

Development of Flavor Preference in Man and Animals: The Role of Social and Nonsocial Factors

BENNETT G. GALEF, JR.
McMaster University

I. Introduction: Behaviorism, Hedonics, Biology, and Flavor Preference Development	412
II. Inherent Sensory-Affective Bias	414
III. Effects of Postnatal Experience on Flavor Preference	416
A. Simple Exposure	416
B. Association Learning	417
IV. Social Factors in Development of Flavor Preference	418
A. Social Factors in Development of Flavor Acceptance	419
B. Social Factors in Development of Flavor Rejection	424
V. Conclusion: Preference Development in Animals and Man	425
References	427

The present chapter concerns the ontogeny of response to gustatory stimuli in both animals and man.¹ More specifically, it is about the

¹ Whereas it is both convenient and conventional to compare the behavior of man and animals, any conclusions drawn from such comparisons must be extremely tentative. Nearly a century of study has provided an incomplete picture of the feeding behavior of a few mammalian species, an inadequate sample, selected in large measure for reasons of experimental convenience, from among the 4237 extant mammalian species (Morris, 1965). It would have been more accurate, if less interesting, to title the present chapter "Preference development in domesticated Norway rats and man."

development of acceptance and rejection responses to gustatory sensation; and more specifically still, it concerns the contribution of both nonsocial experiences and of social interactions to the ontogeny of diet preference.

The organization of the chapter reflects the fact that it is the individual organism that ultimately selects items for ingestion. Social influence acts only indirectly in the development of taste acceptance or rejection by affecting processes that channel flavor preference development in the individual. Thus, discussion of the mechanisms underlying development of flavor preference in individuals is a necessary antecedent to discussion of the ways in which social factors influence the development of individual response to gustatory stimuli.

I. INTRODUCTION: BEHAVIORISM, HEDONICS, BIOLOGY, AND FLAVOR PREFERENCE DEVELOPMENT

The major function of the sense of taste is to enable organisms to use chemical cues to select appropriate items for ingestion from among the multitude of nutritive, nonnutritive and toxic objects encountered in natural habitats. Possession of a sensory system able to detect chemical properties of potential ingesta would be of little use to the detecting organism without a concomitant behavioral capacity to either accept or reject items as food on the basis of their sensed chemical properties. Consequently, discussion of the development of the functioning ingestive system requires consideration of the development of two capacities: the capacity to sense gustatory stimuli and the capacity to respond behaviorally to gustatory sensations. The present chapter concerns the development of behavioral response to gustatory stimuli. (For a discussion of the development of gustatory sensation per se, see Mistretta, Chapter 15, this volume.)

The phenomenon with which I am concerned is easily described: any organism will more readily accept some items for ingestion than others. Clearly, the ontogeny of such flavor preferences can be discussed in terms of observable behavior without reference to hypothetical underlying internal states. However, recent interest in internal process oriented interpretations of behavior (Griffin, 1976) and hedonic models (Cabanac, 1979) has produced a second vocabulary of use in discussion of data relevant to questions concerning development of flavor preference. Although there is reason to prefer explanations of behavior stated in terms of observable events to those invoking hypothetical internal states as explanatory concepts, the vocabulary of hedonic

models can be useful in clarifying conceptual issues relevant to the ontogeny of responses to gustatory stimuli.

In particular, I find it helpful in thinking about the ontogeny of response to tastes to conceive of gustatory stimuli as evoking response in two relatively independent dimensions: a discriminative dimension and an affective one (Cabanac, 1979; Young, 1959). The discriminative dimension describes the detectability and identifiability of a stimulus, whereas the affective dimension describes the amount of pleasure or displeasure that a stimulus arouses in a sensing organism. Within hedonic models of perception, it is usually assumed that there is a direct relationship between the affective dimension of perception and behavior. Pleasurable stimuli elicit approach and acceptance, whereas displeasure induces avoidance and rejection. One advantage of conceptualizing the discriminative and affective responses to gustatory stimuli as distinct from one another is that such conceptualization permits separate discussion of the ontogeny of each dimension of response.

The assumption that organisms respond affectively to gustatory stimuli implies the existence of physiological systems that produce sensations of pleasure and displeasure in response to taste. These physiological systems may be conceived of as species-typical features, evolved to promote efficient utilization of food resources by species members in their natural habitats. On this model, natural selection is seen as having acted to produce physiological systems that cause sensations of pleasure in response to gustatory stimuli frequently predicting the presence of needed nutrients and sensations of displeasure in response to gustatory stimuli frequently predicting the presence of toxins. Within such a framework, one can consider organisms as selected to choose ingesta maximizing pleasant, and minimizing unpleasant, gustatory sensation.²

As a general rule, molecules that serve as energy carriers, such as sugars, are perceived as pleasant tasting by man and tend to be accepted by both humans and animals. Unpleasant sensations and rejection responses are induced by bitter substances, for example, alkaloids and glycosides that are characteristically useless or even dangerous to ingest. This tendency to accept substances described by man as "sweet" (Pfaffman, 1975) and to reject those perceived as "bitter" is extremely widespread phylogenetically (Garcia & Hankins, 1975; Young, 1968) and probably represents a set of convergent mechanisms for biasing diet

² On this model, homeostatic or regulatory influences on dietary selection are conceived of as acting via changes in perceived palatability (see Cabanac, 1979, for relevant discussion).

selection in natural habitats in adaptive directions (Longhurst, Oh, Jones, & Kepner, 1968). Evidence that species introduced by man into alien ecosystems often succumb to unfamiliar toxic plants that are rejected native species is consistent with the hypothesis that at least some biases in diet preference are the product of natural selection (Arnold & Dudzinski, 1978, p. 119). Species that typically do not respond positively to sweet tastes, such as sucrose (e.g., cats and chickens) (Beauchamp, Maller, & Rogers, 1977; Gentle, 1972; Kare, 1961), or respond positively to generally aversive tastes, such as bitter, pose interesting but as yet unresolved problems in behavioral ecology and comparative physiology (see Young, 1968).

