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APPETITE, PALATABILITY AND FEEDING HABIT: A CRITICAL REVIEW[1]

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In 1941 the writer (64) published a critical review of researches upon appetite. Since that date the investigation of problems relating to food acceptance has developed rapidly. Again he wishes to survey experimental studies and to bring his own work into relation with that of others.

Some General References

Experimental methods and results in the study of food habits have been reviewed and a useful bibliography compiled by Dr. Patricia Woodward for the Committee on Food Habits of the National Research Council (78). The principles and theories underlying Richter's work have been generalized in several papers (45, 46, 47, 48). The work of the Food Acceptance Laboratory of the Quartermaster Food and Container Institute at Chicago has been described in a recent paper by Dove (19). From the point of view of food technology the book by Crocker (10) is of general interest. The previous review by the writer (64) contains references to some of the earlier studies and his text (65, p. 125) presents a general statement upon bodily need and appetite. The chapter on bodily needs in Morgan's *Physiological Psychology* (35, p. 437) contains a very clear statement of the facts relating to bodily needs and specific hungers and some useful references.

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Bodily Needs and Homeostasis

Dietary Requirements

A useful summary of the dietary requirements of laboratory animals can be found in Loosli (29). He has listed these requirements under the following headings: protein and amino acids, fat, vitamin A and carotene, vitamin D, vitamin E, thiamine, riboflavin, pantothenic acid, pyridoxine, biotin, niacin, vitamin K, choline, ascorbic acid, other vitamins (not yet isolated), calcium and phosphorus, magnesium, manganese, iron and copper, potassium, sodium and chlorine, cobalt, zinc, and iodine. Water and oxygen are omitted from the list probably because too obvious to mention. A similar summary has been made by McCoy (30).

It is of interest to inquire what a nutritionist means when he states that a rat *needs* a particular substance. The answer is fairly simple and might be illustrated many times over from the literature: Every nutritional need is defined in terms of the symptoms or syndrome resulting from a specific deficiency in the diet. One could readily tabulate the various metabolic disturbances and the deficiency diseases which result from withholding one or another of the essential dietary elements. Such a tabulation, however, would be mainly of nutritional rather than psychological interest.

Here is a single illustration: We read that vitamin A is essential for all mammals, that it is important for growth, for normal vision and the maintenance of normal epithelial tissues. Vitamin A deficiency results in keratinization of epithelia, a disturbance of bone growth, sterility and cessation of growth, and, importantly, in night blindness. Vitamin A plays an essential rôle in the metabolism of visual purple. A deficiency, in addition to producing night blindness, may result in a structural breakdown of the retina itself.

In human nutrition the deficiency conditions are commonly described by reference to the symptoms or diseases produced by the want. The vitamins are often described in terms of what they prevent (20). Thus vitamin A is antixerophthalmic and antiinfective; vitamin B_1 is antiberiberi and antineuritic; vitamin C is antiscorbutic; vitamin D is antirachitic; vitamin E is antisterility; vitamin B_2 is antipellagric and antidermatitic.

Discussion of such deficiency conditions usually contains a statement of the minimum daily intake of a substance required to prevent the appearance of the symptoms of deficiency. Thus, in discussing the need for thiamine, Loosli states that this need is shown by the deficiency in the metabolism of carbohydrate; there is polyneuritis, cardiac

dysfunction, muscular atrophy and anorexia. One of the studies indicates that 10 micrograms of thiamine per day will cure the polyneuritis and permit satisfactory growth of rats but normal lactation requires a minimum daily intake of 120 micrograms.

Now the vast literature in the field of nutrition is interesting and important for its own sake—but it is not psychology. The nutritionist, being both a physiologist and a biochemist, thinks objectively in terms of growth, reproduction, and a host of developmental abnormalities which result from dietary deficiencies. The developmental abnormalities however, often have very definite behavioral manifestations.

In the past few years, to illustrate, psychological studies have been made upon the effects of amino acid deficiency on the behavior of the rat (**52**), the effect of vitamin B_1 deficiency on the conditioning of eyelid responses in the rat (**6**), convulsive seizures associated with pyridoxine deficiency (**37**), effects of excess glutamic acid on learning in the rat (**32**, **77**), spontaneous activity in relation to the diet (**55**).

Animals, in general, exhibit changes in the level of activity when in want of food. Nutritional deprivation is usually shown by a rising level of activity as it is also shown by a decline in weight. Although high running is a typical sign of want, it is not an invariable sign. Wald and Jackson (**59**) have shown that with the deprivation of magnesium in the rat there is a lowering of the level of general activity. After 1 to 2 weeks of magnesium deprivation running declines to a very low level. Magnesium, therefore, is one indispensable component of the diet the lack of which does not stimulate increased activity. The same appears to be true, Wald and Jackson state, for the deprivation in total inorganic ions, and in vitamin A. Apparently, then, if changes in the activity level are ruled out, there remains no single behavioral manifestation of metabolic need, no invariable and dependable sign of need in behavior.

At present there is a fairly large and growing literature upon the psychological manifestations of bodily need. This kind of work, obviously, should be carried on in close collaboration with the nutritionist or biochemist.

Bodily Need and Homeostasis

In his Harvey lecture Richter (**46**) developed the thesis that the behavior of the total organism contributes to the maintenance of a constant internal environment, or homeostasis. The thesis is illustrated by numerous examples:

> If the parathyroid glands are surgically removed, rats develop tetany and die within a few days. When parathyroidectomized rats are given free access to a solution of calcium lactate they ingest large quantities of it, keep themselves free from the symptoms of tetany and survive indefinitely. Along with in-

creased calcium intake there is simultaneous decrease in the intake of phosphorus. If parathyroidectomized rats are forced to ingest a high phosphorus diet the mortality is 100 percent but when given a choice they select a low phosphorus diet and survive indefinitely (50).

Again, if the posterior lobe of the hypophysis is removed, there is general dehydration due to loss of an anti-diuretic hormone. The rats compensate for the loss of water by drinking large amounts.

If a toxic substance, such as mercuric chloride, is presented in threshold concentrations of 0.001 to 0.003 percent, the rats reject it and select distilled water even though the total amount of the drug is too small to have any detectable physiological effect.

Adrenalectomized rats ingest quantities of sodium and survive indefinitely. This, Richter believes, is due to chemical changes within the taste buds. When the taste nerves are sectioned adrenalectomized rats no longer increase their intake of sodium and as a consequence they die just as they would have done without access to the sodium chloride. (Work upon adrenalectomy is considered below.)

In general, these and other illustrations show that the behavior of rats is an aid in maintaining a stable *milieu interne.* The drive to maintain internal balance, Richter argues, is one of the most powerful of the biological urges.

Richter's theory is important because, if it is correct, the appetites of laboratory animals can be used in the experimental study of bodily needs. The self-selection method has been employed, in fact, in studies of metabolism as related to endocrine function. It has been used to investigate changes of intake in relation to pregnancy and lactation, age, gustatory function, and other processes. Self-selection feeding has been tried with success upon the human infant.

Nutritive Instincts

Is there a nutritive instinct or group of instincts?

In an interesting discussion Remington (39), a nutritionist, has denied that man has any instinct which enables him to select a diet according to his needs. The likes and dislikes of man, he states, are not a dependable guide in the selection of a diet. In a positive and vigorous way Remington points out that the foods which man eats are dependent upon the geographical region in which he resides. The soil and the climate determine what can and cannot be obtained for food. Man of necessity eats what he is able to find in his environment. Further, religious customs and taboos regulate the acceptance of food and determine the manner of its preparation. In modern times Remington continues, economic factors are of basic importance in determining what an individual can and cannot obtain as food. Another determinant is propaganda, in the form of advertising, which builds up attitudes of ac-

ceptance or rejection toward foodstuffs. Thus geographic, economic, and social factors regulate the feeding processes of man. Remington remarks wistfully that up to the present time our knowledge of chemistry, physiology and the science of nutrition has played a relatively minor rôle in directing the eating habits of the human species.

