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Food Selection: Problems in Understanding How we Choose Foods to Eat

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GALEF, B. G. JR. *Food selection: Problems in understanding how we choose foods to eat.* NEUROSCI BIOBEHAV REV **20**(1) 67–73, 1996.— Understanding food selection will require considerably more than reductionist analyses of the internal workings of individual animals. To understand food choice we will have to examine not only the physiology and behavior of individuals, but also the biological and social environments within which individuals select items to ingest. The biological environment determines patterns of food availability and, over evolutionary time, provides selective pressures which shape sensory–affective responses to flavors, making them adaptive with respect to local conditions. Direct experience of the consequences of ingesting potential foods and interaction with conspecifics that have eaten various foods both affect food choices. These multiple influences, acting at different levels of organization, can bias food selection by individuals in either adaptive or maladaptive directions, depending on the characteristics of the environment in which feeding occurs. The need to understand the relationship between internal organization, individual and social experience and ecological demands may make food choice the most difficult of the core aspects of feeding behavior to analyze satisfactorily.

Food selection Dietary generalists Dietary specialists Hedonic responses Individual learning Social learning

INTRODUCTION

UNDERSTANDING THE feeding behavior of animals with complex nervous systems requires analysis of physiological and behavioral systems that support three related activities: (1) selection of items to eat; (2) initiation of ingestion; and (3) termination of ingestion. For a variety of reasons, practical, historical and intellectual (43) studies of meal initiation and termination have captured the lion's share of academic attention for the last decade. When we do return to the study of food preference and choice, as we inevitably must, we will find it the most difficult of the three core aspects of ingestive behavior to analyze satisfactorily because understanding food selection requires more than a natural-science-based, reductionist analysis of the internal workings of organisms. To understand food choice we are going to have to look not only at the physiology of individuals, but also at the interaction between the individual and the ecological and social environments in which it feeds. Study of ecology will be necessary because patterns of food availability are major determinants of which foods organisms eat. Study of social influences on food choice will be important because, especially in our own species (but in other species as well), social or cultural factors are major determinants not only of which foods are available, but also of which available foods are selected for ingestion.

To understand food selection, we will also have to deal with the fact that, over evolutionary time, the relative abundance and scarcity of particular nutrients, as well as the presence of toxic secondary compounds in some potential foods, have shaped congenital hedonic responses to both flavors and textures. Unhappily for the student of ingestive behavior, environments that prevailed when the hedonic responses of humans (and of many economically important animals) were shaped by natural selection no longer exist. Consequently, we can only speculate about the selective pressures which shaped hedonic responses to flavors both in our own species, in which cultural innovations from agriculture to cuisine have markedly altered feeding choices, and in the many pest species that currently exploit either the agriculture production or waste of humankind.

I am not optimistic that our understanding of food selection by species like rats, mice, Herring gulls or human beings, which today occupy ecological niches markedly different from those in which their hedonic responses to flavors and textures evolved, will ever be as complete as our understanding of the physiological processes that support initiation and termination of feeding bouts promises to be. However, regardless of the difficulties, investigations of food selection must eventually share center stage with studies of the physiology of food intake because practical problems in feeding behavior are a result not only of eating inappropriate amounts, but also of inappropriate choices of substances to ingest (20, 26, 59).

Further, nature has not permitted us the luxury of treating food selection and feeding bout initiation and termination as independent processes. Varying the foods eaten during a meal or selecting highly palatable foods to eat can influence the duration of meals, the number of calories consumed and the body weights of individuals (9, 30, 40, 42–44, 50, 56). Similarly, choosing to eat foods with much of their caloric content in fat rather than carbohydrates or proteins can increase intake and body weight (26, 31, 59).

DIETARY GENERALISTS AND DIETARY SPECIALISTS

As those who have read any of Paul Rozin's excellent reviews of diet selection (46, 48, 49) are surely aware, it is traditional to organize discussion of the topic of food choice in terms of two broad classes of animals: dietary specialists that, in their respective natural habitats, eat only a single type of food, and dietary generalists (sometimes referred to as omnivores) that, in nature, regularly ingest a variety of different substances.