II. INHERENT SENSORY-AFFECTIVE BIAS

If natural selection has acted to produce physiological mechanisms that bias naive individuals toward experiencing certain gustatory stimuli as more pleasurable than others, one would expect to observe species-typical acceptance and rejection responses to various flavors in the newborn.

Although empirical evidence of affective bias in response to taste in neonates is rare, the results of studies with human infants are consistent with the view that such biases are present immediately following birth. Steiner (1974, 1977) has photographed the facial expressions of human infants in response to their first extrauterine gustatory experiences. He reports that application of 0.5 ml of concentrated solutions of sweet, bitter, and sour flavorants onto the central area of the dorsal tongue surface elicits reliably different responses. Administration of a 25% sucrose solution produced a slight smile, followed by licking and sucking; similar exposure to 0.25% quinine-sulfate solution elicited tongue protrusion, splitting, and depression of the mouth angles. Sour taste (2.5% citric acid) elicited pursing and protusion of the lips, accompanied by nose wrinkling.

Such observations are consistent with the hypothesis that the physiology of the organism, as it develops in the normal uterine environment, predisposes the infant to experience certain gustatory sensations as more pleasurable than others. It is admittedly an extrapolation from these data to infer that the facial expressions of human neonates reflect affective states similar to those of adults. However, the observed differential response to sweet, sour, and bitter certainly indicates an ability of human infants to discriminate among the various flavors immediately following birth and suggests that some of these flavors may be more pleasurable to infants than are others.

If human infants are born with affective biases with respect to gustatory sensation, they should exhibit alterations in intake as well as changes in facial expression in response to the taste of potential ingesta. Surprisingly, investigators of the ingestive responses of human neonates to sweet, bitter, and sour solutions have found that, although addition of sugars to water results in enhanced solution intake, the addition of urea (bitter taste) or of citric acid (sour taste) does not reliably result in decreased intake (Desor, Maller, & Andrews, 1975; Desor, Maller, & Turner, 1973; Maller & Desor, 1974; also see Nisbett & Gurwitz, 1970).

Two conclusions are suggested by Desor and Maller's and Steiner's data considered together. First, receptor response, hedonic response, and augmentation of intake in response to sweet sensation are all intact and functional in the human neonate shortly after birth. Second, response to bitter flavor, and perhaps to sour as well, are not in the adult state in the infant. Although, as Steiner's data show, the infant human can detect sour and bitter, either the neonate does not find sour or bitter aversive or the sucking mechanism is not subject to inhibition by unpalatability. One might therefore expect a postnatal development of the sour-bitter rejection system in humans absent in the sweet acceptance system.

Comparable evidence on the development of response to tastes in infrahuman species is not presently available. However, a series of recently devised techniques should greatly facilitate future study of the development of response to gustatory stimuli in infant animals.

Johanson and Hall (1979) have developed a procedure allowing a 1-day-old rat pup to exhibit discriminated learning of a lever press response for rewards of small infusions of fluid into its mouth. Minor modifications in apparatus, providing the opportunity for pups to choose between infused solutions of varying taste, would permit both determination of flavor preferences shortly after birth and study of the development of both discriminative and affective functioning. Grill and Norgren (1978a,b) developed a system for describing the movements of the tongue, jaw, and face of adult rats in response to the infusion of small quantities of flavored solutions into their mouths. Extension of this descriptive system to neonatal rats would permit experiments with infrahuman subjects analogous to Steiner's previously described work with human infants.

Also, recent innovations in the measurement of the heart rate profiles of neonatal rats in response to olfactory stimuli could be adapted to the study of response to gustatory cues, permitting the monitoring of alterations in response to tastes resulting from experience (see Martin & Alberts, 1979; Alberts, Chapter 11, this volume). The development

of such techniques for behavioral measurement in neonatal animals provides the opportunity for a very rapid expansion of information concerning both the taste preferences of organisms immediately after birth and the effectiveness of experience in altering infantile preferences.

III. EFFECTS OF POSTNATAL EXPERIENCE ON FLAVOR PREFERENCE

Even if neonates experience certain gustatory sensations as pleasant and others as unpleasant, this does not mean that response to gustatory sensation at either the hedonic or behavioral level cannot change as the result of experience. Genotypes predisposing the individual to develop palatability preferences typical of its species can only be adaptive with respect to the mean properties of that species' ecological niche (Williams, 1966). Behavioral plasticity in response to gustatory cues enables individuals to adapt to the special demands of the particular area in which they are located. Because potential ingesta are frequently heterogeneous across a species' range, one would expect the physiological systems underlying affective response to taste to be "open-programs" in Mayr's (1974) sense. That is, one would expect these systems to be subject to modification by experience during the life of the organism so that the individual would have the capacity to learn to ingest nutritive substances or to avoid toxic substances idiosyncratic to its particular home range.

A wide variety of studies indicate that the same gustatory stimulus may be responded to by an individual as either pleasant or unpleasant depending on that individual's previous experience. The term "alliesthesia" has been suggested as a label for such changes in hedonic response, a "negative alliesthesia" being an increase in the perceived unpleasantness of a fixed stimulus and a "positive alliesthesia" the reverse (Cabanac, 1979). Current evidence suggests that two very different types of experience can produce profound alliesthesias.

A. Simple Exposure

Data from studies of both animals and humans indicate that, as a general rule, familiar tastes are preferred to novel ones. Effects of familiarity on taste preference, measured either in terms of intake (in infants or animals) or by preference ratings (in adult humans), can be profound and familiarity can result in what those of us lacking a given exposure-induced preference might consider perverse hedonic response. For example, Moskowitz has reported that north Indian laborers describe quinine-sulfate (bitter) solutions as exceptionally pleasant at

low concentrations and find citric acid, a sour taste, like sweet taste (sucrose), increasingly pleasant with increasing concentration. These hedonic responses contrast markedly with those generally exhibited by other human subjects. (Both Americans and Indian medical students report that sourness and bitterness become increasingly unpleasant with increasing concentration and neither finds bitter taste highly palatable at any concentration).

