URGES TO EAT AND DRINK IN RATS

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Studies of nutrition usually depend upon the animal's urges to eat and to drink. But little has been done to find what factors of the diet modify those urges. When body weight is employed as a measure of nutritive state, the observer ordinarily is assuming that intake has been sufficient to supply whatever is available. If weight has been lost he often assumes that the diet is inadequate qualitatively and not quantitatively. To what extent is this confidence in the urges toward maintenance justified?

The following aspects of intake are here investigated: effect of dilution of food by roughage, effect of flavoring, effect of dilution of food by water, forcing of water intake by mixture of water with food, and after-effects of partial or complete privation of food, or of water, or of both. The investigation was designed to ascertain how an animal solves conflicts, and practices priorities, in its bodily maintenance. If it be obliged to ingest an excess of water while obtaining food, how much excess will it take? If more than the requirement of some constituent cannot be avoided, will the total intake be in excess of metabolic uses? In general, how much excess of A in the diet will reduce or stop the intake of B? How are conflicts of metabolisms compromised, and do the urges of intake correspond to a pattern that favors maintenance of the individual, without or with the connivance of the machinery of outputs? By answering such questions, even in part, the physiological organization of the animal body can be partially described. In a general way it is recognized (1) that mammals often gauge intakes according to certain nutritive values, in spite of inequalities of form and substance in various diets. But it is also known that some constituents of food or drink act as deterrents to ingestion, as is illustrated by substitution of sea water for fresh water (2).

The investigation included attempts to induce rats to ingest large quantities of water, simply by mixing the water with the food available to the animals. As a consequence, a general method was worked out of forcing into the metabolism of an animal considerable quantities of various ingested materials that would ordinarily be refused.

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Mixtures of food with roughage. What characteristics of foods may guide rats' food consumption? Are the textbooks correct in suggesting that alimentary fill is a chief requirement of the animal? Male white rats were furnished first with an adequate dry food (chow) ad libitum, then later given the same food thoroughly mixed with a form of roughage (cellulose or kaolin). Water was
separately available. The food consumption and the water consumption were measured in 24-hour periods.

Of a constant sample of food, the consumption was highly uniform. Thus, chow was taken by one individual rat to the extent of 6.1% of the body weight each 24 hours (mean of 94 days), water being available ad libitum. The amount of food taken daily varied in this rat by $\pm 0.65\%$ of the body weight, hence its intake had a coefficient of variation of $\pm 10.7\%$. The variation was no greater among 7 individuals (table 1) than it was in 1, providing male rats of 150 to 300 grams weight were alone considered.

Cellulose. Cellulour is reported (3) to contain no utilizable material, to be 79% cellulose and 17% pentosan. The chow is stated by its manufacturer to contain 4% of crude fiber, 12% of water and 23% of protein.

<table>
<thead>
<tr>
<th>TABLE 1. Intakes of two foods by rats</th>
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<tr>
<td>The same 7 male individuals were given each food for 77 and 114 rat-days, respectively.</td>
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<tr>
<td>Potential energy of food</td>
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<tr>
<td>Food consumed/day</td>
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<tr>
<td>Potential energy consumed/day</td>
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<tr>
<td>Protein consumed/day</td>
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<tr>
<td>Water drunk/day</td>
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<tr>
<td>Water drunk/food consumed</td>
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<tr>
<td>Water content of food</td>
</tr>
<tr>
<td>Water of oxidation + content in food</td>
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<tr>
<td>Total water available</td>
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When the chow was diluted by adding diverse proportions of powdered cellulour to it, the total bulks eaten increased or decreased (fig. 1), depending upon the mixture. Only in the middle range of nutrient proportions (25 to 33% nutrients) was the transition gradual; in others the whole transition was made on the first day of the new diet. The mean quantities eaten varied chiefly with the extent of dilution (fig. 2). If the object of a regime be to force the ingestion of cellulose, the optimal food mixture would evidently be about 33% nutrients. In general, a food mixture furnished to the rat a diminished stimulus to eat bulk whenever the utilizable material was less than 25% of the dry weight. When no nutrient was added to the cellulose, practically none was eaten.