A somewhat different view is that of Dove (11) who has emphasized gene-determined individual differences in the ability to select foods wisely. When given the same choice among several foods some chicks appear to select and balance their diet wisely, as indicated by growth and reproduction, and other individuals appear to be less wise in their choice. The same is true of dairy cattle, laboratory rats, and other animals.

Dove (14) coined the phrase "aggridant type" to designate the nutritionally superior type of individual within a group. The aggridant type is characterized by superiority in physical form and size, rate of reproduction, longevity, efficiency in the use of foods and consistency in reaction. By preparing dietary mixtures for the group as a whole according to the pattern of foods selected by the aggridant type, Dove (13) reports that he was able to produce growth as much as 30 per cent above the standard. He believes (12) that the food selections of the aggridant type are useful in providing an optimal environment because these choices have been shown to be nutritionally wise.

Young has consistently stressed the uniformity and consistency of food selections by laboratory rats. Instead of lawlessness and chance the analysis of food acceptance reveals exact quantitative relationships. Consistent individual differences in food acceptance, however, have been observed (73) and at the present time no explanation of them is possible.

The work of Blakeslee (7, 54) upon the genetics of gustatory thresholds suggests that innate differences in sensory structures, especially in the senses of taste, smell, and touch, may explain why some individuals select food wisely and others do so less wisely.

Dependence of Food Acceptance upon the Organic State

Adrenalectomy and the Appetite for Sodium

As noted above, an increased intake of sodium by adrenalectomized rats has been used by Richter to illustrate the wisdom of the body in the area of food selection. Inasmuch as considerable evidence is available, a more detailed examination of the facts will be profitable.

Increased intake of sodium chloride by adrenalectomized rats has been reported by Richter (41, 44), Richter and Eckert (49), Mark (31),

Clark and Clausen (**9**), and others. Richter has shown that when adrenalectomized rats are maintained upon a salt-low diet they die but when given opportunity to choose between water and a 3 percent solution of sodium chloride they select the latter, ingesting six or more times the normal amount of sodium chloride, and they survive indefinitely.

Mark (**31**) reported that the treatment of adrenalectomized rats with desoxycorticosterone acetate (synthetic adrenocortical hormone) decreased their intake of sodium chloride to normal levels. Then Rice and Richter (**40**) observed that the treatment of normal rats with desoxycorticosterone acetate resulted in an approximately 7-fold increase in the intake of 3 percent sodium chloride. Presumably, they argued, the drug created an increased *need* for salt and this resulted in an increased *appetite*. The polydipsia which the treated animals revealed was regarded as a secondary effect.

Not only do adrenalectomized rats ingest more salt than normals but, according to Richter, their sensitivity to salt is greatly increased. Richter (**42**) has reported that the salt taste threshold is lowered by adrenalectomy. A group of 20 normal rats revealed an average salt taste threshold of 0.055 percent; a group of 8 adrenalectomized rats had a salt taste threshold of 0.003 percent. The adrenalectomized rats showed a sensitivity to salt offered in amounts which could not possibly have a beneficial physiological effect and, "The results indicate that adrenalectomized rats ingest more salt, not because they learn that salt relieves their deficiency discomforts, but because of chemical changes in the taste mechanisms in the oral cavity, giving rise to an enhanced salt discrimination."

That the taste mechanisms are primarily involved can be shown by sectioning of the taste nerves. After cutting the glossopharyngeal nerve and the lingual branches of the trigeminal (including the chorda tympani) rats no longer were able to recognize the difference between water and salt solutions. When this operation was performed on adrenalectomized rats the section of the lingual nerve resulted in death with a mortality rate of 100 percent (**43**).

The study of salt ingestion of adrenalectomized rats has been carried forward in two (as yet unpublished) doctoral investigations.

1. Bare (**3**), at Brown University, confirmed Richter's result that the preferential salt threshold of adrenalectomized rats is lower than that of normal animals. Bare's normal rats revealed a preferential salt taste threshold of about 0.060 percent and his adrenalectomized rats a threshold of about 0.016 percent.

Bare drew an important distinction, however, between the absolute *sensory* threshold and the relative *preferential* threshold. Following the technique of

Pfaffmann (38), Bare cut the chorda tympani nerve in the anesthetized rat. The nerve was lifted onto a pair of moist-wick electrodes. Potentials from the cut nerve were amplified and reproduced on a cathode-ray oscilloscope and a loud speaker, making it possible both to see and to hear the impulses. The activity on the face of the oscilloscope was photographed with a movie camera to obtain a permanent record. The rat, placed in a shielded cage with tongue protruded, was stimulated by one drop of stimulus solution at constant temperature. Action currents produced by the stimulation were observed and recorded.

When tested with this technique normal rats responded to solutions of sodium chloride with concentrations of 0.007 to 0.009 percent (average 0.008). Adrenalectomized rats responded to concentrations of 0.005 to 0.017 percent (average 0.010). Although the adrenalectomized rats were somewhat more variable than normals, their absolute gustatory thresholds, as tested with the electrophysiological method, were not significantly different.

The preferential salt taste thresholds of adrenalectomized rats, however, were lower than those of normal animals. The interpretation of this fact is uncertain. It may be, in the light of the findings of Richter and MacLean (51) with human subjects, that the preferential threshold corresponds to a concentration at which the solution first tastes salty. Human subjects recognize a *difference* in taste between distilled water and very weak salt solutions at concentrations lower than those which yield a salty taste. Richter believes that rats make a preferential selection of salt solutions at concentrations which first yield a salty taste.

Since rats cannot make introspective reports, it is difficult to determine the concentration which first yields a taste of salt. There may be some other explanation of the lowering of the preferential threshold in adrenalectomized rats.

In any event, Bare is entirely correct in pointing to the difference between sensory and preferential thresholds. If a rat discriminates preferentially between two solutions, we can assume that sensory discrimination between them is possible. If he fails to discriminate preferentially, we are still in the dark concerning the sensory threshold. Under other motivational conditions the rat might make a discrimination.

2. The second doctoral investigation, taking its point of departure from Richter's work, is that of Chaplin (8, 76) at the University of Illinois. Chaplin was interested in the preferential selections of adrenalectomized rats among salt solutions of different concentrations.

Chaplin maintained groups of rats upon a complete self-selection diet. In each cafeteria cage he presented either a single 3 percent solution of sodium chloride or a group of 8 solutions of these concentrations: 0.1, 0.2, 0.4, 0.7, 1.5, 3.0, 6.0, 12.0 percent. The average daily intake of each solution was measured both for normal and for adrenalectomized rats.

Chaplin found that there was a marked preference for the solution with a concentration of 0.7 percent which, incidentally, agrees with a result reported by Nelson (36). When sodium chloride was obtainable at a concentration of 0.7 percent the rats ingested from 62 to 82 percent of their total sodium chloride from this solution alone. If we assume, with Richter, that the intake at 3 percent concentration indicates bodily needs, then the rats ingested from one

and a half to three and a half times as much salt as they needed when the optimal concentration (approximately 0.7 percent) of solution was available.

Strikingly, however, the optimal concentration for the acceptance of salt was the same for pre-operative and post-operative rats and the optimal concentration was the same as that found in another experiment upon normal animals (74). Chaplin had expected that adrenalectomy might lead the animals to prefer saltier solutions but this was found not to be the case.