The north Indian laborers studied by Moskowitz and his colleagues subsist on a sparse diet that contains many sour fruits. The tamarind fruit, which tastes extremely sour and slightly bitter, is chewed by the laborers as a confection and is used by them as a flavorant in staple foods (Moskowitz, Kumraiah, Sharma, Jacobs, & Sharma, 1975). Whereas it is possible that genetic inbreeding among the laborers has yielded a population with anomalous inherent biases toward sour and bitter, it seems more likely that they, like Mexican peasant populations whose members exhibit strong preference for "hot" foods, do so as a result of gradual familiarization with the relevant flavorants (Rozin, 1977; Rozin & Schiller, 1980).

Data from animals support the generalization that simple exposure to a diet can enhance intake of that diet and, presumably, change hedonic response to it. In a particularly striking demonstration of the effects of brief exposures on preference in animals, Siegel (1974) exposed different groups of rats to either coffee or vinegar solutions for 30 min and either 7 or 24 days later measured the intake of all subjects of the two solutions in a series of five daily simultaneous choice tests. Subjects ingested approximately twice as much of the preexposed flavor as the novel one in each test. Although Siegel's methods resulted in the demonstration of long-lasting and robust effects of brief exposure to a flavor, his results are, so far as I know, exceptional in the duration of the effects observed. Attempts to demonstrate long-term changes in taste preference in animals as the result of simple exposure to a flavor generally have not been successful (Capretta, 1977; Capretta & Rawls, 1974; Rozin, Gruss, & Berk, 1979; Warren & Pfaffman, 1959). The effects of exposing animals to a given flavor seem to gradually dissipate if the subject has the opportunity to sample other flavors of greater species-typical acceptability. Information on the factors effecting the duration of exposure effects on palatability and preference in animals are both lacking and much needed.

B. Association Learning

There are, of course, experiences other than simple exposure to a gustatory stimulus that can profoundly affect an organism's acceptance

or rejection of that stimulus. A flavor, even a highly palatable one, that has been experienced prior to an experimentally induced illness, will subsequently be rejected (Garcia & Ervin, 1968; Garcia & Koelling, 1966). Whether this rejection results from an hedonic shift (e.g. a sweet taste actually becoming perceptually unpleasant), as Garcia and Hankins (1977) have argued (see also Rozin, 1967; 1979), or from an association of the flavor with illness (Revusky, 1977), or from a more cognitive process in which the subject learns that a flavor is not safe (Kalat & Rozin, 1973) is not yet clear.

Just as the association of a flavor with illness reduces subsequent ingestion of the illness-associated flavor, association of a flavor with recovery from illness can enhance intake of the recovery-associated flavor (Zahorik, 1977; Zahorik, Maier, & Pies, 1974). Demonstrations of enhanced intake of a flavor as the result of association of that flavor with beneficial postingestional consequences such as recovery from illness (Green & Garcia, 1971), recovery from morphine withdrawal (Parker, Faylor, & Weidman, 1973), or reduction of caloric deficit (Holman, 1969; Siqueland, 1965), are far less common in the literature than demonstrations of reduced intake following flavor-illness pairing and are generally of lesser magnitude and duration (Zahorik, 1977). Again it is not known whether the alteration in intake subsequent to flavor-beneficial consequence pairings results from an allesthesia or some other process.

IV. SOCIAL FACTORS IN THE DEVELOPMENT OF FLAVOR PREFERENCE

Whereas much of the development of flavor preference in animals depends on the experience of individuals feeding in isolation, members of many vertebrate species eat in the presence of conspecifics and all mammals experience their first ingestive episodes during periods of interaction with their dam. Such social interactions during feeding can profoundly affect flavor preference and diet selection.

The field literature is rich in examples of animal social groups which feed in an unusual way or select unusual items for ingestion (Galef, 1976). There is a tendency on the part of field observers to attribute such idiosyncratic group behaviors to the action of social learning processes. However, the range of possible causes of differences in feeding behavior among members of different subpopulations of a species living in uncontrolled environments is too great to permit uncritical attribution of idiosyncratic patterns of food selection to social causes. In fact, recent

evidence suggests that several well-known instances of idiosyncratic group feeding patterns, frequently discussed in the literature as examples of social learning in animals, may be due to other causes. For example, Green (1975) has reported observations suggesting that the behavior of dipping sweet potatoes in saltwater, exhibited by a long-studied troop of Japanese macaques (Kawai, 1965; Kawamura, 1959), results from shaping by human provisioners rather than observational learning among the monkeys. Similarly, it has been suggested that apparently traditional patterns of feeding on molluscs in colonies of wild rats (Gandolfi & Parisi, 1972, 1973; Parisi & Gandolfi, 1974) may result from differences in colony access to alternative food resources, rather than to learning by imitation (Galef, 1980). One must be cautious in attributing the development of feeding behaviors to social processes, particularly observational learning or imitation, until alternative explanations have been excluded (Hall, 1963).

