

Handbook of Behavioral Neurobiology

Volume 10 Neurobiology of Food and Fluid Intake

Edited by

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PLENUM PRESS • NEW YORK AND LONDON

Diet Selection and Poison Avoidance by Mammals Individually and in Social Groups

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INTRODUCTION

There is great diversity in the feeding behavior of mammals. Some are essentially monophagous, feeding on a single food or class of foods; others are eclectic in their ingestive behavior, composing exceptionally varied diets.

True ingestive specialists, such as vampire bats (*Desmodus rotundus*), sustained entirely by mammalian blood, acquire nutritionally balanced diets simply by identifying and then eating their staple food. Omnivores cannot compose an adequate diet so easily. Be they men, rats, gulls, or roaches, omnivores must ingest a suitable mix of different foods if they are to thrive outside the laboratory.

Lát (1967) has proposed that the need for omnivores to ingest selectively a number of different foods arises from the fact that, for an omnivore, there is no single natural food that contains adequate amounts of all the constituents required for optimal living. The same fact, that most free-living omnivores live in areas in which no single food provides an adequate diet, can be viewed quite differently. Development of an ability to compose an adequate diet by selectively eating a number of different foods allows omnivores to occupy areas in which no single satisfactory food is available and in which no monophage could sur-

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vive. Omnivory thus both broadens the range of environments in which mammals can live and requires greater sophistication in selective ingestion than does monophagy.

Because ingestive specialists can meet their nutritional requirements by identifying and ingesting a single class of foods, they have little need to contact or ingest potential toxins. Omnivores, sampling broadly among foods in an attempt to locate sources of needed nutrients, should be exposed to any toxic agents in an environment more frequently than are specialists. In consequence, life as an omnivore could be facilitated not only by the ability to choose a balanced diet but also by the ability to identify and reject toxic substances (Rozin, 1976b). Each omnivore must steer a narrow course between the Scylla of dietary insufficiency and the Charybdis of ingestion-induced toxicosis, neither selecting such a restricted range of foods that it fails to include all required nutrients nor sampling so widely that it ingests harmful quantities of toxins.

Selecting an adequate diet and avoiding ingestion of toxins, the two main behavioral challenges faced by omnivores as a consequence of their omnivory, usually have been treated as separate problems. Investigators working on diet selection and those studying poison avoidance have developed different research paradigms, contributed to relatively independent literatures, and employed different theoretical perspectives.

In a landmark series of papers, Rozin (1965, 1967a, 1967b, 1968, 1976a, 1976b; Rozin & Kalat, 1971) provided an integrative framework that, quite unlike Richter's (1943) earlier model, permitted discussion of diet selection and poison avoidance as a unitary problem. Richter (1943) had hypothesized that each of the dozens of nutrients required by omnivores is regulated by an innate mechanism that detects a specific deficiency state, detects a needed nutrient in foods, and motivates its ingestion. Rozin proposed that although intake of three critical dietary elements (e.g., water, sodium, and calories) was controlled in the manner Richter had suggested, intake of most nutrients was not so controlled. On Rozin's model, sensitivity to the novelty or familiarity of a food, together with a capacity to respond behaviorally to the physiological consequences of eating a food, underlies both selection of an adequate mix of unregulated nutrients and avoidance of repeated ingestion of toxins. For example, an omnivore maintained on an inadequate food develops an aversive deficiency state that is similar to toxicosis. This aversive deficiency state produces a learned aversion to the taste of the inadequate diet. Conversely, eating an isolated meal of an unfamiliar food that produces recovery from illness leads to a learned preference for the flavor of the unfamiliar food.

If diet choice is to be optimized, consequences of ingestion must be associated with food-related stimuli despite long delays between eating a food and experience of consequences. Normally, association of stimuli with their consequences does not occur when they are separated by more than a few seconds. Rozin argued from data provided by Garcia and his co-workers (Garcia & Koelling, 1966, 1967; Garcia, Kimeldorf, & Hunt, 1961) that the learning of dietary aversions and preferences rests on two adaptive specializations of a more general Pavlovian learning process: first, attribution of changes in internal state to the consequences of ingestion ("belongingness"), and, second, a capacity to tolerate long delays between ingestion and the onset of the consequences of ingestion ("long-delay learning"). On this view, belongingness (Revusky, 1971) and long-

delay learning have evolved expressly to facilitate solution of the problems of diet selection and poison avoidance faced by omnivores in natural habitat.