While the distinction between dietary specialists and generalists has proven useful, it has been trivialized to some extent by the tendency, when discussing dietary specialists, to treat them as a collection of interesting but rare and behaviorally primitive animals that need be mentioned only for the sake of completeness or because of the belief that somewhere in the sophisticated feeding machinery of the dietary generalist, there lurks a primitive specialist seeking salt and water.

Unfortunately, once an animal species has been assigned to the class of dietary specialist (a fate most frequently suffered by the koala, *Phascolarctos cinereus*),* it is implicitly assumed that the food choices of members of that species are understood and no longer pose important or interesting questions. This is, of course, not true. In our rush to get on to study of the feeding behavior of animals that, like *Homo sapiens*, are more eclectic in their selection of substances to consume than are vampire bats or anteaters, we often ignore the fact that we know little about either the psychology or physiology of feeding by dietary specialists.

Animals that, to survive and reproduce, need simply *choose* among nutritionally balanced items which differ only in size, probability of encounter, and difficulty of capture and dismemberment, pose problems for the student of food choice as important as those posed by species that must *compose* nutritionally balanced diets by ingesting a multitude of different foods, each of which lacks one or more necessary nutrients.

ANIMALS THAT CHOOSE AMONG NUTRITIONALLY SIMILAR ITEMS

Predators (carnivores, piscivores, insectivores, etc.) choose among nutritionally equivalent food items that vary in size and availability rather than compose diets from items having markedly different nutritionally value. Consequently, predators face a less diverse set of challenges in selecting items to ingest than animals either lower on the food chain or more catholic in their tastes.

Broadly speaking, for a lion, each zebra or gazelle is a naturally occurring, mobile Purina pellet that contains the full range of nutrients that lions must ingest to survive and reproduce. A lion need not worry about basic food groups; to survive, it need only select places to hunt and prey to pursue with sufficient wisdom so as to capture food items providing more energy than was expended in their capture and consumption.

Of course, competition for resources and consequent natural selection have resulted in evolution of lions that can do far better than merely achieve energy balance. Indeed, it is not unreasonable to assume that natural selection will have driven lions as it has driven members of every species, towards that combination of traits that exceeds all others in its contribution to fitness. Although natural selection will not produce lions that are perfect hunters, it should consistently favor the best hunting phenotypes allowed by phylogenetic constraints and restraining trade-offs that act upon the evolution of lions. In fact, analyses of patterns of food choice by a variety of predatory animals reveal that many select prey in a fashion close to the theoretical optimum, maximizing their rate of net energy gain (see 28, 55 for reviews). As developed over the past 20 years, quantitative optimality models have provided a method for raising the study of evolutionary design of predators and other animals that choose food items, rather than compose diets, from the ingenious story telling that many scientific reductionists find objectionable to a level where quantitative hypotheses can be derived and experimentally tested.

I've spent more time than is customary discussing food choice by specialists to make clear that animals that choose among nutritionally similar food items, like those that compose diets, face problems in food selection that require analysis and to remind you that our colleagues in behavioral ecology have developed a method for analyzing patterns of food choice which those of us interested in feeding in animals that compose their diets have seldom used to advantage

*In its natural environment, even the koala, the prototypic dietary specialist, appears to face all the problems of food selection faced by generalist, diet composers. Koala feed on 50 or more of the 600 species of Australian eucalyptus which vary markedly both in caloric content and in the secondary compounds that they contain (23). Ten to 12 of the eucalyptus species that koala feed on are preferred food sources, koala particularly liking smooth barked trees of high oil content such as Blue and Grey gums. Koala also feed on approximately 10 plant species that are not eucalyptus.