The body weight was maintained only in the richer mixtures of food (fig. 2). At 33% of nutrients or less, the intake of nutrients was clearly inadequate and weight was steadily lost. The loss of weight was at the same rate as when the food intake was limited (in paired feedings) to the amounts of undiluted food actually obtained. It may be supposed that the rat was partially limited by
its alimentary capacity from handling every day more than one-fourth of its body weight of bulk (solids plus water) and one fourteenth of its weight of roughage. But below it will be shown that when the bulk is mainly composed of water, five fold as much total ingesta are taken. Factors other than bulk are believed to participate in limiting the intake.

**Fig. 1.** Daily ad libitum intakes of solids by rats transferred at zero day from chow diet to chow mixed (in various fractions) with powdered cellulose. Each point is the mean of 3 to 5 tests; each line is drawn to fall within the standard error of all the points that belong with it. In this and subsequent graphs each intake is represented at the end of the 24-hour period to which it applies.

**Fig. 2.** Daily intakes of available nutrients, solids, and water, and changes of body weight, in rats maintained on various mixtures of chow and cellulose. Each point is the mean of 12 to 24 days, and the standard errors among these days are represented by the vertical lines.

**Fig. 3.** Daily intakes and changes of body weight in rats maintained on various mixtures of chow and kaolin.

**Fig. 4.** Effect of adding small quantities of flavored nutrients to kaolin, upon the daily acceptance of the kaolin mixture. This figure also amplifies the left-hand portion of figure 3.

There appears to be evidence that in the rat’s alimentary tract some cellulose is decomposed (4). The products of decomposition are not such as to furnish nutrients to the rat, however. The usual assumption is that among mammals only ruminants derive energy from ingested cellulose, since they alone are believed to harbor symbionts that digest cellulose to utilizable sugars.

**Kaolin.** For comparison, another diluent of the food, kaolin, was chosen as one from which no utilization of energy was possible. When diverse mixtures
of chow and kaolin were presented, increased bulks were again eaten. Approximately the same relations of amounts ingested to concentrations of nutrients were found (fig. 3) as for cellulose. Slightly more kaolin was accepted in the region of 15% nutrient and slightly more cellulose at 50% nutrient. But for both the maximal roughage ingested in one day was one-fourteenth of the body weight.

It may be concluded that the proportion of nutrients in a food mixture plays a predominant role in eating, and that cellulose as a non-nutrient is not preferred to clay. Within limits, rats eat for calories.

It is notable that from dilutions of food with roughage, less nutrient material was taken than from undiluted food. To this small degree, bulk of food is a factor. Or it may also be said that only of concentrated food did the rat eat more than it needed for maintenance of body weight. In fact, for the equilibrium of weight a food of low nutrient concentration (50% utilizable) was sufficient. But to increase the body weight a highly concentrated nutrient was apparently required. In natural conditions also it is likely that a rat does not maintain its weight on a food mixture whose nutritive content is less than half. A high fraction of utilizable material is widely understood to be an important factor in edibility and acceptance. The above experiments demonstrate that this factor constitutes a necessity and not a mere preference.

Cellulose as diluent leads to more consumption of water than kaolin does. Probably the cellulose swells as it enters the alimentary tract. With kaolin mixtures the water consumption was linearly related to consumption of nutrients in the same manner as with direct partial privation of food.

It might be supposed that the ingestion of roughage could be increased by previous privation of food. This was not the case. In general, as shown below, rats deprived of food but not of water for 1 to 6 days consumed about the same amount of food per day after privation as they did before privation. So also, when food mixed with roughage, containing 33, 50, or 67% of nutrients, was offered before and after 3 days of privation, no individual ate more in 1 day subsequently than previously. Inanition is not a significant stimulus to subsequent ingestion of more roughage-containing food in the rat.

In numerous instances the rats attempted to scatter the diluted foods from the food cups, whereas they made no attempt to scatter concentrated ones. In the present tests deep jars were used as food cups so that scattering was rarely possible. In deep jars the rats often burrowed through the food mass, churning it over, as though hunting for more concentrated portions within it. Low nutrient concentrations evidently induce overt action in ways other than that of eating more; the action indicates that the low quality of the food is recognized before ingestion.

