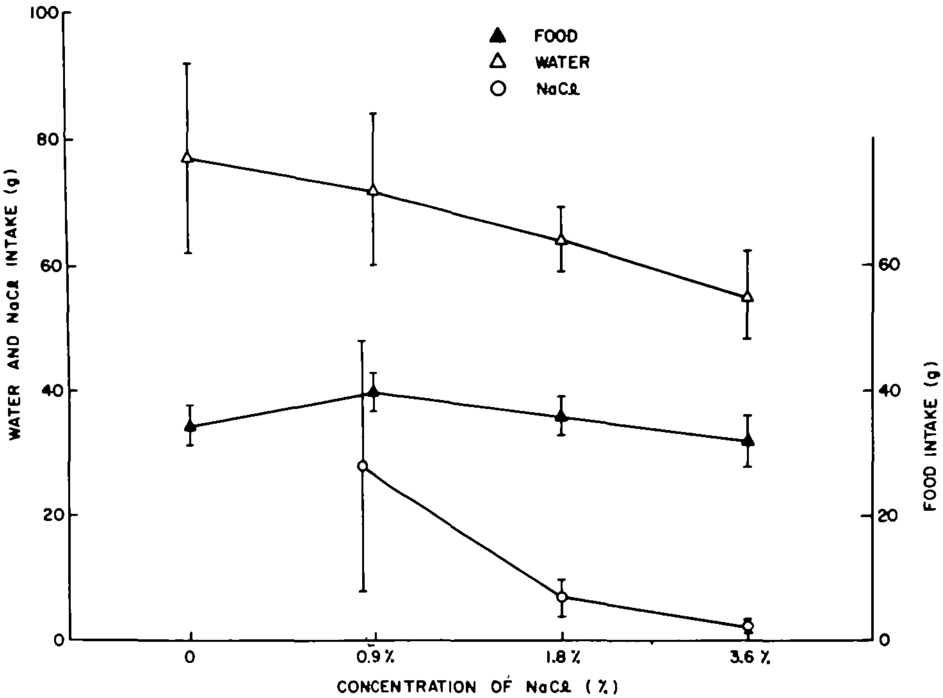

Fig. 4. Average 24 hr intake of various sodium chloride concentrations. Water and food intake are also shown. (Horizontal bars represent standard error of the mean).

intake of sodium saccharine so low, the solution was neutralized by making the solution in a buffered base. This, however, did not change the curve.

3.3 Sodium chloride

Figure 4 represents the average of four monkeys only. Sodium chloride intake was always lower than water intake and decreased to almost nothing at the 3.6% concentration. Total food and fluid intake did not show any appreciable change with sodium chloride concentration.

Two of the monkeys which consumed rather larger and variable amounts of sodium saccharine also took more of sodium chloride even at higher concentrations. Since all other monkeys did not like sodium saccharine and these two took more both of sodium saccharine and sodium chloride, it was felt that perhaps the monkeys were drinking for the sodium salt. Their blood along with all others was, therefore, tested for serum sodium. The results indicated that the mean value of serum sodium in these two monkeys was 121.8 meq/L as compared to the mean value of 141.4 meq/L in the other four monkeys, thus suggesting that the two monkeys might have been drinking the sodium saccharine and sodium chloride solutions in order to compensate for a low level of serum sodium.