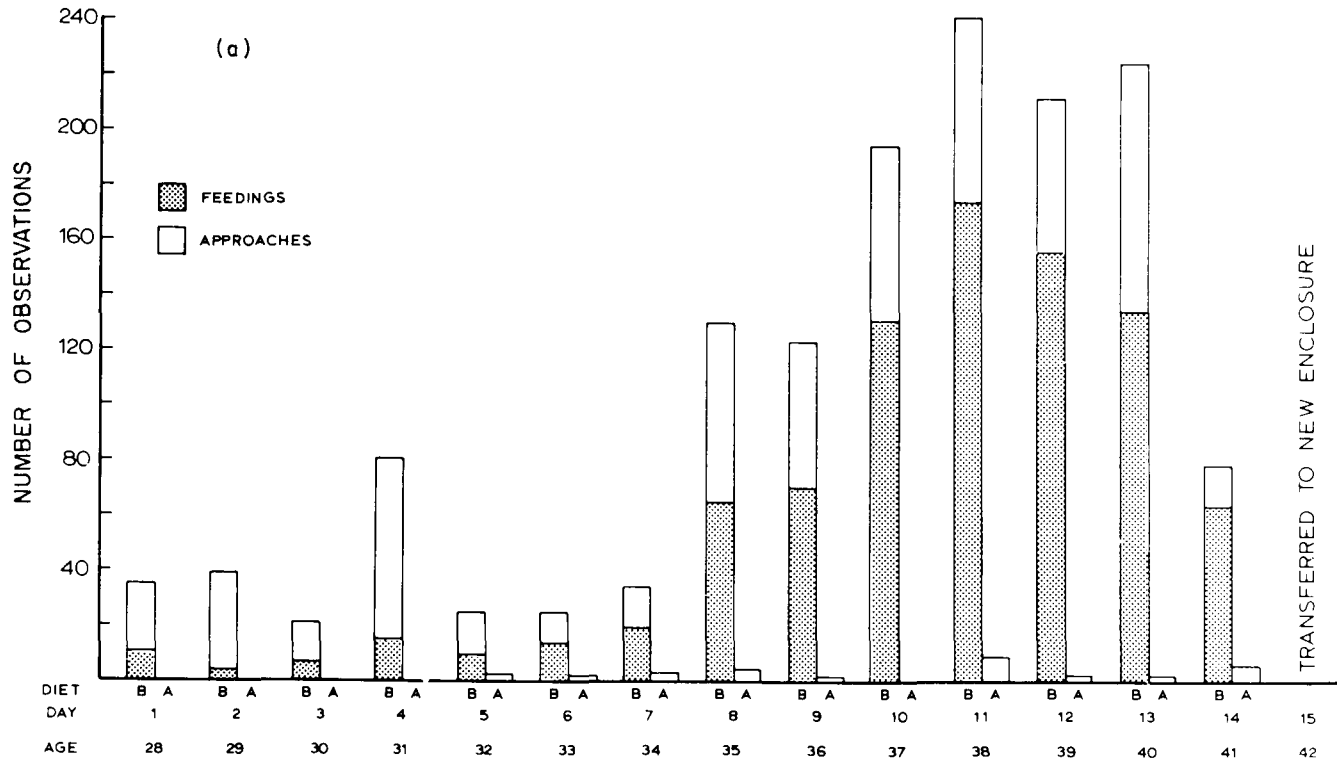
As we shall see from what follows, animal analogues of human traditions in feeding behavior do exist. However, those instances that have been carefully studied seem to depend on rather subtle social influences acting on simple exposure and associational processes of the type discussed in the preceding section, rather than on processes such as observational learning or direct imitation.

A. Social Factors in the Development of Flavor Acceptance

One of the more extensively studied cases of naturally occurring differences among populations in diet selection, involves the development of food preferences in wild rats. Fritz Steiniger, who worked for many years on problems of rat extermination, reported in 1950 that naive young rats, born to colonies that have learned to avoid ingesting a particular poison bait, absolutely reject the diet that their progenitors have learned to avoid without ever even sampling it.

In our laboratory analogue of Steiniger's field situation, colonies of adult wild rats were trained to eat one of two distinctive, nutritionally adequate diets (Diets A and B) and to avoid the other by introducing sublethal concentrations of poison into the samples of one of the two diets offered to each colony (Galef & Clark, 1971). Under these conditions, members of our adult colonies rapidly learned to avoid ingesting the diet into which poison was introduced and continued to avoid uncontaminated samples of that diet for several weeks.

Experiments began when pups born to colony members left their nest sites to feed on solid food for the first time. We observed adults



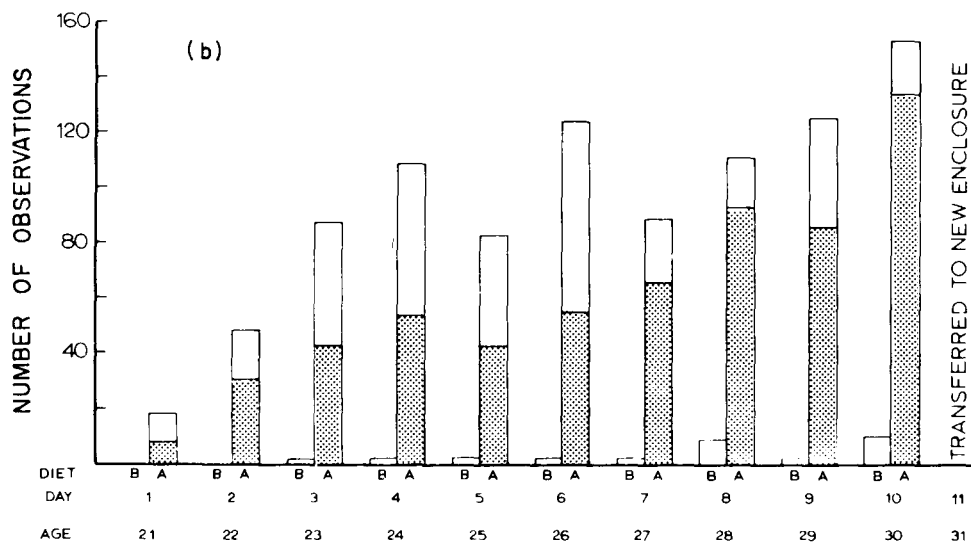


Fig. 14.1 Number of observed approaches to and feedings from Diets A and B by wild rat pups whose parents had been poisoned on either (a) Diet A or (b) Diet B. Shaded area indicates feedings; white area, approaches.

and pups throughout daily 3-hr feeding periods and recorded the number of times pups approached and ate each of the two available uncontaminated diets. After the pups had been feeding with the adults for several days, they were transferred to new enclosures, separate from the adults, and again offered uncontaminated samples of Diets A and B.