The experiment differs from threshold studies in that there was at no time a need for salt. The rats, both before and after adrenalectomy, had unlimited access to salt solutions. Under these conditions, incidentally, the adrenalectomized rats were able to survive indefinitely and in seemingly good health and activity.

The diet employed in Chaplin's experiment contained two sources of sodium: sodium chloride and sodium phosphate. The results indicated an inverse relationship between the intake of these two minerals. When sodium chloride was available at the optimal or near-optimal concentration (0.7 percent) the intake of this solution was at a high level and simultaneously the intake of sodium phosphate was at a low level. When sodium chloride was presented at a single 3 percent concentration less sodium chloride was ingested but the intake of sodium phosphate was heightened. The inverse relation between the intake of sodium chloride and sodium phosphate was observed with both normal and adrenalectomized rats. The result recalls the finding of Richter and Eckert (49) that there is an appetite for sodium rather than for chlorine.

Chaplin's demonstration that the intake of sodium chloride varies with the concentration of solution, both with normal and adrenalectomized rats, reveals an important distinction. Intake is dependent both upon the organic state (functioning of the adrenal gland) and upon the external characteristics of the food stimulus (concentration of solution). One can argue that rats take what they *need* to maintain homeostasis. One can also argue that rats take what they *like* (find palatable) regardless of need.

Sickness and Health

References to anorexia and parorexia are widely scattered through the medical literature and, so far as the writer is aware, no one has attempted to bring them together.

An incidental observation is mentioned here because it is of theoretical interest. In one investigation (72) an epidemic of bronchopneumonia swept through the colony of rats during the last part of the experiment. Most of the animals were affected but the experimental program was continued. During the epidemic the rate of running upon the apparatus declined; the rats were less active than normal. Further, they became less discriminating between the pairs of test-foods presented for choice. The percentages of preference for all pairs of test-foods dropped toward the 50 percent, or indifference, level. Since tests of preference had been given before the epidemic developed, it was possible to demonstrate that the relative preferences among the test-foods

remained unchanged during the sickness. We are justified in concluding that the bronchopneumonia rendered the animals less active and less discriminating than normals in the selection of food.

Hunger and Thirst

Hull (24) and Leeper (28) have shown that rats can learn to take one path to food when hungry and another to water when thirsty, discriminating on the basis of their organic state. Young (70) confirmed this finding with two methods of testing preferential discrimination.

Hull explained the facts by postulating persistent drive stimuli either from the empty contracting stomach (hunger) or from the tissues of the mouth and throat (thirst). The total pattern of stimuli from the environmental situation and the organic state differed with hunger and thirst. To one total pattern the animal learned, through conditioning, to respond by turning to the right. To the other pattern he learned to respond by turning to the left.

Evidence published by Kendler (27), however, presents a difficulty to this internal drive theory of discrimination. Kendler trained rats upon a simple T-maze when they were simultaneously hungry and thirsty. Water was presented in one goal box and food in the other. The experimental procedure was such that all animals would have equal opportunity to explore the contents of both goal boxes. In the critical test series the rats were made either hungry or thirsty but not both hungry and thirsty.

Kendler found that the rats, trained under simultaneous hunger and thirst, were able to respond appropriately during the test trials when they were made either hungry or thirsty. He argued that since there was a single pattern of drive stimuli—that provided by the organic state of simultaneous hunger and thirst—present during training, the hypothesis that rats learn to respond differentially to different patterns of drive stimuli is untenable.

A further argument against Hull's theory is found in the important experiment of Spence and Lippitt (56). They trained rats to run a simple Y-maze under thirst motivation. One path of the maze led always to water and the satisfaction of thirst. The other path led to a goal box containing food for half of the rats and nothing at all for the other half. All of the rats could explore the maze but since there was no hunger the rats which found the food did not accept it. There was thus no reinforcement of behavior through contact with food.

When the motivation was changed from thirst to hunger on the first trial with hunger motivation all of the animals continued to go down the

water alley despite the inappropriateness of this behavior. Further, in learning subsequently to go to food when hungry there was no difference between the groups. The animals which had found food in the goal box during exploration (but did not eat it) learned to go to food no faster than the animals which found the goal box empty.

Spence and Lippitt interpret their result to mean that learning depends upon actual reinforcement. "Knowledge," in Tolman's sense, is ineffective apart from reinforcement. Food-seeking habits, therefore, are formed on the basis of actual effects produced by the acceptance of foodstuffs.

Satiation and Deprivation in Food Selection

The above experiments of Hull, Leeper and Young upon the hunger-thirst problem were carried out under the assumption that an internal need creates a specific drive. But another explanation is possible. The hungry rats were also water-satiated and the thirsty rats were also food-satiated. Satiation, whatever its neural mechanism, is revealed by the inhibition of further ingestion. If two patterns of behavior (going to food and going to water) are equally well learned, the inhibition of one pattern through satiation will make the other pattern more likely to appear in a situation which has repeatedly called out both behavioral patterns.

The importance of satiation as inhibitor in food selection is indicated by experiments of Young (70) who, in fact, has had to abandon the need-drive hypothesis for one which stresses proprioceptive tensions based upon previous affective reactions (palatability effects). According to the prevailing theory, represented by the above view of Hull, specific food-seeking drives originate in local tissue conditions which provide drive stimuli.

The argument against the local origin of specific food-seeking drives may be summarized as follows:

1. In the experiment of Young and Chaplin (75) there was no evidence that protein starvation created a specific urge in the animal to go out and seek the needed protein. The evidence indicated that specific habits of food selection are based directly upon effects of contact with the food via the head receptors. The palatability effects are in some way related to bodily needs.

2. An experiment upon the hunger-thirst balance with different periods of total deprivation demonstrated that the percentage of choices of purina (the preferred nutrient) varied with the number and distribution of reinforcements with apparent disregard for the carefully planned periods of total deprivation (69, p. 145). A preference of purina to water developed steadily with practice despite an increasing period of total deprivation from 5 to 144 hours. It was

difficult to reconcile the facts with the view that independent appetites (hunger and thirst) were being balanced one against the other.

3. Control experiments upon hunger and thirst showed that as the period of total deprivation increased from 24 to 72 hours, the rats became increasingly indiscriminate. Position habits dominated behavior more and more rather than the quality of the incentive. In extreme depletion rats were quite indiscriminate in their choice between food and water.

If we abandon the view that contractions of the empty stomach are essential for the hunger drive and that stimulations from the dehydrated mouth and throat are essential for the thirst drive, then we are in a position to look for some other bodily mechanism which can explain differential food-seeking behavior. The nature of this mechanism is indicated by evidence which constitutes another argument against the local-stimulus theory of drive.

Although we have found it difficult to reverse an established preference by creating a need for the non-preferred food, we have repeatedly reversed food preferences by satiating rats upon the preferred food of a pair (63). Satiation reduces to zero the acceptability of a food but satiation does not produce an immediate change in food selection as one would expect on the basis of the local-stimulus theory of hunger. Satiation produces a gradual preferential trend toward reversal, but reinforcements are necessary for the preference to reverse. When through controlled pre-feeding a preference has been reversed the cessation of pre-feeding does not produce an immediate return to the original preference but it does produce a preferential trend in that direction.

Apparently some reinforcement is necessary to establish a specific food-seeking drive and the effectiveness of a food as a reinforcing agent varies with the period of deprivation starting from complete satiation as the zero point.

The hypothesis on which we are working is that the inhibition of specific food acceptance through satiation can explain the selection and balancing of a diet in accordance with bodily needs just as adequately as the hypothesis that every need creates its own specific hunger which drives the animal to go forth and seek the food which is needed.