Rozin's model of food choice explains the results of many laboratory experiments in which rats succeeded in avoiding repeated ingestion of toxic foods or in selecting from among several diets the sole diet permitting redress of a deficiency state. Although we accept Rozin's general view of the causes of rats' successes both in selecting adequate diets and in avoiding poisons, we believe that it is incomplete in one important respect.

Rozin's model was designed to explain how omnivores select adequate diets and avoid eating poisons; it neither pays much attention to nor offers any explanation of their failures. We argue below that consideration of failures, both of diet selection in the laboratory and of poison avoidance in the field, may be of considerable importance in understanding the capacity of omnivores to select foods successfully in either setting.

It is important to keep in mind, especially when discussing Norway rats or other mammalian species capable of rapid rates of population growth (Pianka, 1970), that individuals often fail to respond adequately when challenged by the environment. Failure to find shelter, failure to avoid predators, failure to find safe and adequate food, failure to resist disease, failure of some sort results in the death of more than 90% of rats before they reproduce (Brooks, 1973). Such failures can be as instructive as less frequent successes in understanding the feeding-related behavioral capacities of omnivores. Focus on failure may also provide a useful cautionary message in this age of Panglossian explanations of apparently ubiquitous behavioral optimality. Animals fail when their behavioral capacities are insufficient to respond to environmental demands, and failure is common.

DIET SELECTION

CAN RATS SELF-SELECT ADEQUATE DIETS?

It has long been known that rats choosing from a cafeteria of purified nutrients can select a diet adequate for normal rates of growth. In a classic study, Richter, Holt, and Barelare (1938) found that rats offered 11 containers, each containing a different, relatively purified nutrient (casein, dextrose, olive oil, baker's yeast, water, salt mix, etc.) gained weight more rapidly and on fewer calories than did a control group of rats maintained on a standard laboratory chow. Young (1944) confirmed this result in groups of 12 rats, each group having access to the 11-food cafeteria used by Richter *et al.* (1938). Clearly, under some circumstances, rats can self-select an adequate diet from among a variety of potential foods.

Richter had expected his subjects to be successful in the cafeteria feeding situation. "The survival of animals and humans in the wild state in which the diet had to be selected from a variety of beneficial, useless and even harmful substances is *proof* [emphasis added] of this ability . . . to make dietary selections which are conducive to normal growth and development" (Richter *et al.*, 1938, p. 734). In Richter's view, the laboratory data illustrated a capacity for diet selection that could be deduced from the survival of omnivores in the natural world. Consequently, when omnivores failed to self-select an adequate diet in some

experimental situation, the failure was interpreted by Richter as the result of an artifact of one sort or another: the use of complex natural foods (Richter *et al.*, 1938), inherited defects of the sensory system in domesticated subjects, age-related exhaustion of regulatory functions, or, in humans, perverse cultural influences (Richter, 1943).

Yet, review of the literature on dietary self-selection by rats in cafeteria feeding situations reveals that failure, as indicated by markedly slowed growth, is at least as common as success (Kon, 1931; Scott, 1946; Pilgrim & Patton, 1947; see Epstein, 1967; Lát, 1967, for reviews). Such failures to self-select, together with the theoretical considerations discussed below, suggest that Richter's deduction from the fact of the persistence of omnivores in nature, of a capacity for dietary self-selection in cafeteria feeding situations, was overdrawn.

Members of any species, even those as cosmopolitan in distribution as Norway rats or "primitive" *H. sapiens*, are not found everywhere within their respective species' ranges. By definition, individuals can survive only in those portions of the environment that both provide all resources necessary for life and lack insurmountable threats. An area would be devoid of rats if it contained either lethal substances that rats were unable to learn to avoid or a necessary nutrient only in a form that rats couldn't learn to eat. Existence of an omnivorous species in nature tells us little about the range of environments in which species members have the ability to self-select nutritionally adequate, safe diets. Persistence of omnivores outside the laboratory shows only that there exist portions of the environment where the behavioral capacities of species members are sufficient to permit development of a dietary repertoire conducive to self-maintenance, growth, and reproduction. In particular, existence of an omnivorous species in nature does not suggest that in the laboratory omnivores should be able to select nutritionally adequate diets from among a cafeteria of purified dietary components.