Flavors. In addition to the factors of bulk and of utilizable nutrients, some factors of taste were tested. Food acceptance of an adequate diet is often believed to depend upon tastes and odors; yet the amounts of an adequate food mixture taken by rats are influenced only to moderate though significant extents by added substances (5). The question in our experiments was: Could a rat be
induced to ingest non-nutrients when they were suitably flavored? Some of the flavoring materials tested had no nutrient value; others contained considerable nutrient. The experiments show that flavors of the first sort (diacetyl, butyric acid) induced no more eating than their absence, though saccharin did lead to a barely significant increase in eating. Hence it seems difficult to fool a rat into accepting a non-nutrient by such means. Flavors that furnished nutrients in small amounts induced eating in close proportion to their nutrient contents (fig. 4), taking chow as the standard of comparison. It is still possible that flavors may make a greater impression where choices among foods are allowed. It is also possible that more impelling flavors will be found.

Kinds of food. Two standard foods were compared, dried whole milk and chow. The two have very different contents of potential energy (table 1), the dried milk yielding 3/2 as much energy per gram of weight as the chow. When the voluntary consumptions of the two foods were compared, the richer in energy was ingested in smaller amount. The Calories actually consumed ad libitum turned out to be slightly greater in the richer food. The water consumed was proportional to the energy supplied by the food eaten. The dried milk is richer by virtue of its higher fat content, the protein representing 21% of the potential energy in milk and 28% in chow. Again it is suggested that the bulk ingested played a moderate role, but that the principal guide to the amount of ingestion was the caloric value.

The transition from one food to the other was characterized by a significant change of body weight. In passing from chow to dried milk, 2.7% of the weight was lost in 24 hours. In passing from milk to chow, 3.8% was gained. The difference between 3.8 and 2.7 corresponded roughly to the daily weight gain on constant diet. The change of weight represents, probably, the increased alimentary fill that prevails on the chow diet, since it remains longer in the alimentary tract.

SUMMARY. Mixing of diverse materials with adequate nutrients is, it appears, a method of forcing the ingestion of substances that are ordinarily refused. In other researches the method has been used incidentally for rats; as an example, Gamble et al. (6, 7) forced urea and various salts, in amounts that constituted up to 18% for sodium chloride and 36% for urea, of the weight of food eaten. In each of these instances the full standard quantity of food as measured in terms of its potential energy was ingested.

The conclusion from the above experiments is that both bulk and nutritive value are factors in food consumption. But a compromise between them is regularly made, according to a pattern that is uniform among many individuals. Satiety makes itself felt both in the alimentary tract and in the metabolizing tissues, and both factors then influence the motor activity of food ingestion.

Mixtures of food with water. A further development in the study of mixtures of non-nutrients with nutrients concerned the dilution of food with water. Would a rat increase its water intake to any lengths in obtaining food? At what point would mixtures be treated by the rat as though they yielded diminishing returns? Would there be any relation between water intake and the capacity for excreting water?
For this study milk fortified with copper, iron and manganese (8) was the sole diet. It was furnished ad libitum either dry (klim), or in blended dilutions of the same, or in equivalent dilutions of a uniform condensed milk (formulac), or of fresh cow's milk. Tap water was always available. Whereas the dried milk was presented in a deep beaker, the liquid milk was furnished in an inverted flask or cylinder with drinking tube. The outlet was usually arranged so that any spilled food did not enter the urine funnel. Care was taken to present the same drinking tube to any one rat each day; the cylinder was refilled with fresh materials each 24 hours and sometimes twice daily. Sodium benzoate (0.2%) also prevented coagulation and separation of the milk which stood at 26°C.

In the first 24 hours on diluted food the rats took nearly, but not quite, as large amounts of it as in subsequent days (fig. 5). They therefore lagged slightly in adjusting to the diluted food. They continued to take uniform amounts for at least 6 days, except that of the lowest dilutions (0 and 0.65% solids) less was taken after the third day. Therefore, only the extreme dilutions offered any progressive discouragement to ingestion. The amounts ingested were accordingly averaged for each entire period of 3 to 6 days.

The amounts of liquid taken by the rats increased progressively with dilution of the food from 30% solids down to 2.6% solids. With further dilution less was taken, and with tap water alone the ingestion was small indeed. Of 2.6% dilution the rats were regularly ingesting more than their own body weights of water every 24 hours.