According to the satiation theory of food selection an animal ingests a food until a need is met and perhaps more than met. Some inner mechanism (not clearly understood) puts on the brakes, inhibiting further ingestion at satiation. As a matter of fact, Richter's self-selection method is one which permits a rat to eat to satiation. The changes in intake which Richter observes are changes in the quantity of food required to satiate a rat and to keep him satiated throughout a 24 hour period.

PALATABILITY AND THE ENVIRONMENTAL DETERMINANTS OF FOOD ACCEPTANCE

In an experiment upon the choice of protein food Aschkenasy-Lelu (2) found that factors other than bodily need are important determinants of food acceptance. There are native individual differences in food acceptance but environmental factors such as the position of food, its familiarity, or novelty, were found to play a part in selection.

The environmental determinants of food acceptance can conveniently be classified under two headings: palatability factors and non-palatability factors. Since our main concern in the present section is with palatability, it would be well at the start to recognize factors other than palatability which are important determinants of food acceptance.

Laboratory experimenters have repeatedly found that the position of a food is an important factor. On the preference apparatus, for example, a rat may persistently take the food located at his right or that at his left with little regard for its quality. If food objects differ in size, as with grains of corn, wheat, or barley, the larger grains are preferred to the smaller. The number of grains (quantity of reward) makes a demonstrable difference in the motivation of the animal. The accessibility of a food is an important factor. Accessibility varies with the kind of container in which a food is presented and with the amount of work which must be done to obtain the food.

Wholly apart from the food itself are environmental conditions which affect the rate of acceptance. One experiment shows that the rate of food acceptance falls gradually as the room temperature rises from 65 to 90 degrees F; above 90 degrees the rate falls rapidly. The rate of water intake makes a sharp rise at temperatures above 90 degrees F.[2] A good many experiments have utilized electric shocks to block food-seeking behavior. If the shock is weak, it may simply retard the rate of food acceptance. More intense shocks may produce an emotional blocking of the feeding reaction. Other environmental factors such as illumination, distraction, humidity, odor, etc., doubtless have a measurable effect upon the process of feeding.

When Richter uses the term *appetite* he is thinking of intra-organic conditions but his index of appetite is intake per rat per day. If the daily intake of calcium increases significantly, the appetite for calcium is said to increase; if the intake falls, the appetite is said to decrease.

[2] Personal communication from Dr. John R. Brobeck, Yale University School of Medicine. For an abstract of Dr. Brobeck's work see: "Food intake as a mechanism of temperature regulation in rats," *Fed. Proc. Amer. Physiol. Soc.*, 1948, 7, 13.

The criterion of intake per rat per day was used by Young (**74**) in an experiment upon the critical concentrations (preferential threshold, optimal concentration, indifference concentration) for solutions of sucrose and sodium chloride. The experiment showed that for sucrose the optimal concentration was approximately at 8.5 percent. For sodium chloride it was at approximately 0.7 percent. When concentrations were above or below the optimal value the rats ingested definitely less of the fluid than at the optimal concentration.

In terms of the theory that intake indicates bodily need one would expect the average daily intake of a substance to be approximately constant under the same set of intra-organic conditions. But actually the quantity of fluid ingested varied markedly with the concentration of the solution. For sucrose and sodium chloride the optimal concentration was one at which there was a maximal intake of water. The maximal intake of the solute occurred at a concentration well above the optimal. The maximal intake of sucrose, in grams, was at a concentration of approximately 18 percent. The maximal intake of sodium chloride, in grams, was at a concentration of about 2 percent.

These variations of intake, depending upon the characteristics of the food stimulus when intra-organic conditions are constant, demonstrate convincingly the factor of palatability. The term *palatability* refers to the acceptability of foodstuffs as determined by the characteristics of the food stimulus. When organic conditions are held constant food ingestion is found to vary with the kind of food presented, with the concentration of solution, with temperature, texture, flavor, and other properties of the food stimulus. Collectively these characteristics of the food stimulus define palatability as distinct from organic appetite.

Relative palatability is revealed not only in terms of intake per rat per day but also by Young's method of immediate choice. In the experiment under consideration tests of preference were given with solutions of sucrose and sodium chloride differing only in concentration. For solutions of sodium chloride the near-optimal concentration of 0.5 percent was preferred to distilled water and both of these fluids were preferred to a 3 percent solution. The method of immediate choice gave results agreeing completely with those obtained when intake was used as a criterion of palatability.

With sucrose solutions, however, the two methods gave different results. Following 24 hours of total deprivation the method of immediate choice revealed that a 50 percent sucrose solution is preferred to a 4 percent sucrose solution and that both of these solutions are preferred to distilled water. In other words, the higher the concentra-

tion the higher the rating in palatability. But with intake as a criterion of palatability the 4 percent solution, being nearest to the optimal concentration, was preferred to the other two fluids.

The explanation of this discrepancy is simple. Richter's method implies that rats ingest a food up to the limit of satiation; the daily intake is a measure of the quantity of a food required to keep a rat satiated throughout a 24 hour period. Less of the 50 percent sucrose solution than of the 4 percent solution is required to keep a rat satiated for a day. Young's method implies deprivation rather than satiation; satiated rats would not run upon the apparatus. Following a day of total deprivation the sweeter solution was preferred to the less sweet. We have no doubt, however, that this preference could be reversed by permitting the rats to pre-feed upon sugar prior to a test (**63**).

Richter has argued that average daily intake indicates bodily need. His results show that rats ingest much more of a substance than the bare minimum required to prevent deficiency symptoms. There is a large margin of safety. But it is also true that a rat accepts what he *likes*.

Richter has used the intake of a 3 percent sodium chloride solution as a measure of the need for sodium. But if the intake at 3 percent is an adequate measure of bodily need, then it can be shown that rats ingest from one and a half to three and a half times as much sodium chloride as they need when the salt is obtainable at the optimal concentration of 0.7 percent. In a brief report Nelson (**36**) has stated that when salt is obtainable at a concentration of 0.8 percent rats ingest much more salt than they need and, moreover, they develop symptoms of excess—enlarged kidneys and other organs, retardation of growth. Incidentally, Nelson's report suggests the interesting possibility of investigating experimentally the symptoms of excess by presenting foods under conditions of optimal palatability.

If rats are given a single salt solution as the only source of water, the result depends upon the concentration. The following tabulation is based upon an experiment by Heller (**23**):

Concentration of sodium chloride	*Result*
0.5–1.0 percent	Normal growth
1.5 "	Subnormal growth, some die
2.0 "	The young die
2.2–2.5 "	Old and young die
3.0 "	Sudden loss in weight, diarrhea, rough hair, death
3.5 "	Young and mature die soon
4.5 "	Die at once

Animals can adapt to salty drinking water to some extent. Rats 4 weeks of age and weighing 50 grams, when placed on 1.5 percent salt solution nearly always died. The ones surviving passed through a stunted period, in time started growing, and in some cases grew normally.

It is an interesting fact that the 3 percent concentration which has been repeatedly employed to indicate need would be lethal if there were no other source of water in the self-selection diet. It is also an interesting fact that the optimal concentration, according to Nelson, may lead to the appearance of symptoms of excess.

In view of the above facts a question can be raised as to whether the concepts of appetite and palatability are both necessary. We tried in a series of experiments to demonstrate a difference between two kinds of preference—one based upon palatability and one upon organic appetite—but we failed to do so (70). And now, relying upon Richter's criterion of average daily intake, we are forced to conclude that intake reveals differences in palatability as truly as it reveals differences in appetite and bodily need. An animal accepts what he *likes* as well as what he *needs* and it is an open question as to how far what he *likes* agrees with what he *needs*.