Typical results of these experiments are presented in Figs. 14.1 and 14.2. Figure 14.1a presents data describing the feeding behavior of a litter of wild rat pups born to a colony trained to eat Diet B; Fig. 14.1b presents data describing the behavior of a litter of pups born to a colony trained to eat Diet A. As is clear from comparison of the data presented in the two histograms, the learned feeding preferences of adult colony members profoundly affected the feeding preferences of their young. While in contact with adults of their colony, wild rat pups ingested only the diet that the adults of their colony ate and rejected alternatives.

Furthermore, as shown in Fig. 14.2, the acquired diet preference of adults continued to affect the feeding preferences of their young for 8–10 days following transfer of the pups to enclosures separate from adults. As can also be seen in Fig. 14.2, the effects of interaction with adults were transitory. All subjects, independent of rearing experience,

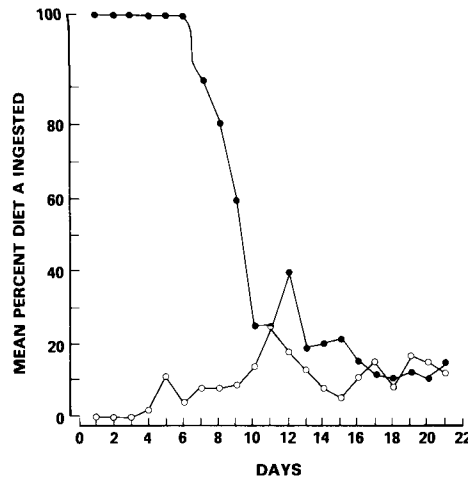


Fig. 14.2 Amount of Diet A eaten, as a percentage of total intake of Diets A and B, by pups following removal to a new enclosure isolated from adults. Pups whose parents were poisoned on Diet A indicated by ○; parents poisoned on Diet B, by ●.

eventually showed a stable preference for Diet B rather than for Diet A, presumably reflecting an inherent sensory–affective bias.

The analytic problem is to determine the behavioral mechanisms that: (a) lead rat pups to wean onto a diet that adult members of their colony are exploiting; and (b) cause the juveniles to exhibit continued avoidance of alternative diets even after they have been removed from direct adult influence. To begin, it is important to determine whether the juveniles are learning to avoid the diet that the adults of their colony have learned to avoid or are learning to eat the diet that the adults of their colony have learned to eat. The mechanisms responsible for each of these types of learning, either of which would be sufficient to produce the homogeneity of adult and pup dietary preference observed in our basic experiment, obviously would differ markedly.

Our data (Galef & Clark, 1971) are consistent with the view that rat pups learn to eat the diet that the adults of their colony are eating rather than to avoid the colony-avoided diet. If, for example, one rears wild rat pups in a colony having access only to Diet A and subsequently tests these pups with a choice between Diets A and B, they are just as hesitant to eat Diet B as are pups reared by a colony trained to eat Diet A and avoid Diet B. The important environmental factor during ontogeny, influencing pups diet preference in our experimental situations, appears to be socially induced exposure to the diet that adult colony members are eating.

My co-workers and I have found three ways in which adult rats can influence pups of their colony to wean to a diet that they are exploiting:

1. The physical presence of adult rats at a feeding site attracts pups to that feeding site and markedly increases the probability of young rats initiating weaning on the foodstuff located there (Galef & Clark, 1971, 1972).

2. Adult rats deposit residual olfactory cues in areas that they visit and pups prefer to explore and eat in an area soiled by conspecifics rather than in a clean area (Galef & Heiber, 1976).

3. The milk of a lactating female rat contains gustatory cues directly reflecting the flavor of her diet and, at weaning, isolated pups exhibit a preference for a diet of the same flavor as the diet that its mother has been eating during lactation (Galef & Clark, 1972; Galef & Henderson, 1972; Galef & Sherry, 1973).

We have also examined a number of potential routes by which adult rats could influence the food choices of their young, but which do not, in fact, appear to be effective. For example, it does not seem to be the case that pup ingestion of the anal excreta of adult colony members results in an enhanced preference for the diet of those adults (Galef & Henderson, 1972; Galef, 1979a).

There is a sense in which each of the three mechanisms effective in modifying pups' food preferences is simply a way in which adult rats can influence their young to become familiar with the properties of one diet rather than another. If, as is the case (see, e.g., Galef, 1977c), young rats exhibit a preference for a familiar diet when selecting items for ingestion, anything that an adult rat does to increase pup familiarity with the properties of a given diet will increase pup ingestion of it. I believe one can understand the initial preference of pups for the diet that the adults of the colony are exploiting as a result of an enhanced familiarity with that diet consequent on social interaction with adult colony members (Galef, 1977a,b; 1979b).

Adults of a number of species other than the rat are also known to be able to bring their young to wean to diets that they would otherwise avoid. For example, mother hens use a special food call to attract their young to a feeding site, and a food-calling hen can induce her chicks to ingest mealworms, a food that they would otherwise avoid (Hogan, 1966). Similarly, meerkat females with weanling young will run to and fro in front of their kits holding food in their mouths and elicit a food-snatching response from the young, thereby inducing the kits to ingest food, such as bananas, that they would normally ignore (Ewer, 1969).

And both kittens and 3½-year-old human infants can be induced to eat novel foods that they would otherwise reject, by interaction with a conspecific adult eating those foods (Harper & Sanders, 1975; Wyrwicka, 1978). The ability of adults to bias young of their species to wean to diets that they are exploiting and, as a result, to become familiar with those diets appears to be a common mode of social influence on the development of flavor preference in vertebrates.

B. Social Factors in Development of Flavor Rejection

If members of a given group tend to select the same foods for ingestion, then by definition, they also tend to reject the same potential ingesta. Whether the mechanisms serving to produce homogeneity in group typical rejection responses are dependent upon or independent of those producing group-typical acceptance responses is open to question. Rozin (1977) has suggested, following examination of the anecdotal evidence, that human reluctance to ingest unusual foods results in large part from an aversion to novelty itself when selecting items for ingestion. Similarly, I have proposed (Galef, 1971; 1977b) that the prolonged avoidance by wild rat pups of alternative diets, once they have become familiar with the diet that the adults of their colony are eating, is the result of their extreme reluctance to ingest novel foods (Barnett, 1958; Galef, 1970; Rozin, 1968). The general line of argument, based on the animal experiments and extrapolated to humans, is that individuals do not learn to avoid specific flavors as a result of interacting with conspecifics; rather, they are socially induced to eat some subset of potential ingesta and subsequently reject other ingesta because they are hesitant to ingest unfamiliar foods.