CAUSES OF FAILURE IN SELF-SELECTION

In discussing selection of foods containing nutrients other than salt, neither Rozin (1976b) nor Richter paid much attention to the relative palatability of foods. The flavor of a food is not necessarily a reliable indicator of its nutritive content. Consequently, selection of foods on the basis of their flavors cannot explain successful diet selection. Palatability may, however, be an important determinant of failure of self-selection (Richter, 1943). As Epstein (1967, p. 201) concluded in his review of the literature on dietary self-selection by rats, "Rats tend to eat what they like, and what they like is determined largely by the palatabilities of the foods they are offered." In laboratory cafeteria feeding studies, growth rate has been determined largely by protein intake (Lát, 1967). As Scott (1946, p. 403) indicated, "[individual] rats either do or do not like casein; if they like it, they eat an average of 3 grams a day and grow well; if they do not, they eat less than 0.1 gram per day, lose weight, and die within a short period."

Such laboratory findings can be extrapolated, with caution, to extralaboratory environments. How successful animals are in selecting an adequate diet will depend on their intake of the relatively less palatable available foods that contain necessary nutrients. If an animal eats enough of a relatively unpalatable food to allow evaluation of the consequences of eating that food, then the problem of dietary self-selection can, at least potentially, be solved. If an animal cannot

overcome its initial aversion to the taste of some food so as to eat sufficient amounts of the food to permit its evaluation, then a capacity to learn about consequences of ingestion will be of no use.

The question "Can omnivores self-select adequate diets?" is unanswerable in that form. In benign ingestive environments, such as the one constructed by Richter *et al.* (1938), the relative palatabilities of the foods provided may lead directly to selection of an adequate diet by all individuals. In the Richter *et al.* (1938) study, the presence both of multiple sources of protein and of a relatively unpalatable carbohydrate (Epstein, 1967) probably rendered the problem immediately soluble (Scott & Quint, 1946). In less benign environments, spontaneous sampling, coupled with response to positive postingestional consequences, suffices to permit most subjects to overcome their initial avoidance of the least-palatable needed food or foods. In yet more challenging situations, no individual's spontaneous behavior may be sufficient to overcome the flavor-induced avoidance of one or more needed foods.

Failure to solve a diet-selection problem can result from the unpalatability of foods containing one or more necessary nutrients limiting ingestion of valuable foods to the point that discovery of their beneficial properties is unlikely. Results of several classic studies of diet selection in which rats were taught to solve cafeteria feeding problems they did not solve spontaneously suggest that rats often fail to solve problems that are, in principle, soluble. For example, when six of 12 rats selecting among four purified diet components (casein, sugar, salt mix, and fat) steadily lost weight because of low protein intake, McDonald, Stern, and Hahn (1963) fed them only casein for 4 weeks and then returned them to the choice situation. All subsequently ate casein and showed excellent weight gain. Similarly Harris, Clay, Hargreaves, and Ward (1933) found that vitamin-B-deficient rats, unable to select a single vitamin-B-rich food from among ten foods, could solve the problem after 2 or 3 days of access only to that food rich in vitamin B. The initial problem was not insoluble. Rather, the rats' behavioral proclivities were not sufficient to produce an ingestive pattern leading to a solution.

Contradictory outcomes both within and between studies of dietary self-selection are consistent with the view that both the particular foods offered to subjects and individual differences in dietary preference are significant determinants of success. One should not ask whether rats can select adequate diets but rather inquire as to the characteristics of foods that affect the probability of adaptive dietary selection by individuals with differing dietary preferences. In benign ingestive environments, like that of Richter *et al.* (1938), the palatability spectra of many animals may be sufficient to produce a relatively immediate solution. In less benign environments, spontaneous sampling and sensitivity to the consequences of ingestion can sometimes produce solutions. In harsh environments, animals are unable spontaneously to create situations leading to identification of needed nutrients.

The results of Davis' (1928) pioneering studies of diet selection by human infants, like the results of Richter's studies of dietary self-selection by rats in cafeteria feeding situations, have frequently been interpreted as providing evidence that naive omnivores can instinctively select a well-balanced diet from a cafeteria (Story & Brown, 1987). Davis herself, however, was well aware that human infants could self-select an adequate diet only when nutritious unsweetened foods were offered as choices. As Davis (1939, p. 261) stated, "Self-selection can have no, or but doubtful value, if the diet must be selected from

inferior foods." In humans, as in rats, the capacity to self-select adequate diets depends on the diets offered for choice. The provision of an assortment of nutritious, roughly equipalatable foods rather than a capacity to self-select needed foods probably underlay much of the success of Davis' subjects (Rozin, 1976b).