Correspondingly, the urinary output was greatly augmented by food dilution (fig. 6). In the presence of the dilution that was ingested most copiously, each rat was excreting its body weight of water every 24 hours. Evidently food dilution constituted an easy method of increasing enormously the turnover of water. The greatest output was obtained by furnishing to the rat only 2 to 3% of solids in the food.

The difference between intake of water and output of urine is not an accurate measure of evaporative losses of water, since variable amounts of urine were lost during its collection. On the average the urine collected was 78% of the water ingested. In these tests, water intake appeared to be the sole determiner of urinary output. The concentrations of the urine excreted reflected the great dilution of the excretory substances by the large volumes of water being put out (fig. 7).

If the rat was to obtain the same quantity of nutrients other than water, it would have to double its intake every time the concentration of mixture was halved. It almost did so from mixtures containing 15% to 2.5% of solids. Of smaller concentrations it obtained less and less food, as shown in the upper portion of figure 6.

Nevertheless, the body weight was approximately maintained upon the smaller
caloric intakes down to a concentration of 2.6% of milk solids, though only after a slight loss of weight in the first 2 days. Upon lesser concentrations the body weight was not maintained; the two smallest concentrations yielded little advantage over pure water.

FIG. 5. Daily ad libitum water intakes of rats transferred at zero time from solid milk to eat, plus water to drink, to milk diluted with three different proportions of water. Each point is the mean of 10 tests in the uppermost curve, and of 3 tests in the other 2 curves.

FIG. 6. Daily exchanges of available nutrients, ingested water and urine in rats maintained, each for 3 to 6 days, on various concentrations of milk. A logarithmic scale is used for the concentrations of the food mixture. Free water was always present in addition to the food mixture. Each point is the mean of 18 to 36 days, with its standard error.

FIG. 7. Mean specific gravity of urine in relation to rate of water intake when food (milk) was diluted to various extents.

FIG. 8. Daily intakes of water from three kinds of milk preparations in similar dilutions.

It seemed possible that gradual and progressive dilution of the food with water (set C) would lead to some sort of adjustment in intake and body maintenance. No such adjustment was noticable, however, and the same amounts of liquid food were taken of each concentration as when the rats were suddenly transferred to each of the concentrations (sets A and B). In fact, no simple method was found of modifying the amount of each dilution that the rats accepted.

Body weight did not increase appreciably during the transition from pure
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food to diluted food. Hence the retained water was insufficient to detect in terms of body weight as ascertained at daily intervals. Comparison of three preparations of milk in equal dilutions showed no consistent differences of water intake among them (fig. 8).

Limiting factors. What is the significance of the maximal rate of water intake? Is it feasible for the rat to ingest still more of the dilute food and thereby to maintain its weight? The amount taken might be limited by the alimentary tract, or by the excretory system, among other possibilities. Within the alimentary tract, digestion of the proteins or fats might be limiting, thereby making the nutrients unavailable in dilute foods. Or absorption from the alimentary tract might reach a maximal rate. That absorption of the water was not limiting in the present tests is suggested by the fact that no more diarrhea prevailed when rats ingested diluted milk than when they ingested dried milk.

Table 2. Maximal rates of water exchange in adult rats

<table>
<thead>
<tr>
<th>Maximal water ingestion</th>
<th>% of body weight per hour</th>
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<tbody>
<tr>
<td>Hypophysial injury (Richter)</td>
<td>4.5 (7) 5.0</td>
</tr>
<tr>
<td>Food dilution to 2.6% solids</td>
<td>5.2 (32) 10.0</td>
</tr>
<tr>
<td>First hour after 48-hours' water privation</td>
<td>7.5 (12) 10.1</td>
</tr>
<tr>
<td>First hour after 48-hours' of M/2 NaCl</td>
<td>6.7 (8) 12.4</td>
</tr>
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Maximal water excretion

| Hypophysial injury (Richter) | 3.9 (7) |
| Food dilution | 4.1 (32) 7.5 |
| Water by stomach (Dicker and Heller) | 6.2 |
| Hourly water by stomach (Richter) | 4.2 (4) 5.9 |
| Hourly water by stomach and epinephrine under skin (Gaunt et al.) | 5.1 (14) |