When we are considering the dependence of food acceptance upon intra-organic conditions, such as deprivation, states of satiation, or disturbances of intake related to the endocrine glands, the term *appetite* is appropriate. But when we are considering the dependence of food acceptance upon the food stimulus, its kind or temperature or concentration or texture, the term *palatability* should be employed. Food acceptance is dependent upon two groups of conditions, the one intra-organic and the other environmental.

Experimental Methods for the Analysis of Food Acceptance

The experimental methods which have been employed in the analysis of food acceptance are considered below under three headings: the method of immediate choice, the rate of ingestion, methods dependent upon measurements of intake.

1. *The method of immediate choice.* Two main forms of the method of immediate choice have been employed. In the *foods-apart* method the test-foods are widely separated and in fixed positions as in a T- or Y-maze. The point of choice is beyond the range of the head receptors. In the *foods-together* method the test-foods are presented side by side in accessible containers and their relative positions are alternated from trial to trial (67, 70). The latter method has a distinct advantage in that it reveals at once the difference between food preference and position habit.

In the foods-together method the absence of a preference is indicated either

by the consistent acceptance of the food in a fixed position (right or left) or by alternate nibbling of both foods. If the test-foods are exposed for a time longer than that required for choice, the rat may alternately sample the foods. At first we thought that this kind of alternate eating indicated a sampling reaction prior to choice. But we found that when the exposure period was lengthened the alternate eating continued. The pattern is probably best described by Hull's (25) phrase "behavioral oscillation."

The rule in testing preferences by the method of immediate choice is that the test-foods should be exposed no longer than the minimum time required for choice. Since choice is the criterion of preference, the method must require choice and not permit continued feeding.

In the writer's recent work the unit of a preference test has been a pair of successive trials in which both spatial arrangements of the foods are presented. This pair is easily rated as indicating preference for one of the foods or as showing no preference at all.

We have relied upon percentages in studying preferential trends, reversals of preference and the like. These percentages indicate that foods arrange themselves in a truly transitive series such that if A is preferred to B and B to C, then A is preferred to C. When, however, percentages are used to measure distances of separation along the continuum of palatability they are found to be inadequate.

The distance $\overline{AC}$ should equal the sum of the distances $\overline{AB}$ and $\overline{BC}$ but often this relationship does not obtain. Dove (15, 16), relying upon the weight of food ingested as a criterion, encountered the same difficulty with percentages of preference.

One difficulty with the percentage of preference is that it varies with too many conditions. It is known to change with practice and with the familiarity of the apparatus. The percentages vary with the degree of depletion, the state of health, the sensory capacity of the animal, the form of apparatus, as well as with the relative palatability of the test-foods. The percentage of preference needs to be supplemented by other measurements of behavior.

2. *The rate of ingestion.* When test-foods are exposed continuously the best measure of the degree of palatability is the rate of ingestion. As an animal eats continuously from maximal hunger to satiation the rate of ingestion steadily drops (under some conditions there seems to be an initial warming-up period). Continuous weighing of a food during the period of feeding yields a curve of approach to satiation which shows changes in the rate of acceptance.

The rate of ingestion varies with practice, yielding curves of the type described by Skinner. The rate of ingestion also varies widely from animal to animal.

In one experiment the rate of running upon the preference apparatus was studied in relation to the palatability of the test-foods. The number and the distribution of reinforcements for three foods (sugar, wheat, casein) were held constant and the experiment was designed so that no food had any consistent advantage of priority for the group as a whole. Under these conditions it was found that high palatability is associated with a high rate of running; low palatability with a low rate of running (72). From the rate of running preferences could be correctly predicted.

A criterion commonly employed by nutritionists is the weight of food consumed during the exposure period but there are certain difficulties with weight

consumed as a criterion (62, p. 568). For one thing foods differ in density and a gram of one food, such as salt, is not comparable to a gram of another, such as wheat. Further, the rate of acceptance declines as an animal approaches satiation and the total weight ingested conceals this important fact. Estimates of preference based upon the weight of food ingested vary with the duration of the exposure period.

Relative eating time has the same disadvantage as quantity consumed as a criterion of relative palatability.

3. *Methods dependent upon measurement of intake.* If the test-foods are exposed for a long period of time, such as a 24 hour period, the animal can ingest *ad libitum* up to the limit of satiation and keep himself satiated throughout the period. When the observation is extended for days, weeks or months the daily intake, in grams or cubic centimeters, becomes a measurement of the rate of acceptance. The rate of acceptance is expressed in terms of grams per day or cubic centimeters per day.

In Richter's method of self-selection maintenance the total diet is broken into its components which are presented separately. The subject is free to accept or reject each component and commonly does so up to the limit of satiation.

In some experiments the subject is given no choice. He is placed in a cage containing a single food and his change in weight, activity, and his life span are observed. In terms of survival times the sustaining value of different foods can be determined.

Beebe-Center *et al.* (4) have described a method in which the per diem consumption of a fluid from a single bottle is measured.[3] Solutions of saccharine (or of vanilla-flavored water) and distilled water are presented on alternate days. The difference between the per diem intake of the test-solution and the per diem intake of water is used as a criterion of perference. When the rats are given a single fluid as a source of drinking water the intake of this fluid varies with the concentration of the solution.

In Richter's method for determining preferential thresholds the animal is given a choice between two fluids—distilled water and the test-fluid. At the start distilled water is placed in both bottles. After a few days for adaptation to maintenance conditions a subliminal solution is placed in one of the bottles. The concentration is then gradually increased, day by day, in small steps, until a concentration is reached at which a preference is revealed. Young has modified this method by using both ascending and descending series of concentrations.

[3] Dr. Beebe-Center has demonstrated to the writer a simple and effective technique for measuring per diem intake which eliminates the costly calibrated bottles and the worries concerning uniformity of calibrations. A standard inverted bottle is placed at the top of an individual cage and a straight glass nozzle arranged so that a rat can drink from it directly. A single graduated measuring beaker is used for the entire experiment. A measured quantity of fluid is poured into the bottle prior to exposure. After a 24 hour exposure in the cage the remaining fluid is poured back into the beaker and again measured. The difference is the per diem intake.

The initial measurement could be eliminated by determining once for all the capacity of the filled bottle. Another possibility would be to make the initial and final measurements in terms of weight and converting the series of weight measurements into volume by a single determination of the density of the fluid.

Chaplin (**8**, **76**) presented 8 solutions of sodium chloride simultaneously to a group of rats. The animals had free access to the salt solutions as well as to the other components of their maintenance diet. This method was found to be a simple and convenient technique for determining the optimal concentration. It doubtless could be used, with low concentrations, to determine the preferential threshold.

THE MOTIVATION OF FOOD-SEEKING AND FOOD-SELECTING BEHAVIOR

The Local-Stimulus Theory of Internal Drive

The local-stimulus theory of internal drive is probably accepted by psychologists today more widely than any other theory of motivation. Anderson (**1**), for example, in his theoretical paper upon the externalization of drive, assumes that a drive such as hunger is originally dependent for its arousal upon internal conditions of the organism and that through conditioning behavior comes to be controlled increasingly by external stimulation. Hull (**24**, **25**), as we pointed out in the above discussion of hunger and thirst, bases his theory of motivation upon primary needs and the local stimuli which they produce in the tissues.

Despite its popularity the local-stimulus theory of internal drive lacks a convincing experimental demonstration.