ARE CAFETERIA FEEDING STUDIES ADEQUATE ANALOGUES OF DIET SELECTION IN NATURAL HABITAT? A DEVELOPMENTAL PERSPECTIVE

For the first few weeks or months of life, young mammals are ingestive specialists, sustained by a single nutritionally adequate diet, mother's milk. At some point in development, each individual's caloric needs outstrip either the energy transduction capacities of its dam (Babicky, Ostradalova, Parizek, Kolar, & Bibr, 1970) or her willingness to invest further resources (Trivers, 1974). It is at this point in development, at weaning, that each young omnivore must undertake the transition to omnivory, the potentially arduous task of developing an adequate diet of solid foods. Although adults may be challenged occasionally by a failure of one or another resource on which they have come to depend, every weanling must deal with withdrawal of its major source of sustenance. Thus, one would expect weanlings to solve laboratory analogues of diet selection problems that occur in nature.

It is, therefore, surprising that weanling rats presented with a self-selection task in the laboratory, even one that adults solve easily, often fail dismally in maintaining their body weight. Tribe (1954, 1955) presented 15 100-g female rats with seven foods (corn starch, glucose, margarine, yeast, casein, salt mix, and cod liver oil). Thirteen solved the problem and grew, but only two of ten rat pups survived placement "at weaning" in the same situation. Scott, Smith, and Verney (1948) offered 12- to 15-week-old rats a choice of but four foods [casein, vegetable oil, sucrose, and salt mix (vitamins were fed by pill)]. Thirteen of 20 12- to 15-week-olds gained weight, and all survived, but only nine of 31 weanlings survived in the same situation. Kon (1931) offered 28-day-old rats three dietary elements (casein, sucrose, and salt mix) supplemented with vitamins by hand. Two of his four weanling subjects died, and one gained no weight for 7 weeks. Such failures of weanling rats to solve dietary selection problems far simpler than one might expect them to face in natural circumstances suggest that the laboratory analogue of dietary selection, the cafeteria feeding experiment, does not capture some important aspect of dietary self-selection as it occurs outside the laboratory.

SOCIAL SOLUTIONS TO SELF-SELECTION PROBLEMS

If the ability to self-select an adequate diet is typical of weaning omnivores, then the not infrequent failure of weanling rats to survive diet selection studies in the laboratory poses a problem. Either the genotypes of domestic strains of Norway rat are deficient, the environment in which rats are maintained in the laboratory is so deviant as to preclude the development of a species-typical behavioral capacity, or the cafeteria feeding situation is not an appropriate analogue of the problem faced by weanling rats in natural circumstances.

One unchanging feature of the environment in which all mammals that survive to weaning age develop, absent in all reported laboratory studies of

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dietary self-selection, is the presence of a dam who, by her very existence and reproductive success, has demonstrated the adequacy of her dietary selections. Data from our laboratory suggest that the presence of an adult that has solved the problem of diet selection can be a major factor in the success of juveniles in composing an adequate diet.

In a recent experiment (Beck & Galef, 1989), we presented individual weanling rats with a cafeteria of four distinctively flavored diets. Three of these diets contained inadequate levels of protein (5%), and one had ample protein (20%) for the support of normal growth. We found (see Figure 1), as had Kon (1931), Scott *et al.* (1948), and Tribe (1954, 1955), that our weanling subjects did very poorly in such a situation. None was able to develop a preference for the protein-adequate diet. Each pup appeared well on its way to a premature demise if we had not terminated the experiment. Weanling rats faced with the same diet selection problem while in the presence of adults previously trained to ingest the protein-rich alternative grew rapidly in the experimental situation. Clearly, information acquired from a knowledgeable adult permitted weanlings to select an adequate diet in what we assume is the normal, species-typical fashion of rats.

Our analysis of the behavioral processes involved in social enhancement of dietary self-selection by weanling rats in a cafeteria situation is still in its early stages (Beck & Galef, 1989). However, enough is known about mechanisms of social influence on diet choice in young rats more generally to propose two alternative pictures of how the results shown in Figure 1 might be produced. First, juvenile rats prefer to eat at locations where adults are feeding rather than at locations that adults are ignoring (Galef & Clark, 1971). The simple presence of an adult rat at a feeding site attracts young to that site and causes them to begin feeding there (Galef, 1971, 1981). Adult rats also deposit residual olfactory cues around and in feeding sites they use, and these residual cues attract weanlings and cause them to eat where adults have eaten (Galef, 1986a; Galef & Beck, 1985; Galef & Heiber, 1983). Such social influences on diet selection are in a sense indirect. The presence or activity of adults at a feeding site attracts young and increases the probability that juveniles will eat the food to be found at the socially enhanced site (Galef, 1977). There is, however, no direct specification of what food to eat.