Koala not only select particular species of eucalypt to eat, they also select individual trees within a eucalypt species on which to browse, though the criteria used in this selection process are not known (23). Within eucalyptus trees that koala are browsing, young leaves of some species contain potentially lethal concentrations of prussic acid and must be avoided (57).

Most interesting, eucalyptus leaves do not provide sufficient calcium for construction of mammalian bone, and koala descend regularly to the forest floor to feed on mineral-rich earth (57). Clearly, koala are diet composers with clear food preferences, problems in poison avoidance, and a need to redress deficiencies in their diets. They should not be thought of as monophageous dietary specialists.

(for an exception, see 10) but which can be used to analyze the feeding behavior of dietary generalists as well as that of dietary specialists (1–3).

ANIMALS THAT COMPOSE NUTRITIONALLY ADEQUATE DIETS

Animals that compose their diets face challenges considerably more daunting than animals choosing among nutritionally balanced food items. In response to those challenges, dietary generalists have evolved a number of behavioral mechanisms that can make substantial contributions to success in diet composition. It is, however, well to keep in mind that, despite the range of relevant abilities possessed by diet composers, they often fail to compose adequate diets (14, 15).

CONGENITAL HEDONIC RESPONSES TO THE CHARACTERISTICS OF FOOD

Selection of foods to eat begins with the detection of textural and structural characteristics of a potential food by the tongue, lips and incisors as an object is held and bitten, and with the near simultaneous activation of olfactory and gustatory systems that both discriminate among and respond hedonically to chemical stimuli introduced into the oral cavity (7, 61).

As a general rule, molecules that serve as energy carriers, such as sugars, are perceived as sweet by humans and tend to be accepted by both humans and animals (37). Rejection responses are induced in animals by substances that humans find bitter or sour, for example, inorganic acids, alkaloids and glycosides, that are sometimes useless, or even dangerous, to ingest (19).

In our own species at least, some acceptance and rejection responses to flavors are congenital and are evident even before experience of the consequences of their ingestion. Just after birth, human infants exhibit vigorous, apparently appetitive responses to sweet tasting substances and equally vigorous responses, that appear to result in expulsion from the mouth, to both sour- and bitter-tasting items (45, 54).

The tendency to accept substances described by adult humans as "sweet" (37) and to reject those perceived as "bitter" is widespread phylogenetically (19,62) and probably results from evolution of convergent mechanisms that bias food selection in the natural habitat in adaptive directions.

Observations suggesting that many members of diet composing species introduced into alien ecosystems poison themselves by eating unfamiliar toxic plants that members of endemic species do not eat are consistent with the hypothesis that at least some biases in flavor preference are evolved responses to local environmental pressures. The difficulties exhibited by animals moved into alien environments (domestic cattle to the grazing lands of North America (24), sheep to Australia (4, p. 119), or Japanese macaques to Texas (11)) in adapting their food selection to the demands of their new homes provide compelling evidence that the gustatory system does not provide

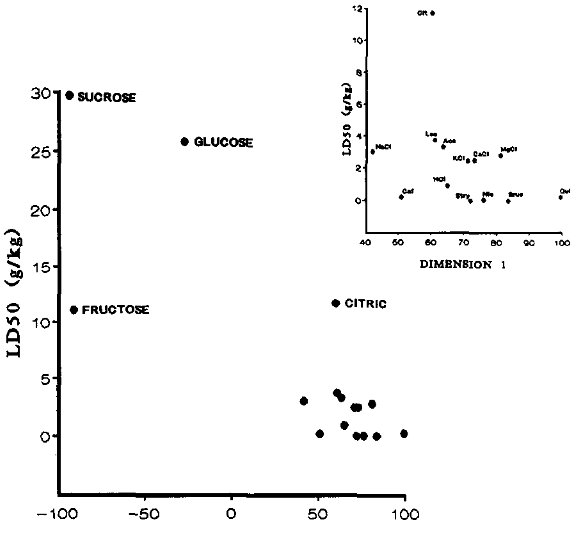

FIG. 1. LD_{50} in g/kg of various chemicals as a function of the profile of response each invokes in the nucleus tractus solitarius when applied to the tongue. Insert is an enlargement of the cluster of points scoring from 40 to 100 on Dimension 1 of response.

anything approaching total protection against ingestion of toxic compounds.

