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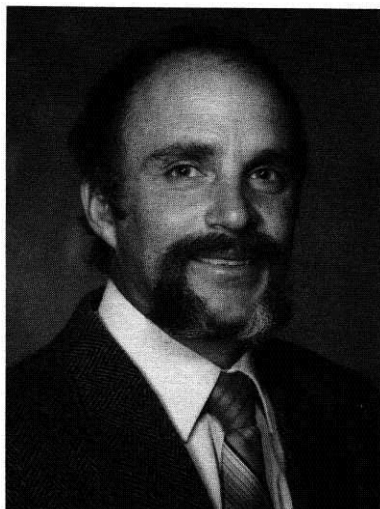
Postingestive feedback as an elementary determinant of food preference and intake in ruminants

F. D. Provenza

Invited Synthesis Paper

The Editorial Board of the *Journal of Range Management* invited Frederick D. Provenza to prepare this synthesis paper.

Fred Provenza was born in Colorado Springs, and raised in Salida, Colorado. He attended college at Colorado State University in Fort Collins, and obtained a B.S. degree in Wildlife Biology in 1973. He worked on a ranch near Salida while attending college, and for nearly two years after college.

Fred moved to Logan, Utah in 1975 and began work on M.S. degree in Range Science, which was obtained in 1978. He subsequently worked on a Ph.D. in Range Science, which was completed in 1982. In 1982 Fred began working on the faculty in the Range Science Department at Utah State University. He is currently a professor in the Department of Rangeland Resources. Fred has taught 3 courses since becoming a member of the Range Science Department; (RS 298, Summer Camp; RS 300, Range Principles; RS 703, Plant-Herbivore Interactions). He also received a grant from the Soil Conservation Service to teach RS 703 as part of their efforts in continuing education.This course was taught for the first time during the summer of 1991, and will be taught on an annual basis for the foreseeable future. The course takes place during a 2-week period and involves field work, lectures, and discussions.

Fred's research interests are in plant-herbivore interactions, with specific interests in how learning affects food and habitat selection by herbivores.

Postingestive feedback as an elementary determinant of food preference and intake in ruminants

FREDERICK D. PROVENZA

Abstract

Ruminants select nutritious diets from a diverse array of plant species that vary in kinds and concentrations of nutrients and toxins, and meet their nutritional requirements that vary with age, physiological state, and environmental conditions. Thus, ruminants possess a degree of nutritional wisdom in the sense that they generally select foods that meet nutritional needs and avoid foods that cause toxicosis. There is little reason to believe that nutritional wisdom occurs because animals can directly taste or smell either nutrients or toxins in foods. Instead, there is increasing evidence that neurally mediated interactions between the senses (i.e., taste and smell) and the viscera enable ruminants to sense the consequences of food ingestion, and these interactions operate in subtle but profound ways to affect food selection and intake, as well as the hedonic value of food. The sensation of being satisfied to the full (i.e., satiety) occurs when animals ingest adequate kinds and amounts of nutritious foods, and animals acquire preferences (mild to strong) for foods that cause satiety. Unpleasant feelings of physical discomfort (i.e., malaise) are caused by excesses of nutrients and toxins and by nutrient deficits, and animals acquire aversions (mild to strong) to foods that cause malaise. What constitutes excesses and deficits depends on each animal's morphology, physiology, and nutritional requirements. This does not mean that ruminants must maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that they can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient or of an excess of toxins or nutrients, to generate behavior to correct the disorder. Extreme states should cause herbivores to increase diet breadth and to acquire preferences for foods that rectify maladies. From an evolutionary standpoint, mechanisms that enable animals to experience feedback, sensations such as satiety and malaise, should be highly correlated with nutritional well being, toxicosis, and nutritional deficiencies, which are directly related with survival and reproduction.

How wisely ruminants select their diets is a contentious issue. On the one hand, there is little evidence that ruminants can directly sense nutritional components in foods, and it is difficult to accept that liking or disliking the flavors of particular foods enables animals to select foods that are nutritious and avoid those that are toxic. In addition, ruminants occasionally die from overingesting substances (e.g., certain toxic plants, grain, lead plates from broken batteries), and they sometimes fail to ingest appropriate minerals which are offered cafeteria style. Given these observations, and the lack of a mechanistic framework to understand food selection, it is difficult to discern how ruminants might ingest foods to meet their nutritional requirements.