If the excretory system is limiting, then it might be that no faster excretion of water occurs under other circumstances than under the present ones. Richter (9) found that rats exhibiting diabetes insipidus after injury to the hypophysis had a highest continued rate of water intake of 120% of the body weight in 24 hours (table 2). Since rats given excesses of water by stomach tube excreted an average of 101%, and up to 140%, of their weights of collectable urine per 24 hours (though this test did not continue for 24 hours), Richter suggested that the excretory capacity for water was the limiting factor in the water turnover of diabetes insipidus. Rates up to 148% per 24 hours (not continued for 24 hours) have been reported by Dicker and Heller (10). We have sometimes collected 200% of the body weight of urine in 24 hours, the highest recorded being 240%. Even that rate is far below the believed glomerular filtration rate of the rat, which amounts to 500% of the body weight per 24 hours as inferred from inulin clearance (10), a clearance which itself appears not to vary in the rat with rate of water excretion.
Unilateral nephrectomy did not diminish the ingestion or the excretion of water below that of control individuals except to halve the turnover upon the day of operation. Tests of this sort will be described in a later report, together with the small amounts of hypertrophy of the kidneys that are initiated.

It can be concluded that the rate of water turnover in rats is not limited by any single known factor.

A rat maintained on ordinary dry food spends about one-twentieth of its time in eating and drinking. On the mixture containing 2.6% of milk solids, the rat can be observed to spend as much as one-fourth of its time in drinking. The actual ingestion, therefore, comes to be a serious amount of physical activity, even in an animal that has nothing else to do.

Dilution of food by water tells the same story as dilution by non-nutrients. The rat's acceptance is apparently guided for the most part by the nutritive quantities. Its intake of bulk is increased in moderate dilutions. But in high dilutions the compromise with bulk is diminished with the futility of the intake. The qualitative similarity with dilution by roughage prevails in spite of the fact that with roughage the diluent does not pass beyond the alimentary tract, while with water both absorption and urinary excretion of the water are concerned in its disposal.

**Interrelations of food intake and water intake.** The experiments described below were designed to reveal the rat's ingestive responses to a) forcing of concentrated food, b) privation of food for various periods, c) privation of food and water for various periods and d) privation of water for various periods. Remarkably reproducible effects are apparent both during the periods of unusual availability and subsequent to them. They reveal additional features of the rat's regulations of supply.

**Excesses of food.** In a few experiments food was forced upon the rat by stomach tube. The most concentrated food that was used had 38 grams of milk solids in 100 ml. of food. When 90% of the control daily nutrient intake was forced upon 5 rats by stomach tube in two portions during one day, other food was practically refused for the remainder of the 24-hour period. On the two subsequent days, 73 and 84% of the control intake was taken respectively.

The same refusal to eat occurred after forced intake following a day of food privation. The administration of food by stomach tube inhibited the eating, whereas water similarly administered did not affect food consumption.

Administration of foods by intraperitoneal injections was not satisfactory. Concentrated solution of glucose and of protein digests were tolerated only in small amounts, and continuous flows of nutrient solutions would have been necessary if the number of injections was to be reduced to a reasonable standard. Nevertheless, injected nutrients reduced the voluntary intake of food by mouth.

The chief conclusion to be drawn at present from the forced-feeding tests is that the intake of food does not depend upon how much has passed through the mouth. Introduction through a stomach tube or by intraperitoneal injection inhibits a corresponding amount of voluntary ingestion. Plethora inhibits eating for many hours, even when the alimentary tract has not been concerned in the creation of the plethora.
Privation of food. Before the question can be answered as to what guides the rat's intake of food, the sequelae of food privation must be ascertained. Two kinds of privation were imposed on rats, partial or entire. When half as much food was allowed for one day as the 10 rats ordinarily ate ad libitum, the subsequent daily food intake was within 5% of the usual (fig. 9). The same was true after food, but not water, was entirely withdrawn for one day (11 rats). Hence there was no indication that the food deficit created on one day was compensated subsequently. Actually the body weight was regained in both experiments without extra intake, solely by the expedient of smaller expenditures. In 2 rats (fig. 9) the partial food limitation was prolonged to 2 days; again the subsequent food intake was the same as before privation, yet body weight was fully

Fig. 9. Food intake was limited to half the voluntary intake in 10 rats for 1 day, and in 2 rats for 2 days. Then both food (F) and water (W) were allowed ad libitum. Mean intakes and standard errors are indicated at the end of each 24-hour period.