Such observations are not easily reconciled with the proposal (53) that the electrophysiological response profiles of certain cells in the brainstem are correlated with the toxicity of chemical stimuli applied to the tongue. Taken at face value, the significant correlation between electrophysiological response and toxicity (53) suggests that the taste system can respond directly to the toxicity of simple chemicals. However, looking at Fig. 1, prepared from data provided in Scott and Mark (53), it is apparent that, although the response

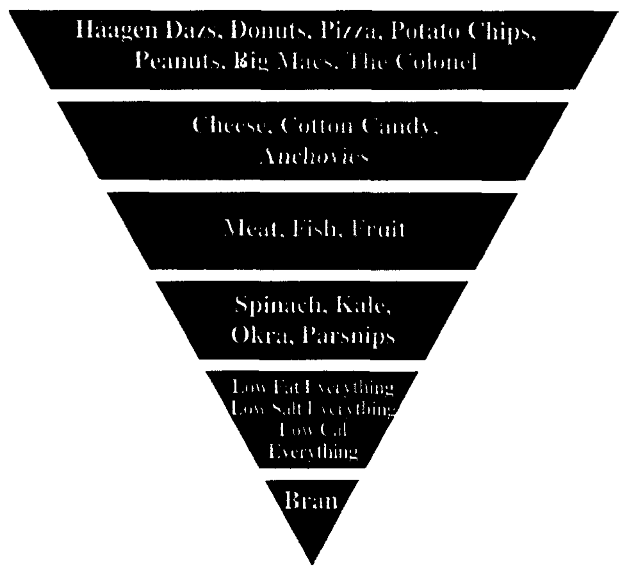

FIG. 2. Hedonic food pyramid.

profile of the nucleus tractus solitarius (NTS) of rats can be used to identify some sugars, the responses of the NTS are not of much use in discriminating among other flavored substances. When selecting foods to eat, I personally would not put much faith in a system which indicated that strychnine is intermediate in toxicity between $CaCl_2$ and $MgCl_2$, or that caffeine is less toxic than either $CaCl_2$ or lactic acid.

The unreliability of the taste system as a guide to ingestion is not limited to toxins; the taste system is also of only marginal use in directing intake toward necessary nutrients. Compare the food pyramid (purported to provide a rough guide to the relative amounts of various types of foods we humans should be eating) with a hedonic scale of the palatabilities of various foods. At the pinnacle of the hedonic scale stand combinations of sugar and fat (candy, ice cream) and salt and fat (potato chips, french fries, Big Macs, pizza, etc.) that so sorely tempt us all, and which we would be well advised to avoid eating entirely, or so the medics tell us. Conversely, at the bottom of the hedonic scale lie the fiber-rich products that should form the basis of our diets, but which many of us do not find particularly palatable even when adorned with fat, sugar or salt.

Our hedonic responses to gustatory stimulation and our associated motivations to seek out certain flavors may have been useful in some ancestral environment, presumably one in which sugars, fat and salt were hard to come by and special motivations to seek such substances were of adaptive value. However, when our motivational system, evolved to cope with an environment in which calorically dense materials and sodium were relatively scarce, interacts with the superabundance provided by commercial agriculture, our hedonic responses tend to produce injurious levels of intake of the sweet, the salty and the greasy. And, because our bodies are not designed to cope with the hedonically driven selection of foods we are motivated to ingest, some of the diseases of the modern world emerge. Tooth decay, rare in non-Western societies, is largely a result of extended exposure of teeth to sugar. Obesity and its sequelae diabetes, cardiovascular disease and, possibly, even cancer of the gastrointestinal system are associated with high levels of fat intake. In some populations, hypertension is aggravated by elevated salt intake, and so on (60).