Although there is convincing data that animals can indirectly influence conspecifics to avoid one food simply by directly influencing them to eat an alternative, evidence suggesting direct social transmission of food avoidance is not available. Lavin, Freise, and Coombes (1980); Coombes, Revusky, and Lett (in press); and Freise and Lavin (1978) have found that a naive rat that ingests a novel palatable food and is then exposed to a conspecific made ill by poisoning, will subsequently reject that palatable food. Cues emitted by a sick conspecific can serve, as does illness itself, as an unconditioned stimulus producing a learned aversion to a novel, palatable flavor with which it is associated. However, it is not known how such a mechanism might act in natural circumstances to reduce the probability of naive group members ingesting a diet that their more knowledgeable fellows found toxic.

Active physical interference in the ingestive behavior of others to prevent them from ingesting potentially noxious foods has not been unequivocally demonstrated in any animal species. Danguir and Nicolaidis (1975) have reported that rats trained to avoid ingesting a toxic solution will physically restrain naive conspecifics and actively interfere with their ingestion of a similar-tasting safe solution. Unfortunately, replication with additional controls has indicated that the observed reduced ingestion of the safe solution by naive subjects did not result from actions of the trained conspecifics (Galef & Dalrymple, 1978). Menzel (1966, p. 134) and Stephenson (1967) have both reported instances of nonhuman primates pulling naive conspecifics away from potentially dangerous objects. These observations deserve further examination, as they suggest a means by which primates might directly induce naive conspecifics to avoid ingesting dangerous foods.

The absence of any animal model of the direct transmission of food aversions appears to have limited consideration of the importance of such processes in the development and maintenance of human traditions of flavor preference. Although there is, so far as I know, no experimental evidence that human facial expressions signaling disgust inhibit others from ingesting substances they might otherwise eat, I would be surprised if disgust signals did not act in this way. Similarly, the active intervention of human parents to prevent their offspring from ingesting substances that the parents' social group defines as unedible (for example, worms, or insects) must influence the child's subsequent selection of items for ingestion (see Rozin, 1978, for discussion). The investigation of such phenomena in both humans and other primates should prove to be fruitful.

V. CONCLUSION: PREFERENCE DEVELOPMENT IN ANIMALS AND MAN

The development of gustatory preference is clearly a multiply determined process.

1. Organisms are born with preferences for certain flavors and aversions to others.
2. Such species-typical affective responses to tastes are modifiable by gustatory experience.
3. Interaction with conspecifics can determine the gustatory experiences that an individual has during ontogeny. Furthermore, both the extent to which postnatal experience can alter gustatory preferences

present at birth and the extent to which social interactions influence postnatal experience probably vary among species.

Present evidence suggests that development of flavor preference in our own species may be more profoundly affected by experiential and social factors than is flavor preference development in other mammals. Humans appear to be unusual in their formation of long-lasting and extremely robust preferences for familiar but inherently unpalatable flavors. For example, human infants, naive children, and adults typically reject bitter or "hot" flavorants, as do naive animals. However, following repeated exposure to horseradish, quinine water, or chili peppers, humans reverse their initial rejection and develop positive responses to such inherently unpalatable substances (Rozin, 1978; Rozin & Schiller, 1980). As can be seen in Fig. 14.2, nonhuman animals have not been found to exhibit analogous long-term reversals in response as a result of simple exposure (see also Rozin *et al.*, 1979). Thus, the effects of exposure to a flavor on preference for it appear markedly different in humans and animals, the former exhibiting far more long-lasting and profound effects of familiarity on taste preference than the latter.

Also, humans appear to exhibit greater effects of social interaction on diet selection than do members of other mammalian species. Food selection in human social groups is profoundly shaped by social tradition, whereas members of other species seem to depend largely on individual experience to select palatable or nutritional substances. Non-human omnivores, like rats, frequently chew and taste available objects. The absence of analogous patterns of oral exploration in human adults, permitting discovery of previously unexploited food resources, must increase human dependence on social interaction for successful identification of foods.

In summary, two of the central factors influencing human flavor preference development, social tradition and repeated exposure, may be of considerably less importance in the development of long-term animal feeding preferences. Animal food selection probably depends to a far greater extent than human food selection on individual sampling and subsequent evaluation of postingestional consequences.

The ultimate causes of anomalous patterns of flavor preference development in man remain obscure, but offer fertile grounds for speculation. One would suspect that there must be some features of human exploitation of food resources, not seen in most other animals, that would require both flexibility and homogeneity in flavor preference among members of a social group. The food sharing, typical of human

social groups, would appear to require at least a degree of homogeneity in group flavor preference. Furthermore, an ability to come to favor whatever foods are readily available would seem appropriate to the opportunistic foraging of a geographically widely dispersed hunter-gatherer species such as our own.

In any case, the importance of social interaction and of postnatal exposure as factors in the determination of human diet selection and their relative lesser importance in other vertebrate species studied to date, casts some doubt on the adequacy of animal models to illuminate some of the most important processes underlying human flavor preference development. Although our species shares with others many features of its food selection behavior (e.g., a reluctance to ingest novel foods, a capacity to form associations between flavors and illness, inherent aversions to some flavors, etc.), at least two important factors in human flavor preference development may be uniquely human. A major part of the contribution of the study of the development of animal flavor preference to the understanding of the same process in man may lie in the identification of those features of the process that are unique to, and can only be studied in, *Homo sapiens*.