On the other hand, studies during the past decades have established ruminants generally select diets higher in nutrients and lower in toxins than the average food available (Arnold and Dudzinski 1978, Provenza and Balph 1990, Rosenthal and Janzen 1979, Raupp and Tallamy 1991, Rosenthal and Berenbaum 1992). Selection occurs even though ruminants' requirements vary with changing environmental and physiological conditions (Church 1988). Thus, ruminants apparently possess some degree of nutritional wisdom such that they are able to select foods that meet nutritional needs and to avoid foods that cause toxicosis.

Young ruminants can learn from mother and peers what is and is not appropriate to eat, and this apparently plays a critical role in the transmission of nutritional wisdom among generations (Provenza 1994a,c). Learning from mother increases efficiency of learning about nutritious foods and reduces risk of overingesting toxic foods. Lambs learn quickly (i.e., 5 min/day for 5 days) to avoid a "harmful" novel food lithium chloride (LiCl) that their mothers were trained to avoid, and to select a nutritious novel alternative, when they were with their mothers who exhibited the appropriate behavior (Mirza and Provenza 1990, 1992, 1994).

There is also evidence that food selection involves interactions between the senses of taste and smell and mechanisms to sense the consequences of food ingestion, such as satiety (experienced when animals ingest adequate kinds and amounts of nutritious foods) and malaise (experienced when animals ingest excesses of nutrients or toxins or experience nutrient deficits). Much remains to be learned concerning how taste and smell are integrated with postingestive feedback. The objective of this paper is to discuss how these factors may be related, thereby identifying some of the mechanisms that may underlie the nutritional wisdom of ruminants. Some of the views are speculative, and are offered in the hope that they will stimulate research on the interaction between the nutritional and behavioral bases of food selection in ruminants.

Models of Food Selection

Four models have emerged regarding food selection of ruminants: (1) euphagia, (2) hedyphagia, (3) body morphophysiology and size, and (4) learning through foraging consequences (Provenza and Balph 1990). Euphagia, the innate ability to taste and smell specific nutrients and toxins in plants, supposedly lets animals select nutritious foods and avoid harmful foods. Nonetheless, it is not likely that animals directly taste and smell most nutrients and toxins in foods because the taste, smell, and texture of each food results from a unique concoction of chemical compounds that make the flavor of each food unique (Bartoshuk

1991, but see conclusions of Provenza and Balph 1990 and Sclafani 1991a). Proponents of hedyphagia argue that animals select foods that are immediately "pleasing" to olfactory, gustatory, and tactile senses and avoid those that are not. According to the argument, evolution operates such that those plant compounds that are nutritious taste good and those that are toxic taste bad. Models based on body morphology and physiology assume that ruminant species differ in their ability to ingest forages with different physical and chemical characteristics. Proponents of these models argue that as a result of evolving in different environments, different ruminant species possess different morphological and physiological characteristics that cause them to ingest forage that differs in physical and chemical characteristics.

The fourth model, learning through foraging consequences, involves feedback mechanisms that provide the flexibility to select nutritious diets in environments where forages vary in concentrations of nutrients and toxins (Provenza and Balph 1990, Provenza and Cincotta 1993). Learning encompasses prominent aspects of the other 3 models. The learning model of foraging assumes that diet selection is a result of positive and negative consequences of foraging. The nutritional and toxicological consequences of food selection are related to an individual's morphology and physiology, which is the essence of the morphophysiology model. Neurally mediated interactions between the senses (i.e., taste and smell) and the viscera enable ruminants to sense the consequences of food ingestion, and these interactions can operate in subtle but profound ways to affect the hedonic value of food (i.e., pleasurable and unpleasurable sensations experienced through taste and smell), which is the gist of the hedyphagia model. Finally, feedback from nutrients and toxins can enable animals to select nutritious foods and limit intake of toxic foods, which is the essence of the euphagia model of food selection.