Fig. 10. Body weights and ad libitum intakes of food (dash lines) and water (solid lines) in rats deprived of all food and water for 1, 2, 4 or 6 days.

Fig. 11. Daily exchanges of total substance (solids and water) in 4 days of total privation of both food and water and 3 days of recovery upon a regime of unlimited food and water. Mean of 7 rats.

Fig. 12. Body weights and daily intakes in 3 rats which, starting on day 7, for 23 days were allowed half their initial daily intakes of water. Straight broken lines indicate expected values that might have intervened if water intake had not been restricted.
regained. Prolongation of complete food privation to 6 days made no difference in subsequent intake; after prolongation to 7 days the rats failed to eat much and died from delayed effects of the inanition.

Limitation of food intake that was voluntary, as a result of low proportion of nutrients in the cellulose-rich mixtures described above, also resulted in little extra food intake when concentrated food was subsequently made available. Evidently the marked deficits of nutrient intakes consistently aroused no compensatory intakes of significant extra amounts of straight food.

Rather similar results prevailed when water as well as food was denied (fig. 10), but differing in certain details. After this total privation for only one day, 40% extra food was taken as compared with the control period. No greater excess of food was taken after total privation of any longer duration. The intake of 40% extra food differs by a significant amount from the intake after one day's privation of food only, as indicated in the previous paragraph.

From the changes of body weight each day and from the measured intakes, one can compute the total losses (fig. 11). During 4 days of total privation, the losses were greatly reduced. By continuing the reduced rates of loss for one subsequent day upon which full intake was resumed, rats secured nearly all the recovery from inanition that ever occurred. A food deficit was never paid off by subsequent over-consumption.

We conclude that previous privation of food is little or no stimulus to eating. If we call the rat's state one of hunger, then over a 24-hour period hunger does not much augment the animal's intake of food. Though the body be deficient in weight, that weight is restored only slowly through the device of utilizing new food more economically.

Another aspect of this economy was illustrated by Forbes et al. (11) who measured the oxygen consumption of rats that were ingesting food at 0, ½, 2, and 1 of their usual voluntary intake. Those on half food almost succeeded in maintaining themselves in energy, for they utilized a larger percentage of the food eaten and expended only 27% more energy than they ate. Those on 2 food expended only 2% more energy than they ingested. Those on full diet used most of the additional utilizable food in extra combustions. Hence a rat has a large margin of dispensable metabolism below what it ordinarily employs upon an ad libitum diet.

Great generalizations cannot be made about the response among species to previous privation of food. In caged dogs the intake was augmented during recovery so that little or no deficiency of intake remained (12, p. 324). Instead the food debt was fully paid off. In rabbits an intermediate situation prevailed (13); in recovery they resembled rats more than dogs.

Water availability. When water was denied rats, the amount of food ingested was greatly reduced. The denial was either partial or total.

In one experiment 3 rats were kept for 23 days upon half of their original ad libitum water intake (fig. 12). A new and lower rate of food intake was then set by them, amounting to 75% of the original. Body weight was lost in the first week, but thereafter was slowly regained. Upon restoration of water in-
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take ad libitum, the food intake as well as the water intake was markedly increased for 5 days, the food ingestion upon the second day attaining 143% of the original ad libitum rate. But whereas 88 grams of food were missed by each rat during the period of limitation, only 10 grams extra were eaten subsequently, which was less than one control day’s intake. Similarly only 23% of the missed water was taken in excess during the recovery. After the water limitation the rats approached but did not attain the meanwhile augmented body weights of control individuals.

More severe self-denial of food was reported by Asher and Hodes (14) in young rats given only one-fourth or one-eight of the usual water intake. Their results and ours are in accord.

When entirely deprived of water, the food intake diminished progressively (fig. 13). After the third day it was less than one-tenth of the original. This

![Fig. 13. Ad libitum intakes of food (dash lines) and water (solid lines) in rats deprived of all water for 1, 2, 4 or 6 days.](http://ajplegacy.physiology.org/)

![Fig. 14. Relation of change in body weight to intake of nutrients by rats. The data are derived from figure 2. Intake was limited by direct partial denial of food in only one of the four series. Water was always available ad libitum.](http://ajplegacy.physiology.org/)

self-denial of food effectively conserved body water, of course. When water was again furnished, only a small excess of water was ingested. This over-all limitation of water ingestion is comparable to the voluntary dehydration that we have described in man. By it the rat economizes in its water requirement. In contrast, a dog economizes very little, since it subsequently drinks most of what it has missed (15); and a man does not economize appreciably in his over-all consumption. To some extent these species differences are related to food intakes during water privation and to body sizes.