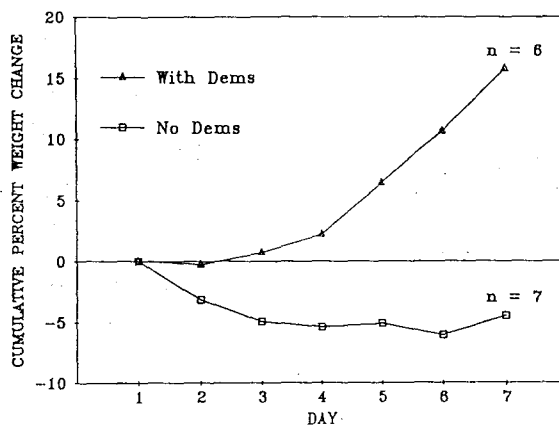


Figure 1. Mean cumulative percent weight change seen in juvenile rats choosing among four diets in the presence and absence of knowledgeable demonstrators.

There is, in addition, considerable evidence of social effects acting directly on diet selection by naive rats. If one rat (a "demonstrator") eats a diet and then interacts with a naive rat (an "observer"), the observer rat subsequently exhibits a markedly enhanced preference for the diet its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983).

In sum, a naive rat pup can exhibit socially enhanced intake of a diet for one of two reasons: either an adult induced the pup to begin feeding at a location where a particular food is found, or an adult directly induced an enhanced preference in the pup for a food that the adult was eating. Either direct or indirect induction of eating of the protein-rich diet could be responsible for the social facilitation of protein ingestion shown in Figure 1.

The fragility of weanling rats and their frequent failure to self-select adequate diets when alone in laboratory cafeteria feeding studies has imposed a research strategy on laboratory investigators of dietary self-selection by rats. Investigators extend the young rat's period of total dependence on others for diet selection by weaning pups from mother's milk to a nutritionally adequate chow compounded by nutritionists. Weaning from milk to chow maintains animals in a state of naiveté with respect to problems of nutrient selection. Adults maintained on chow from weaning and faced for the first time with a need to self-select nutrients have served as model systems for studying a process that normally occurs at the time of weaning from mother's milk.

Naive adult rats, like naive weanlings, often have difficulty in solving even relatively simple diet-selection problems. McDonald *et al.* (1963) offered 12 individually housed 90-day-old rats a four-choice cafeteria (sugar, salt mix, casein, and vegetable oil), and six lost weight. Similarly, Schutz and Pilgrim (1954) found that 21 of 43 young adult rats were losing weight 3 weeks after being offered a four-choice cafeteria similar to those used by Scott (1946) and Pilgrim and Patton (1947). Rozin (1968) offered ten thiamine-deficient rats a choice among three novel diets only one of which contained thiamine, and four of his ten subjects failed to select the thiamine-rich food.

Adult rats, like weanlings, will show facilitation of diet selection when in the presence of knowledgeable adult conspecifics. As can be seen in Figure 2, when individually housed adult rats were offered a choice of four novel diets, only one

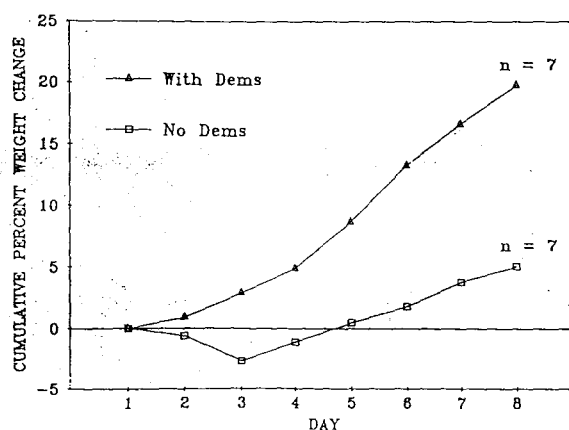


Figure 2. Mean cumulative percentage weight change seen in adult rats choosing among four diets in the presence and absence of knowledgeable demonstrators.