ACKNOWLEDGMENTS

Preparation of this chapter was greatly facilitated by financial support provided by the National Science and Engineering Research Council of Canada and the McMaster University Research Board. I thank Harvey Weingarten, Paul Rozin, Mertice Clark, and Jeff Alberts for their thoughtful reviews of earlier drafts of this manuscript.

REFERENCES

- Arnold, G. W., & Dudzinski, M. L. *Ethology of free-ranging domestic animals*. Amsterdam: Elsevier, 1978.
- Barnett, S. A. Experiments on "neophobia" in wild and laboratory rats. *British Journal of Psychology*, 1958, **49**, 195-201.
- Beauchamp, G. K., Maller, O., & Rogers, J. G., Jr. Flavor preferences in cats (*Felis catus* and *Panthera* sp.). *Journal of Comparative and Physiological Psychology*, 1977, **91**, 1118-1127.
- Bronstein, P. M., & Crockett, D. P. Maternal rations affect the food preferences of weanling rats: II. *Bulletin of the Psychonomic Society*, 1976, **8**, 227-229.
- Cabanac, M. Sensory pleasure. *The Quarterly Review of Biology*, 1979, **54**, 1-29.
- Capretta, P. J. Establishment of food preferences by exposure to ingestive stimuli early in life. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection*. Waco, Tex.: Baylor University Press, 1977.

- Capretta, P. J., & Rawls, L. H., III. Establishment of flavor preference in rats: Importance of nursing and weaning experience. *Journal of Comparative and Physiological Psychology*, 1974, **86**, 670-673.
- Coombes, S., Revusky, S., & Lett, B. T. Long-delay taste aversion learning in an unpoisoned rat: Exposure to a poisoned rat as the US. *Learning and Motivation*, in press.
- Danguir, J., & Nicolaidis, S. Protection d'un rat naif de la consommation d'une solution par des congénères ayant appris à la refuser. *Académie des Sciences. Comptes Rendus Hebdomadaires des Séances. Series D.*, 1975, **280**, 2595-2598.
- Desor, J. A., Maller, O., & Andres, K. Ingestive response of human newborns to salty, sour, and bitter stimuli. *Journal of Comparative and Physiological Psychology*, 1975, **89**, 966-970.
- Desor, J., Maller, O., & Turner, R. Taste in acceptance of sugars by human infants. *Journal of Comparative and Physiological Psychology*, 1973, **84**, 496-501.
- Ewer, R. F. The "instinct to teach." *Nature*, 1969, **222**, 698.
- Freise, B. G., & Lavin, M. J. The effects poisoned rats have on modifying flavor choices in non-poisoned conspecifics. Paper presented at the meetings of the Eastern Psychological Association, Washington, D.C. March, 1978.
- Galef, B. G., Jr. Aggression and timidity: Responses to novelty in feral Norway rats. *Journal of Comparative and Physiological Psychology*, 1970, **71**, 370-381.
- Galef, B. G., Jr. Social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. In J. S. Rosenblatt, R. A. Hinde, E. Shaw, & C. Beer (Eds.), *Advances in the study of behavior* (Vol. 6). New York: Academic Press, 1976.
- Galef, B. G., Jr. Mechanisms for the social transmission of food preferences from adult to weanling rats. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection*. Waco, Tex.: Baylor University Press, 1977. (a)
- Galef, B. G., Jr. Mechanisms for the transmission of acquired patterns of feeding from adult to weanling rats. In J. M. Weiffenback (Ed.), *Taste and development: The genesis of sweet preference*. Washington, D.C.: U.S. Government Printing Office, 1977. (b)
- Galef, B. G., Jr. Social transmission of food preferences: An adaptation for weaning in rats. *Journal of Comparative and Physiological Psychology*, 1977, **91**, 1136-1140. (c)
- Galef, B. G., Jr. Investigation of the functions of coprophagy in juvenile rats. *Journal of Comparative and Physiological Psychology*, 1979, **93**, 295-305. (a)
- Galef, B. G., Jr. Social transmission of learned diet preferences in wild rats. In J. H. A. Kroeze (Ed.), *Preference behavior and chemoreception*. London: Information Retrieval, 1979. (b)
- Galef, B. G., Jr. Diving for food: Analysis of a possible case of social learning in rats (*Rattus norvegicus*). *Journal of Comparative and Physiological Psychology*, 1980, **94**, 416-425.
- Galef, B. G., Jr., & Clark, M. M. Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *Journal of Comparative and Physiological Psychology*, 1971, **75**, 341-357.
- Galef, B. G., Jr., & Clark, M. M. Mother's milk and adult presence: Two factors determining initial dietary selection by weaning rats. *Journal of Comparative and Physiological Psychology*, 1972, **78**, 220-225.
- Galef, B. G., Jr., & Dalrymple, A. J. Active transmission of poison avoidance among rats? *Behavioral Biology*, 1978, **24**, 265-271.
- Galef, B. G., Jr., & Heiber, L. The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *Journal of Comparative and Physiological Psychology*, 1976, **90**, 727-739.