When water was given to rats after water privation, moderate excesses of food were eaten; but few exceeded by 40% their original food intakes, and none compensated for all the food self-denied. Water privation thus led to reduced intake of food. This food reduction may be responsible for the moderate amounts of overeating in the recovery period when water was again available in unlimited quantities. Yet, curiously, water privation led to subsequent overeating with
much greater certainty than did food privation per se. It is particularly difficult to emphasize any one accompanying difference, since privation of either food or water led to self-denial of the other. Partial privation of food led to no over-eating during recovery, yet the partial self-denial of food that accompanied total privation of water did.

Self-denial of food in proportion to the allowed water intake was reciprocated when limitation of food intake was imposed. Both situations illustrate the tendency of intakes to be relative to one another. The animal's urges to eat and to drink result in an approximate preservation of proportions in its bodily contents. Only when intakes are not limited by the experimenter does inherent volume control express itself. The tendency to proportionality among intakes is also widely found when other constituents of the diet, such as an amino acid or a vitamin, are unavailable; the consumption of all other food items is proportionately self-denied.

Excesses of water intake led to no extra intake of food (fig. 7), even in mixtures of the two in which it would be easy for the rat to ingest extra nutrient in the form of the mixture. Numerous further experiments were done in which water was forced upon the rats, either by stomach tube or by intraperitoneal injection. In those experiments the intake of food over periods of 24 hours was not modified. Of course, in them the excessive water was eliminated by diuresis lasting about 4 hours, leaving 20 hours of the period free of its influence. In contrast to the forcing of food by stomach tube, which inhibited eating for many hours, the forcing of water by stomach tube did not interrupt the periodic ingestion of food.

**Comment.** Food acceptance and the urge to eat in rats are found to have relatively little to do with a 'local condition of the gastrointestinal canal,' little to do with the 'organs of taste,' and very much to do with quantitative deficiencies of currently metabolized materials. It would be satisfying to know how these deficiencies act in the neuromuscular system that carries out the ingestion. At present there is no sure knowledge of particular sensory areas or afferent pathways. It may be remembered that all kinds of animals have urges to eat, but few have any one pattern of structures.

Evidently the urges to eat form a system of reciprocal relationships among many functions of tissues and organism. Each urge is a resultant of factors whose study, one at a time, is but the beginning of an adequate description. Yet the urges are sufficiently fixed so that the variability of ordinary food intake (± 10% among daily periods) is one of the smallest of physiological variabilities, and so that every rat regularly maintains its body weight or increases it slightly each day. Further, the rat returns to its standard intake after each denial of food. The facility and precision with which the organism balances its intake and its output are widely assumed; the assumption needs analytical investigation.

No one characteristic of food guides the rat's intake of it. The investigator gains the feeling that some complex of internal compositions intermittently drives the animal to eat so that some resultant concentration or stimulus is kept just above or below a threshold value. The intake of nutrients may be decreased
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by modifying circumstances, but the intake of non-nutrients alone can be increased by changing the composition of the food.

The experiments show how an animal solves several dilemmas that affect the maintenance of its body. In acquiring food, the rat was forced to accept too much roughage or too much water. According to the pattern that was found in these experiments, the rat accepted too much water with little reduction in its caloric intake, until only 2% of its intake was solids and 98% of its intake was water. Thereafter, the weak mixture appeared to furnish diminishing returns from its intake.

When cellulose or kaolin diluted the food, the dilemma was solved by a compromise of a different order. The animal ingested more bulk but stopped before it had ingested a full quota of nutrients. The limited ability to handle roughage in the alimentary tract then became a factor in the animal's urges to eat.

The daily increment of body weight was uniformly related to the potential energy of the food ingested, whether the ingestion was limited by partial privation of nutrients of by offering ad libitum the prepared mixtures of food with cellulose, kaolin or water (fig. 14). The several compromises among physiological components can be expressed as ratios of the excessive intake to the deficient bodily constitution; but none of the other factors studied here actually yield constant ratios.