The magnitude of the problems posed by the maladaptiveness of hedonically driven food selection is nowhere better illustrated than in the Pima Indians of the American southwest who, historically, were athletic people famed as long-distance runners. Today, 50% of adult Pima men and women exceed the 90th percentile on a US age-specific index of body mass. Consequently, although 100 years ago, diabetes was essentially unknown among the Pima, today, their rate of diabetes is 19 times greater than that found in comparative Caucasian populations. The Pima have the highest rate of diabetes-related amputation and kidney dialysis in the USA (52). Increasing the range of foods and beverages available to the Pima (and other Indians of the American southwest as well as many of the indigenous peoples of the Pacific with genetic affinity to the Pima) created an hedonically driven, diet-selection-based health catastrophe (27).

The message here is that, although a congenital pattern of hedonic response to flavors may well have been effective in guiding food choice in adaptive directions in the environment in which that pattern of hedonic response evolved, there is no reason to expect members of species whose ranges and food choices have expanded dramatically in the last few thousand years to be able to identify either toxins or desirable foods on the basis of their sensory qualities. In particular, there is no reason to expect the "wisdom of the body" to lead humans to make wise food choices when faced with the superabundance of the modern supermarket or rats to select balanced diets when allowed to choose from among purified foods in laboratory cafeteria feeding situations (14). The problem currently faced by humans is particularly acute given the extensive work of food manufacturers on the ethology of feeding and the design of superoptimal releasers of feeding behavior, from Big Macs to Twinkees.

THE ROLE OF PLASTICITY IN SELECTION OF FOODS

If reflexive hedonic responses of the olfactory/gustatory system were particularly effective either in guiding animals to valuable foods or in protecting animals from ingesting toxins, one would expect the olfactory/gustatory system to be relatively resistant to modification by experience, to be in Mayr's (34) terminology a closed system. Instead, we find that responses to tastes can be altered by a range of experiences. Such plasticity in response to flavors is central to much of whatever success in diet composition that diet composers enjoy.

Simple Exposure Effects

Prolonged exposure to a congenitally distasteful flavor can produce not just acceptance, but a perverse preference for otherwise unpalatable tastes. For example, Moskowitz et al. (35) reported many years ago that north Indian laborers describe quinine-sulfate (bitter) solutions as exceptionally pleasant at low concentrations and find citric acid (a sour taste), like a sweet taste (sucrose), increasingly pleasant with increasing concentration. Similarly, as Rozin and his co-workers have demonstrated, humans come to exhibit a liking for the congenitally aversive burn of capsiacin following repeated exposure in social situations to foods containing that irritant (47).

On the other hand, within a meal, frequent exposure to a food can lead to a decrease in liking for that food (56). We know relatively little about the conditions that result in either exposure-induced liking (63) or exposure-induced avoidance of flavors and foods.

Effects of Associative Learning

Experiences other than repeated exposure to a congenitally unpleasant or neutral gustatory stimuli can lead to increased intake of substances containing such stimuli. Pairing a flavor with any of a variety of positive events—recovery from morphine withdrawal

(36), reduction of a caloric deficit (5, 51) or experience of a palatable substance (22, 64)—can enhance preference for that flavor. It is not clear whether alteration in intake subsequent to association with a beneficial consequence results from a change in hedonic response (6) or from some other process.

Not only can congenitally aversive substances become more acceptable as a consequence of simple exposure, but congenitally palatable flavors can become aversive, if they are paired with certain sorts of illness (17, 18, 20). Again, it is not obvious whether rejection following induction of taste aversion is the result of an hedonic shift (e.g., a sweet taste becoming perceptually unpleasant), as Garcia and Hankins (19) originally proposed, a consequence of conditioned induction of illness by the taste CS (38) or the result of a more cognitive process by means of which subjects learn that a flavor is not safe to eat (25). Also, why some agents which induce illness in animals produce taste-aversion learning, while others do not (17, 39), is not clear.