- Galef, B. G., Jr., & Henderson, P. W. Mother's milk: A determinant of the feeding preferences of weaning rat pups. *Journal of Comparative and Physiological Psychology*, 1972, **78**, 213–219.
- Galef, B. G., Jr., & Sherry, D. F. Mother's milk: A medium for the transmission of cues reflecting the flavor of mother's diet. *Journal of Comparative and Physiological Psychology*, 1973, **83**, 374–378.
- Gandolfi, G., & Parisi, V. Predazione su *Unio pictorum* L. da parte del Ratto, *Rattus norvegicus* (Berkenhout). *Acta Naturalia*, 1972, **8**, 1–27.
- Gandolfi, G., & Parisi, V. Ethological aspects of predation by rats, *Rattus norvegicus* (Berkenhout), on bivalves *Unio pictorum* L. and *Cerastoderma lamarckii* (Reeve). *Bollettino di Zoologia*, 1973, **40**, 69–74.
- Garcia, J., & Ervin, F. R. Gustatory-visceral and telereceptor-cutaneous conditioning—adaptation to internal and external milieus. *Communications in Behavioral Biology*, 1968, **1** (Part A), 389–415.
- Garcia, J., & Hankins, W. G. The evolution of bitter and the acquisition of toxiphobia. In D. A. Denton & J. P. Coghlan (Eds.), *Olfaction and taste V*. Academic Press: New York, 1975.
- Garcia, J., & Hankins, W. G. On the origin of food aversion paradigms. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection*. Waco, Tex.: Baylor University Press, 1977.
- Garcia, J., & Koelling, R. A. Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 1966, **4**, 123–124.
- Gentle, M. J. Taste preference in the chicken (*Gallus domesticus* L.). *British Poultry Science*, 1972, **13**, 141–155.
- Green, K. F., & Garcia, J. Recuperation from illness: Flavor enhancement in rats. *Science*, 1971, **173**, 749–751.
- Green, S. Dialects in Japanese monkeys: Vocal learning and cultural transmission of locale-specific vocal behavior? *Zeitschrift fur Tierpsychologie*, 1975, **38**, 304–314.
- Griffin, D. R. *The question of animal awareness*. New York: Rockefeller University Press: 1976.
- Grill, H. J., & Norgren, R. The taste reactivity test I. Mimetic responses to gustatory stimuli in neurologically normal rats. *Brain Research*, 1978, **143**, 263–279. (a)
- Grill, H. J., & Norgren, R. The taste reactivity test II. Mimetic responses to gustatory stimuli in chronic thalamic and chronic decerebrate rats. *Brain Research*, 1978, **143**, 781–797. (b)
- Hall, K. R. L. Observational learning in monkeys and apes. *British Journal of Psychology*, 1963, **54**, 201–226.
- Harper, L. V., & Sanders, K. M. The effect of adults' eating on young children's acceptance of unfamiliar foods. *Journal of Experimental Child Psychology*, 1975, **20**, 206–214.
- Hogan, J. A. An experimental study of conflict and fear: An analysis of behavior of young chicks towards a mealworm II: The behavior of chicks which eat the mealworm. *Behaviour*, 1966, **27**, 273–289.
- Holman, G. H. Intra-gastric reinforcement effect. *Journal of Comparative and Physiological Psychology*, 1969, **69**, 432–441.
- Johanson, I. B., & Hall, W. G. Appetitive learning in 1-day-old rat pups. *Science*, 1979, **205**, 419–421.
- Kalat, J. W., & Rozin, P. "Learned safety" as a mechanism in rats' long-delay taste-aversion learning. *Journal of Comparative and Physiological Psychology*, 1973, **83**, 198–207.

- Kare, M. R. Comparative aspects of the sense of taste. In M. R. Kare & B. P. Halpern (Eds.), *Physiological and behavioral aspects of taste*. Chicago: University of Chicago Press, 1961.
- Kawai, M. Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima inlet. *Primates*, 1965, **6**, 1–30.
- Kawamura, S. The process of sub-culture propagation among Japanese macaques. *Primates*, 1959, **2**, 43–54.
- Lavin, M. J., Freise, B., & Coombes, S. Transferred flavor aversions in adult rats. *Behavioral and Neural Biology*, 1980, **28**, 15–33.
- Longhurst, W. M., Oh, H. K., Jones, M. B., & Kepner, R. E. A basis for the palatability of deer forage plants. *North American Wildlife and Natural Resources Conference Transactions*, 1968, 181–192.
- Maller, O., & Desor, J. Effects of taste on ingestion by human newborns. In J. Bosma (Ed.), *Oral sensation and perception: Development in the fetus and infant*. Washington, D.C.: U.S. Government Printing Office, 1974.
- Martin, L. T., & Alberts, J. R. Heart rate change as a measure of associative learning in neonatal rodents. Presented at the meetings of the International Society of Developmental Psychobiology, Atlanta, Ga., 1979.
- Mayr, E. Behavior programs and evolutionary strategies. *American Scientist*, 1974, **62**, 650–659.
- Menzel, E. W., Jr. Responses to objects in free-ranging Japanese monkeys. *Behaviour*, 1966, **26**, 130–150.
- Morris, D. *The mammals*. New York: Harper & Row, 1965.
- Moskowitz, H. R., Kumraiah, V., Sharma, H., Jacobs, L., & Sharma, S. D. Cross cultural differences in simple taste preference. *Science*, 1975, **190**, 1217–1218.
- Nisbett, R. E., & Gurwitz, S. B. Weight, sex, and the eating behavior of human newborns. *Journal of Comparative and Physiological Psychology*, 1970, **73**, 245–253.
- Parker, L., Failor, A., & Weidman, K. Conditioned preferences in the rat with an unnatural need state: Morphine withdrawal. *Journal of Comparative and Physiological Psychology*, 1973, **82**, 294–300.
- Parisi, V., & Gandolfi, G. Further aspects of the predation by rats on various mollusc species. *Bollettino di Zoologia*, 1974, **41**, 87–106.
- Pfaffmann, C. Phylogenetic origins of sweet sensitivity. In D. A. Denton & J. P. Coghlan (Eds.), *Olfaction and taste V*. New York: Academic Press, 1975.
- Revusky, S. The concurrent interference approach to delay learning. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection*. Waco, Tex.: Baylor University Press, 1977.
- Rozin, P. Specific aversions as a component of specific hungers. *Journal of Comparative and Physiological Psychology*, 1967, **64**, 237–242.
- Rozin, P. Specific aversions and neophobia resulting from vitamin deficiency or poisoning in half-wild and domestic rats. *Journal of Comparative and Physiological Psychology*, 1968, **66**, 82–88.
- Rozin, P. The significance of learning mechanisms in food selection: Some biology, psychology and sociology of science. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection*. Waco, Tex.: Baylor University Press, 1977.
- Rozin, P. The use of characteristic flavorings in human culinary practice. In C. M. Apt (Ed.), *Flavor: Its chemical, behavioral, and commercial aspects*. Boulder, Colo.: Westview Press, 1978.