In a previous review the writer (**64**) referred to experiments by Tsang and Bash which demonstrated that local contractions of the empty stomach are not essential to food-seeking behavior. Tsang surgically removed the main bulk of the stomach in seven rats. He found that after one day of fasting the gastrectomized rats were almost as well motivated as normal animals as evidenced by their efficiency in maze running. Bash surgically isolated the stomach from the central nervous system by destruction of the vagi and splanchnic nerves of rats. With afferent impulses from the empty contracting stomach cut off these animals exhibited a hunger drive which was almost normal as shown by their gnawing through cardboard and learning a maze to reach food. Bash concluded that the hunger drive must operate through a noncerebral reflex mechanism which is probably chemical in nature; food ingestion is a chemoreflexive act.

Similarly, experiments by Bellows and Van Wagenen (**5**), by Robinson and Adolph (**53**), and others, have demonstrated the inadequacy of the view that the thirst drive is reducible to neural stimulation from the dehydrated mouth and throat. Bellows and Van Wagenen found that dogs drank water in normal amounts and diabetic dogs drank excessive amounts when (a) in one group the sense of taste was abolished and the pharynx rendered anesthetic, (b) in another group the excitations mediated by the trigeminal nerves were abolished, and (c) in a

third group the sense of smell was abolished. The urge to drink, therefore, cannot be identified solely with any one of the nervous pathways that were interrupted nor with any single type of excitation which they mediate. Robinson and Adolph have shown that with dogs the signal that initiates the drinking response is a deficit of water relative to the other bodily components. When the body is depleted of water by the amount equal to about 0.5 percent of the body weight, water is ingested. The amount drunk at each draft is accurately proportioned to the body's water deficit as determined by body weight.

In view of these and other experiments the prevailing local-stimulus theories of hunger and thirst are seen to be inadequate. The facts of observation upon which these theories rest, of course, remain as facts but a new interpretation is indicated. The contractions of the empty stomach and the associated conscious hunger pang, the inhibition of saliva and dehydration of the mouth and throat with the painful thirst experience—these should be regarded as *symptoms or manifestations of bodily need* but not as a fully adequate explanation of food-seeking and water-seeking behavior.

The theory of specific hungers lacks a demonstration of internal bodily mechanisms capable of arousing an animal, exciting him, so that he will go out and seek the substance which is needed. In his excellent summary of the facts relating to bodily need Morgan (**35**, p. 437) states that there are at least 11 specific hungers. These are the hungers for: carbohydrate, fat, protein, thiamin, riboflavin, oxygen, salt, phosphorus, sodium, calcium, water. Although the list probably requires revision, it can serve to illustrate the complexity of the psychologist's problems.

The criterion for demonstrating the existence of a specific hunger or appetite is that of independent variability. The demonstration can best be made with purified food substances because natural foods are usually complex from the point of view of nutrition. It can be shown that when a rat is satiated or nearly satiated upon one dietary component he still accepts another. This independent variability leads to the assumption that there are independent specific hungers or appetites. But their number does not necessarily equal the number of known metabolic needs since some needs exist without any consistent manifestations in behavior.

The Nature of Specific Food-seeking Drives and Food-selecting Behavior

In all of the work upon food-seeking and food-selecting behavior it is obvious that the animal *learns* those instrumental acts which lead to

food. He learns to run a maze, to press a Skinner bar, to discriminate between black and white, to dig through sand, to open a door, to shuttle back and forth on a preference apparatus. Outside of the laboratory animals *learn* how and where to obtain food. The bear learns to climb over the mountain to the stream where fish may be caught; cattle learn to roam over the plains to the salt licks; the family cat learns to come to the back door for milk, when a particular creaking sound is heard. Specific food-seeking drives are clearly acquired through a process of learning. There is no mystical insight which leads animals to the food which they need.

The next point is that the speed of food-seeking behavior depends upon practice. For example, a group of 19 rats making 100 runs on our apparatus with casein as an incentive increased their average rate from 1.90 runs per minute for the first 20 runs to 2.71 runs per minute for the last 20 runs (**71**, p. 148). That the rate of behavior changes with practice is a fundamental fact of learning.

A further point of theoretical importance is that the rate of running varies with the degree of palatability of the test-food presented as an incentive. If rats are given a single run per day and the time between release from the starting-box and acceptance of food (the approach time) is measured, the time of approach to a highly acceptable food (sugar) is consistently less than the time of approach to a food of low palatability (casein) (**73**).

Summing up the points made thus far, we may state:

1. That specific patterns of food-seeking behavior are learned.
2. That the rate of food-seeking behavior depends directly upon the amount of practice.
3. That this rate varies directly with the level of palatability of the food which serves as an incentive.

Let us now inquire: What kind of a bodily mechanism can account for the above facts of observation?

One hypothesis is that the rat, when repeatedly placed in a situation which yields food, builds up a specific neuromuscular determination which is capable of regulating the pattern of behavior. There is a specific determination to run to food or to do with the laboratory gadgets whatever is necessary to obtain food. This specific determination is related to what Tolman (**57**, **58**) and others have meant by expectancy. When a rat is repeatedly placed in a piece of laboratory apparatus he builds up an expectancy. Our work shows, further, that a rat builds up a running motive *for a particular kind of food.*

A specific determination to run to food is acquired when an animal

is repeatedly placed in the kind of situation which consistently yields food. As a component part of the determination we assume that there is a change in the tonus of muscles and a change in the pattern of neural excitation which determines the tension of the drive to seek a specific food.

Geier (21) has shown that associated with the expectation of food is a measurable bodily tension. He placed rats for one minute prior to feeding (or non-feeding) in an activity wheel and demonstrated that rats expecting food made more revolutions per minute than rats not expecting food. Underlying his technique is the assumption that when a rat is under tension from some internal drive or from frustration he can and does reduce this tension by running in the activity wheel. This is a way to "work it off." Geier assumed that rats expecting food had a higher level of bodily tension than rats not expecting food.

The present argument carries the hypothesis a step further by assuming that the degree of proprioceptive tension, aroused with the specific determination to run to food, varies directly with the degree of palatability of the food which the animal expects to receive. The determination running-to-sugar, as a fact, is more highly motivating than the determination running-to-casein in the same external situation. The former motivation, therefore, is assumed to come from a higher degree of proprioceptive tension. Since proprioceptive tensions can actually be measured, the hypothesis can be put to experimental test.

The above theory of specific food-seeking drives differs from the local-stimulus theory in one obvious respect: The local-stimulus theory of drive looks for the motivation of behavior in tissue conditions produced by need. Although the nutritionist can describe a wide variety of specific symptoms and syndromes produced by various dietary deprivations, no one has been able to describe diverse bodily mechanisms sufficient in number and complexity to explain the facts. The above theory, in contrast, looks to the proprioceptive mechanisms for immediate motivation in all specific food-seeking drives. These mechanisms are capable of directing the organism to different places with different degrees of proprioceptive tension, or physiological drive strength.

The emphasis in the proprioceptive-tension theory of drive is not upon tissue needs but rather upon the reinforcements from the effects of food ingestion. Immediate palatability effects and deferred organic after-effects furnish reinforcement for the acquisition of selective food-seeking drives.

In one experiment rats were maintained upon a standard adequate diet. In their living cages was an unlimited supply of food and water.

Growth, activity, health were normal throughout. No known nutritional need can be said to have existed. The test-foods, sugar and casein, were supplementary to an adequate diet. Under these conditions distinguishable food-seeking drives, running-to-sugar and running-to-casein, developed under identical conditions. These drives cannot be said to rest upon any bodily need nor upon any known deficiency. The rats were well motivated without need for any known substance (73).

Incidentally, psychologists can abandon the view that dietary need is essential for adequate motivation with food. What is necessary is an acceptable reward (sugar) upon which the animals are not already satiated at the time of the experiment. Regular nibbles of sugar can provide adequate motivation to well-nourished rats which are free from metabolic needs.