Evidence of Feedback in Ruminants

In the following discussion of how excesses and deficits of nutrients and excesses of toxins affect food selection and intake, I relied on 3 kinds of evidence to argue that interactions between the senses (i.e., taste and smell) and postingestive feedback are consequential. (1) Esophageally fistulated animals sham-fed various foods or purified compounds show that food flavor (i.e., taste and odor) and postingestive feedback both affect food selection and intake. (2) Other experiments in which animals receive a food or a purified compound, by gavage or ruminal infusion, that causes either aversive or positive postingestive effects, show the importance of feedback. (3) Similar experiments in which animals eat a new food (or a food containing a purified compound), and subsequently decrease or increase intake of the food, provide evidence for the importance of aversive and positive postingestive feedback in food selection and intake.

Excesses of Toxins

Mammals have mechanisms to digest foods, to assimilate nutrients (Church 1988), and to counter toxins (McArthur et al. 1991). The capacity of these systems is seldom exceeded because animals quickly experience internal malaise and limit intake before

toxicosis ensues. Blood flow through the ruminal artery increases within 30 to 60 sec after feeding begins, and peaks about 15 min later (Barnes et al. 1986). Thus, ruminants probably sense many toxins (and nutrients) in the cardiovascular system early in a meal. Sheep acquire aversions to foods containing the toxicant LiCl within 1 hour (Provenza et al. 1993b). Goats learn to limit intake of twigs containing tannins within 1 hour (Provenza et al. 1994c), and learn to limit intake of various sources of dietary nonprotein nitrogen within minutes (Conrad et al. 1977).

Animals eat nutritious plants that contain toxins, but they generally limit intake in accord with the concentration of the toxin. Toxins cause malaise, which in turn causes animals to eat small amounts of a variety of plants (i.e., to increase diet breadth) (Bryant and Kuropat 1980, Bryant et al. 1991). For example, goats prefer older twigs (OG) to current season's twigs (CSG) from the shrub blackbrush *(Coleogyne ramosissima)*, even though CSG contains more nitrogen (1.04% vs 0.74%) and is more digestible (48% vs 38%) (Provenza et al. 1983). CSG contains a condensed tannin that causes aversive postingestive feedback (Provenza et al. 1990), and as a result, goats eat less CSG than OG within a meal (Provenza et al. 1994c).

Aversive postingestive feedback causes cattle, sheep, and goats to decrease intake of foods containing toxins like the alkaloids in larkspur (Olson and Ralphs 1986) and tall fescue (Aldrich et al. 1993, Thompson and Stuedemann 1993), condensed tannins in shrubs like blackbrush (Provenza et al. 1990), glucosinolates in brassica crops (Duncan and Milne 1992, 1993), saponins, coumarins, furocoumarins and anthraquinones in sacahuiste (Rankins et al. 1993), and lithium chloride added to foods (Provenza et al. 1990, 1993a, Lane et al. 1990, duToit et al. 1991, Ralphs and Cheney 1993). Aversive feedback also causes a decrease in intake of poor-quality silage (Buchanan-Smith 1990), leafy spurge (Kronberg et al. 1993), larkspur (Pfister et al. 1990), ponderosa pine (Pfister et al. 1992), bitterweed (Calhoun et al. 1981), and sagebrush (Johnson et al. 1976, Ngugi et al. 1994).

An aversion to a food increases with severity of the illness (Fig. 1), and decreases the longer the delay between food ingestion and illness (Garcia et al. 1974, duToit et al. 1991, Ralphs and Cheney 1993). The longer aversive postingestive feedback is delayed (Burritt and Provenza 1991), and the greater the positive feedback from the food during the delay (Thorhallsdottir 1991, Burritt and Provenza 1992, Ralphs et al. 1995, Villalba and Provenza unpublished), the more likely ruminants will ingest the food. Thus, malaise and satiety can interact across a broad and subtle continuum to affect food selection and intake.

Ruminants often eat nutritious foods containing toxins, an apparent anomaly which may be caused by 2 factors. Enhanced nutrient status may increase their ability to eat foods containing toxins (Illius and Andrews 1994). In addition, ruminants can limit intake to minimize toxicity (Provenza et al. 1994c, Ngugi et al. 1994). For instance, sheep maintain intake of LiCl at approximately 40 to 60 mg/KG body weight, and intake increases as toxicity diminishes (duToit et al. 1991, Launchbaugh et al. 1993). Thus, animals can use food resources whose chemical characteristics vary.