In any case, the failure of animals either to learn to avoid ingesting foods associated with some types of illness (as in the case of quinine or ammonium sulfate poisoning in rats; 39), or to learn to eat foods leading to recovery from illness [as in scurvy in humans (8, 21)], is an obvious limitation on the efficacy of plasticity of response in guiding diet composition in adaptive directions.

Social Influences on Food Choice

The probability that an individual will ingest some food is often affected by interaction with conspecifics that have eaten that food. The importance of such social or cultural influence on food selection by members of our own species has been known for centuries, but it is only relatively recently that analogous social influences on food choice have been demonstrated in a variety of animal species (see 12). Red-wing blackbirds that observe conspecifics eating from distinctively colored containers subsequently prefer to eat from similar containers, while blackbirds that observe conspecifics eating from the same containers and then becoming violently ill are unwilling to eat from them (32, 33). Both Norway rats and house mice that interact with conspecifics that have recently eaten an unfamiliar food develop strong preferences for that food (16, 58). In many species, the presence of conspecifics at a feeding site attracts conspecifics to that site and causes them to begin eating there (see 29 for review).

Interactions Among Effects

Interactions between effects of direct personal experience of consequences of ingesting foods and information about the same foods acquired from conspecifics have the potential to considerably complicate analyses of the development of food choices. For example, Norway rats that interact with a conspecific that has eaten a food show an inhibition of their subsequent probability of learning an aversion to that food (13). Clearly, analyses of the development of patterns of food selection in many species will require study of the social milieu in which food choices are made as well as investigations of species members' congenital hedonic responses and direct effects on individuals' food choices of various sorts of personal feeding experiences.

SUMMARY AND CONCLUSION

Two quite different feeding strategies have evolved in animals. Food selectors, particularly predators that ingest items each of which provide a nutritionally balanced meal, can focus on maximizing their rate of caloric gain. Animals that compose a nutritionally balanced diet by eating a mix of foods that differ in nutritional value have a more complex task; they must select a range of substances to ingest that provide all required nutrients, apportion intake among those substances in order to achieve a nutritionally balanced diet and still ingest more energy than they expend acquiring food.

Diet composers have evolved a range of behavioral mechanisms that facilitate both the selection of foods providing benefits and the avoidance of ingestion of toxins: congenital hedonic responses to stimulation of the olfactory/gustatory system of diet composers provide a rough means of discriminating valuable foods from toxic items to be found in a species' natural habitat. The ability to associate flavors with both positive and negative consequences of ingestion sometimes permits identification of either toxins or substances that redress dietary deficiencies, caloric deficits and illness. Information gained as a result of observation or interaction with knowledgeable conspecifics can lead naive individuals to rich feeding sites and guide them both to ingest valuable foods and to avoid ingesting dangerous ones.

The varied armamentarium that animals employ when attempting to select an adequate diet is, however, no guarantee of success. Physiological and behavioral mechanisms that evolved in response to challenges present in the ancestral homes of today's cosmopolitan species (e.g., rats, mice, cockroaches, gulls or human beings) need not respond adaptively to the conditions that organisms encounter as they move about the world and occupy ecological niches quite different from those in which they evolved. All too often, humans become obese when faced with the panoply of foodstuffs available in countries of the first world. Rats living as human commensals encounter tasteless, slow-acting poisons in palatable baits, ingest lethal amounts of those toxins and die by the tens of millions every year.

The wisdom of the body is not an all-purpose wisdom, it is a wisdom shaped by natural selection over millennia to cope with specific environmental challenges. The wisdom of the body is only locally adaptive, and we are often studying species which, like our own, have only relatively recently become cosmopolitan in distribution. Widely-distributed species encounter potential foods that their ancestors never encountered; they must decide to either eat or reject substances unknown to their forbears. The challenge we face as students of diet selection is to predict and control the ingestive behavior of animals and humans responding to sensory inputs that were never before part of their evolutionary histories.

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