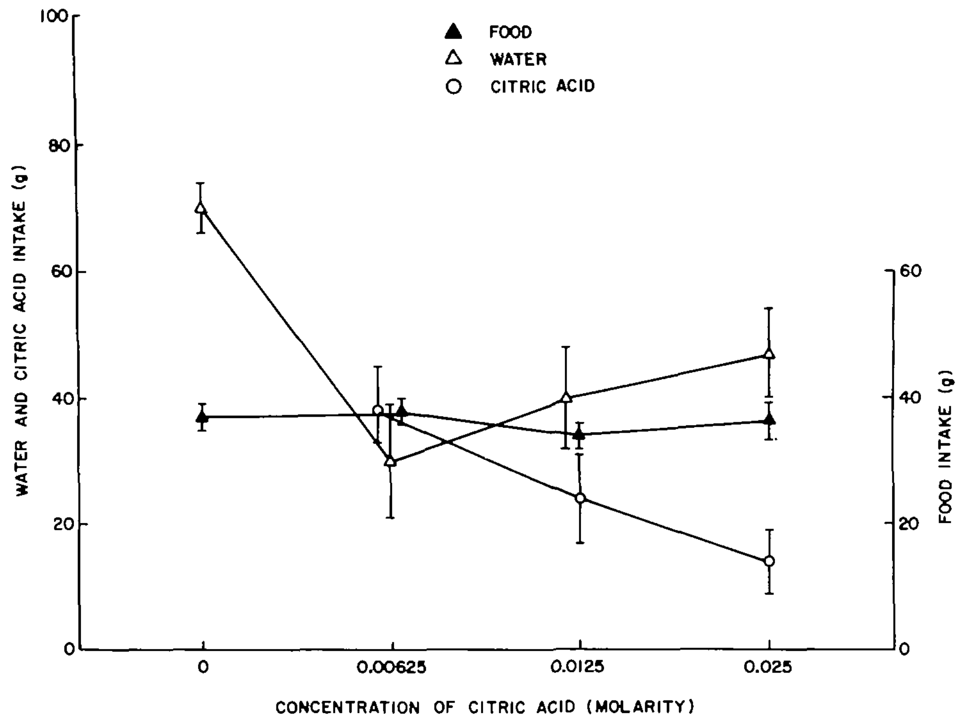

Fig. 5. Average 24 hr intake of various citric acid concentrations. Water and food intake are also shown. (Horizontal bars represent standard error of the mean).

3.4 Citric Acid

The intake of acid solution was less than water at 0.0125 and 0.025 molar concentrations (Figure 5). At 0.00625 *M* concentration, the intake was about the same as water. Total fluid and food intake remained relatively constant across all conditions.

3.5 Quinine and Sucrose Octaacetate (SOA)

Quinine sulfate solutions were preferred over or equally preferred to water at concentrations between 0.001–0.016% with food and total fluid intake showing little change as a function of quinine concentration (Figure 6).

Results for the other bitter solution, sucrose octaacetate, were variable up to 0.008%. There was, however, a definite preference over water for 0.016 and 0.032% concentrations. At 0.064% almost equal amounts of water and SOA solution were taken. No essential change in total fluid or food intake was observed across conditions.

4. Discussion

In wildlife conditions, animals exhibit time feeding habits that vary widely with species