Intake of nutritious foods containing toxins is often cyclical, with sharp declines followed by gradual increases in intake (Pfister et al. 1994). A cyclical pattern of intake also occurs when ruminants eat grain. Production of organic acids from starch digestion evidently causes malaise, which causes intake to decline (Huber 1976, Britton and Stock 1987, Provenza et al.

1994d). Nonetheless, any negative feedback is ultimately followed by positive feedback (i.e., opponent-process theory of motivation of Solomon and Corbit 1974). Thus, when food ingestion is followed by aversive feedback, the aversion to the food diminishes as time passes because the recuperative process gradually counter-conditions the aversion (Garcia 1989).

Considering the millions of bites of food taken by ruminants each day, there are relatively few instances of toxicosis, most of which are probably the result of the failure of feedback and (or) sensory (i.e., taste and smell) systems (Provenza et al. 1992). For instance, toxicosis may occur when phytotoxins circumvent feedback mechanisms responsible for malaise, and when malaise is delayed temporally (several years with some pyrrolizidine alkaloids, Cheeke and Shull 1985). Animals may also be unable to discriminate slight changes in concentrations of a highly toxic compounds, to avoid interactions between toxins in 2 or more plants, and to differentiate nutritious and toxic plants when placed in unfamiliar environments.

Excesses of Energy or Nutrients

Low concentrations of nutrients limit intake, intermediate concentrations cause intake to increase, and excessive rates and amounts of nutrient release cause intake to decrease (Fig. 1, Arnold and Hill 1972). Levels of portal and jugular blood metabolites (e.g., volatile fatty acids, VFAs) that may enable ani-

inadequate (malaise) adequate (satiety) excessive (malaise)

Nutritional Characteristics of Food
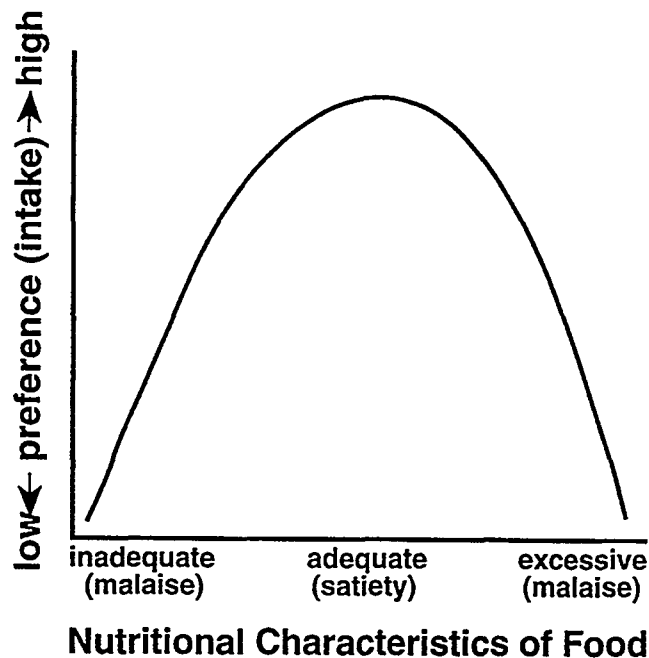
Fig 1. Low concentrations of nutrients adversely affect preference (intake), intermediate concentrations cause preference (intake) to increase, and excessive rates and amounts of nutrient release can cause preference (intake) to decrease. Accordingly, excesses or deficits of nutrients (and excesses of toxins) set a limit on the amount of a particular food that can be ingested within a particular time frame. Feedback enables animals to sense the consequences of food ingestion, which affects preference (intake) for particular foods.

mals to sense the effects of nutrient intake increase within 15 min after ruminants begin to eat (Thye et al. 1970, Evans et al. 1975, Chase et al. 1977, deJong 1981). An excess of energy or nutrients in a food causes ruminants to limit intake of the food, and in turn, can cause an increase in diet breadth. For example, ruminants prefer high-energy foods like grains, but they limit intake of grain and increase intake of alternative foods, once grain is overingested (Britton and Stock 1987, Ortega-Reyes et al. 1992, Phy and Provenza 1994 and unpublished). The decrease in intake is due to postingestive malaise, evidently caused by an excess of byproducts from microbial fermentation (e.g., VFAs like lactate and propionate) (Provenza et al. 1994d). An excess of propionate causes sheep to acquire strong aversions to foods (Ralphs et al. 1995). Thus, byproducts of microbial fermentation such as propionate and lactate can influence food selection and intake.