Feeding Habits

The Basis of Feeding Habits

Although human food acceptance may rest in part upon social pressure, custom and taboo, even upon a sense of duty, these factors do not affect the acquisition of feeding habits by animals.

Habits of feeding rest upon the effects of contact with food. There is, first, the immediate effect produced through the stimulation of the head receptors by the foodstuff and, second, there are remote and deferred after-effects (not clearly understood) which result from the ingestion of food. The term *palatability* refers to the immediate affective reaction (liking or disliking) of an organism which occurs when a food stimulus comes in contact with the head receptors. We know of no general term to cover collectively the various comforts and discomforts, reliefs, and cramps, satisfactions and dissatisfactions, which commonly follow the ingestion of certain foods.

Palatability and the law of effect. According to the law of effect, the satisfaction derived from food acceptance reinforces the patterns of behavior which produce that satisfaction.

Two investigations by Young (72, 73) bear upon the law of effect. Both investigations justify a distinction between the rate of running to food and the rate of learning. The experiments show that at all stages of practice rats *run* faster in approaching a highly palatable food (sugar) than in approaching a food of low palatability (casein). The difference in the time required to approach and accept these foods indicates a motivational difference, a difference in the strength of physiological drive. But if the data are analyzed so that differences in the rate of running are equalized or balanced, the rate of *learning* the habit of

running-to-sugar is the same as the rate of *learning* the habit of running-to-casein. The rate of acquisition depends upon the frequency and distribution of reinforcements rather upon than the quality of the reward. If the frequency and distribution of reinforcements are held constant, then rats do not learn faster for one food incentive than for another, although they undoubtedly run faster to accept a good food than to accept a bad food at every stage of practice.

The data illustrate the distinction between performance and learning. Performance depends upon many factors (practice, motivation, state of health, external temperature, etc.). Learning depends upon practice which is one of these factors.

If learning is defined as acquisition dependent upon practice alone, then the law of effect is not a law of learning, since the rate of acquisition is independent of effect. But this definition of learning, perhaps, is too narrow. Determinations to run (motives) are acquired as truly as motor skills. The determination to run to sugar or to run to casein depends directly upon the effect of contact with these foods.

Therefore, we suggest a broader definition of learning which includes the acquisition of motives (specific food-seeking drives and food expectancies) as well as the acquisition of motor skills (activities which are instrumental in obtaining food). A broader definition would assert that learning is the acquisition of behavior dependent upon (a) practice or (b) effect. Further research on this problem is clearly needed.

Intra-organic after-effects and learning. The experiments of Harris *et al.* (22) point to the importance of intra-organic effects in habit formation. The nature of these after-effects is not clear but they are related in some way to increased rate of growth, more rapid heart beat, change in alimentary tonus, and relief from the symptoms of dietary deficiency.

Harris *et al.* believe that the behavior of a rat in selecting food is due to his experience of some beneficial effect produced by ingesting a particular food. If rats are depleted of vitamin B, they select a food containing the vitamin and begin to gain in weight. When given a choice between diets containing different concentrations of the vitamin they select the food with the higher vitamin content. Rats are able to select the vitamin-containing food whether it is presented in yeast, wheat-germ oil, or marmite, even if a barely sufficient quantity is present in the food.

When several foods (6 to 10) are presented simultaneously some of the vitamin-depleted rats succeed in selecting the food containing the vitamin but most of them, according to Harris *et al.*, fail to make the selection. Two or three days of "education," however, lead them to

select the adequate diet. "Education" consists of letting a rat feed on the vitamin-containing diet until he can experience its beneficial after-effects, *i.e.*, until he can recover from the discomfort of avitaminosis and resume normal growth. In "education" the rats are trained with food of a particular flavor. If the food is associated with recovery, they then continue to select the food of that flavor even if the vitamin is later withdrawn.

In one experiment 4 rats were depleted of vitamin B. They lost weight. Then they were trained to accept a bovril-flavored diet containing an adequate amount of the vitamin. When offered a choice among basal diets of four flavors (basal diet alone, this flavored with lard or with cocoa or with bovril) the animals continued to select the bovril-flavored diet. The vitamin was then transferred to the cocoa-flavored diet but the rats continued to select the bovril-flavored food. They were thus deceived. Through "re-education" on the cocoa-flavored diet, however, they learned to accept it and they gained in weight. This time they continued to select the cocoa-flavored diet when given a choice.

These investigators conclude that the ability of the vitamin-depleted rat to discriminate between diets containing the vitamin and diets deficient in it depends upon an association between some distinctive character of the diet (smell, taste, feel, appearance) and prompt experience of some beneficial after-effect. If the effect is not associated with the food, a rat may fail to make a wise choice.

In an experiment by Young (**70**, pp. 1–17) a single vitamin solution containing thiamin, riboflavin, pyridoxine, nicotinic acid, and pantothenate acid, in the concentrations recommended by our adviser on nutrition, was presented to a group of rats. For some unknown reason the vitamin solution was rejected and the rats began to lose weight. The rats were then forced to drink the vitamin solution by removing for two days all other sources of water. The animals drained the bottles dry, obtaining therefrom on the average 12 c.c. of the vitamin solution per rat per day. After this "education" the original diet was restored. The rats, strikingly, continued to ingest the vitamin solution in sufficient quantity and they gained in weight.

The moral is that the nutritionist, basing his advice upon known metabolic needs, lacked dependable information concerning the palatability of vitamin solutions presented singly and in combination. Hence he could not prepare a compound solution which the rats would accept. But it should be relatively easy, with the behavorial techniques now available, to prepare a solution which rats would accept. The practical art of feeding must rest upon sound psychological analysis of food acceptance.

How Feeding Habits Can and Cannot Be Changed

The committee on Food Habits of the National Research Council has been concerned with the problem of changing food habits (**78**, **79**). Dr. Margaret Mead (**33**, **34**), Secretary of the Committee, and other members, have placed a good deal of emphasis upon social and cultural factors in the causation and change of food habits. Although this emphasis is clearly justified, the review of social and cultural factors is beyond the scope of the present paper.

Our approach is from the point of view of experimental psychology and we ask: What does recent research show about the ways in which feeding habits can and cannot be changed? The question will be considered under four main headings:

1. *Feeding habits stabilize patterns of acceptance.* Rats thoroughly habituated to the selection of sugar in a choice between sugar and casein continued to choose sugar despite a protein starvation of 32 days with marked signs of dietary deficiency. When tested with a different apparatus, however, and with a different technique they at once developed a preference for casein in agreement with their metabolic needs (**75**).

Our first interpretation of this result was that two kinds of food preference existed simultaneously, one based upon immediate stimulation of the head receptors (palatability preference) and the other upon organic need (appetitive preference) (**66**). Subsequent control experiments, however, showed that this interpretation was not correct. We have been unable to demonstrate a difference between palatability preference and appetitive preference (**70**).

The consistent selection of sugar in preference to casein demonstrated the persistence of a well-established feeding habit which happened to be opposed to a bodily need. The consistent selection of sugar was a manifestation of habit alone wholly apart from need and probably apart from palatability (assuming the palatability of casein to have changed with need for this food).

The general principle in this and similar experiments is that established feeding habits tend to persist, to stabilize feeding behavior, regardless of bodily needs but new habits tend to form in agreement with bodily needs (**69**). Change of apparatus forces the animal to become exploratory and more discriminating and the change of environment is favorable to the development of feeding habits which agree with bodily needs (**71**).

2. *The effect of training varies with palatability.* A common human method of attempting to change feeding habits is to force a child to accept a food he dislikes. Is this method effective with animals?