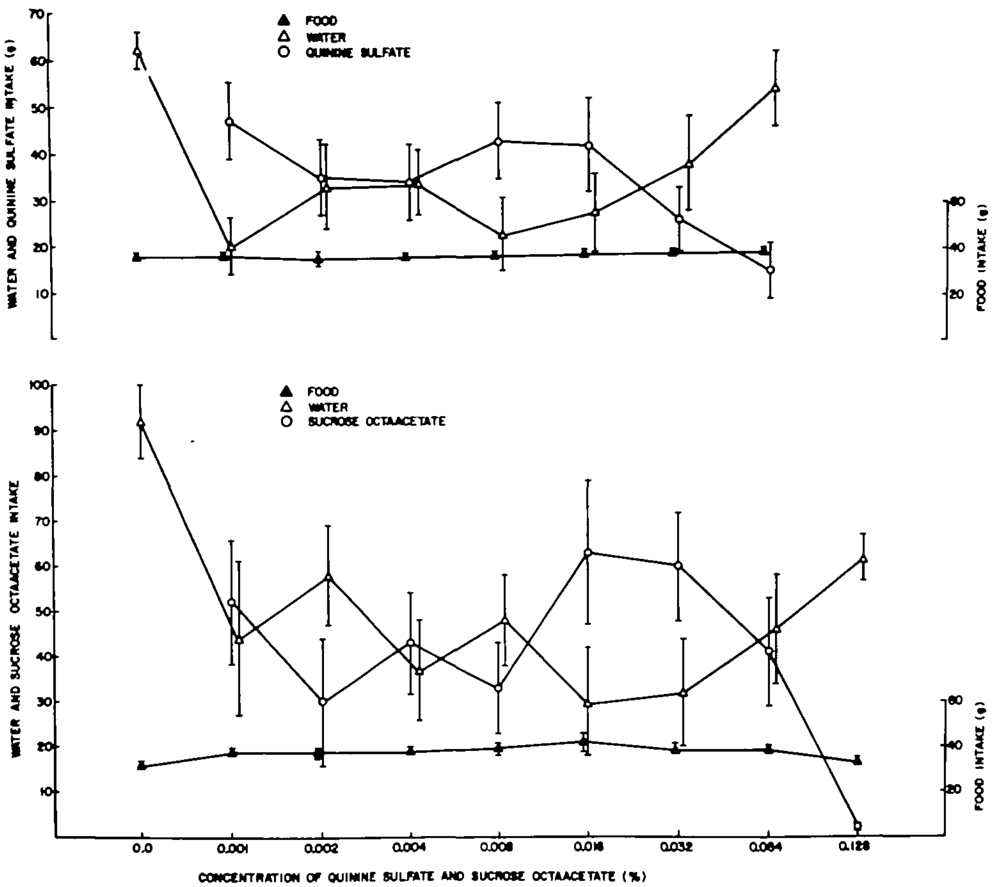

Fig. 6. Average 24 hr intake of quinine sulfate (upper graph) and sucrose octaacetate (lower graph). Water and food intake are also shown. (Horizontal bars represent standard error of the mean).

and are very dependent on ecological factors, availability of the specific foods and modalities of food seeking (Le Magnen, 1967). Depending upon the day–night cycle of feeding activity some animals have been divided into diurnal and nocturnal species. In experimental conditions rat (Bare, 1959; Teitelbaum and Campbell, 1958), mouse (Wiepkema, 1954), and rabbit (Chefillard *et al.*, 1939) are shown to have a day–night feeding cycle and consume 60–80% of their daily intake at night. Squirrel monkeys maintained on *ad lib* feeding under laboratory conditions in the present study consumed about 85% of their water and food during 12 hr day time and only about 15% during the night. These animals thus seem to be diurnal in their feeding habits, preferring to restrict most of their consumption to the day.

The 24 hr water intake of these monkeys was quite variable and averaged 66 g on a typical day. This contrasts with Wuttke (1970), who reported an average daily water intake of 94.3–106.1 ml. However, his three squirrel monkeys were slightly heavier than the monkeys used in the present study and this may partly explain the greater average intake.

The paired-choice 24 hr cumulative-intake method has been used as an index of relative acceptability of various test solutions compared to water. A common criticism of this method is that the 24 hr choice technique does not reflect preferences or aversions that are simply the consequences of the sensory qualities of the solution. Ingestion is influenced substantially by shifts in the water balance of the animal or other post ingestion consequences that occur when solutions of sugar and salts are consumed (Jacobs, 1962; Maller and Hamilton, 1968). It is true that solutions like sugars and salts have post ingestion effects and this may not only change the ratio of solution intake to water intake but may also modify food intake. A substance like quinine, on the other hand, is non-caloric but very bitter in taste. About 20% of the compound appears in the urine unchanged or conjugated with glycuronic acid, and the rest undergoes destruction in the body (Krantz and Carr, 1969). If the animal consumes high concentrations of this taste solution in quantities much more than water or much less than water, without any change in food intake, it would suggest that the animal must be discriminating the solution on the basis of its taste rather than its post ingestional and metabolic consequences. In this sense the intake of certain solutions on a 24 hr basis may in fact be a better indication of acceptability than the short exposure test. This idea is supported by observations on solutions like glucose, where in spite of the caloric need reduction by glucose intake, the animal continues to consume large volumes of glucose solutions. If the animal was only responding to the reinforcing properties of glucose as a substance for caloric need reduction, the intake should have compensated the caloric need only. However, in the present study the monkeys consumed larger volumes of glucose solution, over and above the amount sufficient for caloric compensation, thus indicating that the glucose intake in these cases was being influenced by other factors such as sensory properties or taste. The animal 'liked' the glucose solution and discriminated it on the basis of its taste.