Ordinarily the urge to eat appears to be governed to a large extent in accordance with the potential energy of adequate food. This fact was shown in the comparison of two concentrated foods of unequal bulk, and in the inhibition of eating when the food had been introduced by a route other than the mouth. But when the animal had been deprived of food either partially or entirely, almost nothing was done to pay back the deficit of food that had been contracted. In the rat (but not in some other species), no prolonged urge to eat resulted from the previous privation. A new sort of adjustment was then manifested, an adjustment between intake and output. Body weight was largely recovered by diminishing the outputs of substance instead of by increasing the intakes. No one had guessed that this dilemma would be solved by such a method. Physical activities were correspondingly reduced, conserving energy.

The ingestion of water that is forced upon the rat by mixing milk with water furnishes a simple technique for securing steady ingestion and excretion. Antidiuretics may be assayed in such rats. Correspondingly, antiposics (agents that inhibit water-drinking) may be identified and assayed in such animals.

The water intake was greatly modified by food intake. Intake of dry nutrients was reduced by two procedures, by diluting the nutrients with kaolin and by limitation of amount of food. In both, the ad libitum intake of water was correspondingly reduced; it bore approximately the same quantitative relation to potential energy of the food that was found in the rats of Strominger (16, fig. 3) which were given artificially limited allowances of food.

The rat would ingest much extra water in obtaining its daily quota of food; but it did not ingest excesses of dry food as a means of obtaining the water that was in it or potentially obtainable by oxidation of it. The physiologist knows
that excess of food would dehydrate the rat still further, for water is extracted from tissues by the metabolic products of the food that become available for excretion. The rat without that knowledge still has a pattern of appetites that seems appropriate in the light of the knowledge.

Most dietary experiments imply the assumption that the animal consumes as much of the available food mixture as will improve the animal's nutritive status. Trust is placed in paired feeding as the sole control procedure. The experimenter has no information as to whether or not forced feeding would change the status in one direction or another. The urges to eat must, therefore, be distinguished from the abilities to utilize the nutrients; each requires its own investigation, as is well recognized in studies of human food acceptance.

It seems evident that the regulation of food intake is under many influences. While it receives precedence over many activities of the rat, yet it is also inhibited by some. While intake looks like a simple problem in alimentation when the animal is kept in a sufficiently simplified situation, the animal has a full pattern of priorities and compromises that also solves situations of great complexity. All animals that have been studied, those without alimentary tracts as well as those which have, recognize food, spurn food when it is superabundant, and put forth extra efforts to get it when it is rare. Hence, whatever be the machinery that may fix the pattern of priorities in rats, comparable patterns seem to be endowments of all animals, whether or not they possess specialized neuromuscular or alimentary systems.

SUMMARY

1. Albino rats were furnished food that was mixed with some proportion of cellulose, kaolin or water. In most mixtures the total bulk eaten exceeded considerably the bulk of concentrated food consumed in control periods. The quantity of utilizable nutrients ingested did not exceed that in control periods.

2. In this manner rats were regularly induced to ingest roughages to the mean extent of 8% of their body weights per day, and water up to 125% per day. In the presence of roughages, a compromise was effected between an excessive amount of alimentary fill and a diminished amount of nutrients that depended upon the mixture available. In the presence of water, the upper limit to ingestion was probably not fixed by the maximal rate at which water could be excreted through the kidneys.

3. A variety of flavorings and nutrients in small concentrations did not induce rats to consume greater amounts of roughages.

4. The relations between food intake and water intake were also investigated by limiting the available amounts of one or the other. The intake of the unlimited item (food or water) was regularly reduced but not so greatly as that of the limited item.

5. After complete privation either of food or of water or of both for 1 to 6 days, body weight was subsequently slowly restored with the consumption of very small excesses. Deficits of intake were not paid off; instead, the outputs were reduced for a day or two. Recovery itself was also compromised in such a
manner that animals temporarily deprived did not catch up to the body weights of those not deprived.

6. Patterns of ingestion and excretion were manifested that showed the coordinations among the several factors of turnover. Not only was water ingestion tempered to excretory capacities, but also water ingestion to food ingestion, and food ingestion to absorptive and roughage-handling capacities. These patterns are items in a large complex of regulatory activities concerned in bodily maintenance.

REFERENCES

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