In one experiment two groups of rats, maintained upon the same adequate diet, were trained to run the preference apparatus. One group ran for nibbles of sugar and the other for nibbles of wheat. After training both foods were presented together in a test of preference. The rats trained to run for sugar selected sugar when given a choice although the preference was not stable and some animals changed to wheat. The rats trained to run for wheat continued to select wheat. In other words, the rats tended to select the food upon which they had been trained (**67**).

Since sugar and wheat are nearly equal in palatability, it was decided to see

whether training on a food of low palatability could make it more acceptable than sugar. Rats, maintained upon a complete self-selection diet, were given a choice between sugar and casein following 24 hours of total deprivation. They consistently preferred sugar. They were then given repeated runs for casein alone. Practice up to 1000 runs per rat did not change the initial preference. On the contrary, the preference for sugar increased from about the 60 percent level to a consistent 100 percent preference. There was no evidence that forcing the rats to accept an unpalatable food raised the level of its acceptability. Incidentally, practice in running for casein resulted in an increase in the rate of running. In a series of 900 runs the average rate for the first 20 trials was 0.83 runs per minute and for the last 20 trials 3.98 runs per minute (71).

The two experiments appear to yield contradictory results but it should be remembered that the conditions were different. Sugar and wheat are highly palatable and nearly equal in acceptability to rats. Casein is a food of low palatability. Keeping these differences in mind, we can summarize the two results in a single generalization: If two foods are nearly equal in palatability, the repeated acceptance of one develops a feeding habit which is temporarily effective as a determiner of choice; but if two foods differ widely in palatability, training in accepting the non-preferred food is ineffective in changing the preference.

3. *A preferential habit can be changed by satiating the animal upon the preferred food.* If a preferential habit has been well established, it can be reversed by pre-feeding the preferred food immediately before a test of preference. The reversal does not appear at once but it comes gradually with repeated runs. After a preference has been reversed there is a gradual trend toward the original preference when pre-feeding is discontinued (63).

In one experiment it was found that rats preferred sugar to casein following 24 hours of total deprivation. When the rats were deprived of casein and satiated upon sugar, in the early stages of training, the preference reversed; the rats selected casein in preference to sugar. With continuous casein deprivation of 21 to 25 days the sugar was removed from the diet giving a simultaneous sugar deprivation of 1 to 5 days. Although the rats were weak and inactive, due to the prolonged deprivation, they returned to their original sugar preference (70).

There is no doubt that preferential food habits can be controlled by varying the organic state.

4. *A feeding habit can be changed by changing the palatability of the foods.* Since the rate of acceptance of salt and sugar varies with the concentration of solution, an animal can be made to accept more or less of these substances in his total diet by changing the concentration. When the intra-organic conditions are held constant heightened intake is a mark of heightened palatability (74).

Affective Psychology and the Science of Nutrition

In a critical review of current approaches to affectivity Hunt (26) made two pertinent statements:

It would seem fairly safe to assume that most psychologists today would agree that the concepts, pleasantness and unpleasantness, as used in psychology tacitly refer to general attitudes of acceptance and rejection and that the field of affectivity covers the investigation of these attitudes in their development

and operation. . . . A brief summary would run something like this: The organism may either accept or reject a stimulus. This acceptance or rejection is carried out through appropriate bodily adjustments. These reactions are said to constitute the affective response and are assumed to be a functional entity of some kind.

There are a good many factors which regulate the relative acceptance or rejection of foodstuffs but the investigation of these factors falls squarely within affective psychology.

The nutritionist has a different point of view. The writer recently heard a distinguished biologist describe a method of feeding laboratory mice which was considered ideal from the nutritionist's point of view. A mouse was trained to swallow a food pellet introduced directly into the mouth and throat. The constituents of the pellet could be precisely controlled. No more worries about palatability and habits of feeding!

Dove (17) has attempted to combine the nutritional and psychological points of view. He starts from the *appetite level* of consumption which is the actual level of intake for an individual or a group. It is not enough to limit consideration to the nutritional values of foods in the practical art of feeding men and animals. Dove (18) has stated the proposition clearly: "*Each food must be evaluated not by what is possesses but by what it gives to the consumer;* and it gives to the consumer in gross value its percent value per unit weight times the weight of food accepted." Food acceptance is regulated by psychological factors.

In the Quartermaster Food and Container Institute for the Armed Forces, in Chicago, Dove (19) has been conducting a series of investigations upon problems of food acceptance. The research is comprehensive in scope, embracing analysis of regional differences in food habits due to geographic, cultural, economic, and other determinants, as well as psychological research upon the problems of feeding.

In the war which has just closed the soldier-consumer was provided with a ration calculated by nutritionists to be complete in supplying the necessary minerals, vitamins, proteins, fats, and the requisite calories for energy expenditure during heavy work. But frequently soldiers refused to eat some of the items in the ration and threw their food away! As Dove said has: "when war comes it is easier to dress men alike, even though they come from different regions, with different social, economic, and cultural and racial origins than it is to feed them alike."

Conclusions

1. Dietary need is a nutritional concept. When a component of the diet which is required for normal growth, reproduction, activity, or for survival itself, is removed a pattern of deficiency symptoms appears.

Deficiency symptoms are not drives. No one has been able to demonstrate that for each specific deficiency there exists a specific form of food-seeking or food-selecting behavior.

There are, however, behavioral manifestations of depletion as well as structural changes. A specific deprivation may change the level of activity, the time and error scores in maze learning, the liability to fits, or the functional capacity of the sense organs.

2. Habits of seeking particular foods appear to rest directly upon the effects of ingesting these foods. The term *palatability* implies an affective reaction to foodstuffs which stimulate the head receptors. There are also delayed and remote after-effects of food ingestion which, under some circumstances, may be the basis of dietary habits.

3. An established feeding habit may persist regardless of bodily needs. On the other hand, new habits tend to form which will meet bodily needs.

4. Among the organic determinants of food acceptance the conditions of satiation and deprivation are of prime importance. As an animal steadily ingests a food, approaching satiation as the limit, the rate of acceptance declines. If satiation is the zero point of food acceptance, the acceptability of a food increases with the period of deprivation starting from the zero point of satiation.

As the period of deprivation increases rats become less and less discriminating among foods and more and more determined by position habits.

In addition to satiation and deprivation there are other organic conditions which regulate food acceptance such as the balance of the endocrine glands, age, pregnancy and lactation, sickness, etc.

5. The environmental determinants of food acceptance can be classified as palatability factors and non-palatability factors. Palatability factors are characteristics of the food itself such as the kind of food, concentration of solution, temperature of the food, texture, etc. The experimental study of palatability is of great importance in the practical art of feeding men and animals.

Closely related to palatability in the regulation of food acceptance are such determining conditions as size of food object, quantity of food, position of food, degree of contamination, kind of container, laboratory apparatus through which food is obtained, etc. Environmental factors not directly related to palatability but modifying the feeding process are temperature of the surroundings, distractions, emotionally disturbing shocks and noises.

6. Strength of drive, as measured by the time required to approach

and accept a food, is positively correlated with the degree of palatability of the incentive. Animals run faster in approaching a highly palatable food than in approaching one of low palatability.

The rate of habit growth, however, is not dependent upon the degree of palatability of the incentive. Learning depends upon the frequency and distribution of reinforcements.

7. The conditions which regulate food acceptance are numerous and they are complexly interrelated. There are three main groups of conditions, indicated by the title of this paper, which must be controlled by laboratory workers: conditions within the organism (appetitive conditions); conditions within the nutritive environment (palatability and non-palatability determinants); conditions within the previous behavior of an organism (feeding habits).

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