Both behavioral and physiological methods indicate that in the squirrel monkey sucrose is preferred to water at a weaker concentration than fructose or glucose (Pfaffmann, 1974, Ganchrow and Fisher, 1968). Using different concentrations of glucose, Wagner *et al.* (1965) found that the maximal preference was for 20–30% glucose solution in both 10 or 60 min periods. Clark and Harriman's (1969) monkeys indifferently preferred the sugars over water at low concentrations, significantly preferred fructose, glucose and sucrose and not lactose and maltose at intermediate concentrations, and exhibited decrements in preference for fructose, glucose and sucrose and rejected lactose and maltose at higher concentrations. In the present studies, the 24 hr glucose intake was maximal for 5 and 10% solutions. The 24 hr caloric intake was 7–16% higher than in the water alone condition with concentrations varying from 2.5 to 30% glucose. This increase was manifest in spite of the reduction in caloric intake through food. Maller and Hamilton (1968) have reported similar results in rhesus monkeys. Their animals consumed a large percentage of their calories through the sucrose solution as the concentration increased.

An interesting feature of the interaction between glucose and food intake was the potentiating effect of 1.25% glucose solution on food intake. At this concentration, the food intake increased by about 36%. At all other concentrations the food intake decreased, showing decrements with increasing glucose concentrations. The biological implications of this potentiating effect are not quite clear.

Fisher *et al.* (1965) indicated that squirrel monkeys have a strong preference for dulcin and an aversion for sodium saccharine, while rates showed a preference for saccharine but were indifferent to dulcin, and human subjects preferred both the substances. The present results provide further evidence for species differences in taste preference among various animals (Ogawa *et al.,* 1972). The response to saccharine was not monotonic. The squirrel monkeys preferred sodium saccharine at a lower concentration (0.01%) but showed strong aversion to concentrations of 0.05% and above. These results parallel those of Fisher *et al.* (1965) who observed the threshold for sodium saccharine aversion in squirrel monkeys at $5 \times 10^{-4}\,M$ (0.012%) and above in a bar pressing situation. In the case of rhesus monkeys the preference for saccharine has been shown to be below 0.01 *M* but aversion to 0.04 *M* saccharine was obtained (Weiskrantz, 1960).

Of the three concentrations of sodium chloride tested, 4 of the 6 monkeys always took lower amounts of salt solution as compared to water. The other two monkeys, which showed larger and variable intakes of sodium chloride, also consumed larger amounts of sodium saccharine and showed significantly lower serum sodium levels. It is suggested that these two monkeys might have been ingesting both sodium chloride and sodium saccharine solutions for their sodium salt since the phenomenon of specific appetites is well known and has been shown across species. For example, Beilharz *et al.* (1962) showed a large appetite for sodium solution in their sodium deficient sheep. The low serum sodium of the two high intake monkeys lends support to this notion.

Squirrel monkeys did not seem to care much for the acidic solutions. Citric acid in concentration of 0.00625 *M* was taken in equal amount to water but higher concentrations were taken in much less amount. The low intake of oranges in the laboratory was commensurate with this rejection of acidic taste.

Patten and Ruch (1944) found the response to bitter food in the rhesus monkey or chimpanzee to be especially variable and difficult to quantify. The modal rejection threshold was 0.025% for rhesus monkeys and 0.0062% for chimpanzees. In man and rat the rejection thresholds were much lower and were found to be 0.0025 and 0.0003%, respectively. The results of the present study indicate that the rejection threshold for bitter in squirrel monkeys is higher than the values obtained in rhesus monkeys. In fact, at some concentrations the squirrel monkeys even seemed to 'like' the solution in that they consumed more of the quinine sulphate solutions (up to 0.016%) and of the SOA solutions (up to 0.032%) than water. When an animal consistently drinks more of bitter solution than water on a cumulative 24 hr basis, the animal must prefer the bitter and be able to discriminate between the two solutions. These results are rather interesting in view of the small response shown to quinine by most afferent fibers in the squirrel monkey taste nerve (Frank, 1974). It is quite likely that in the squirrel monkey's natural environment bitter foods are common. There is well documented evidence that cinchona tree, from which quinine is extracted, is indigenous to the forests of South America (Rollo, 1975).

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