Excessive nitrogen in food can also adversely affect intake (Barker et al. 1988). Ruminants eating foods high in rumen-degradable protein experience high levels of ruminal ammonia, suffer malaise, and decrease intake (Prins and Beekman 1989). Microbial fermentation of nitrogen can result in inordinately high amounts of ammonia, which escape from the liver and pass into peripheral circulation where excessive ammonia is toxic (Chalupa et al. 1970, Prior et al. 1970, Fernandez et al. 1990, Schelcher et al. 1992). Ammonia toxicity is mediated by various mechanisms in the brain (Felipo et al. 1993). Toxicosis associated with excessive ammonia explains why intake quickly declines as concentrations of compounds (e.g., urea) that are readily converted to ammonia increase in food (Conrad et al. 1977, Choung et al. 1990). Aversive postingestive feedback causes animals to limit intake of foods paired with excessive amounts of urea (Kertz et al. 1982, see Grovum and Chapman 1988 for discussion related to the taste of urea), and sheep regulate silage intake to maintain blood ammonia nitrogen levels below 2 mg/L (Nicholson et al. 1992).

Aversive feedback from excessive (or inadequate) nitrogen helps to explain how lambs can select a diet that maximizes growth from isocaloric foods that vary in protein (Cropper et al. 1986, Kyriazakis and Oldham 1993, Fig. 2), and why they consume less protein as they age (Cropper et al. 1985). Excessive (or inadequate, see next section) nitrogen content in different foods likely causes various degrees of malaise, which will vary with the concentration of protein and the physiological requirements of the animal. What causes satiety for an animal at one age (e.g., young) may be excessive and cause malaise for another (e.g., older). Young growing animals, as well as adults deficient in protein, probably select diets in direct accordance with their protein requirements (Webster 1993). Changes in food selection likely occur as a result of continuing experience of the effects of foods on the internal milieu (Kyriazakis and Oldham 1993), which could be ascertained on a meal-to-meal basis (Provenza 1994b, Provenza et al. 1994c).

Ruminants also respond to concentrations of minerals in food. For instance, sheep fed an oat hay-lupine mixture containing either 0, 1.7, 3.3, 6.3, 12, or 21% of a mineral mix ate less as the concentration of the minerals increased; most of the sheep in the groups containing the highest concentrations eventually refused to eat the food (Masters et al. 1992). The decrease in intake is mediated by postingestive feedback resulting from increasing osmolality (Bell 1984, Grovum 1988, Grovum and Chapman 1988, Carter and Grovum 1990, Forbes et al. 1992, Anil et al.

1993), which depends on minerals in food and VFAs produced by microorganisms (Bennink et al. 1978). Intake also decreases when NaCl, KCl, Na-acetate, Na-propionate, and PEG are added to the rumen before feeding (Ternouth and Beattie 1971, Grovum and Bignell 1989), which indicates that many osmotically active particles can reduce intake (Carter and Grovum 1990).

Deficits of Energy or Nutrients

Animals acquire aversions to nutrient-deficient diets (Richter 1943), evidently because the effects of nutrient deficiencies resemble those of slow-acting toxins (Rozin 1976). The onset of malaise, and the degree to which it occurs, will depend on the particular nutrient and the severity of the deficiency. Malaise from nutrient-deficient diets should cause animals to increase diet breadth and to acquire preferences for foods that rectify deficits. This is evidently what occurs when cattle increase consumption of supplemental protein when forage is low in protein (Provenza et al. 1983). This may also explain why Angora goats consumed woodrat (*Neotoma lepida*) houses, made of juniper (*Juniperus osteosperma*) bark and twigs soaked with urine (nitrogen), when
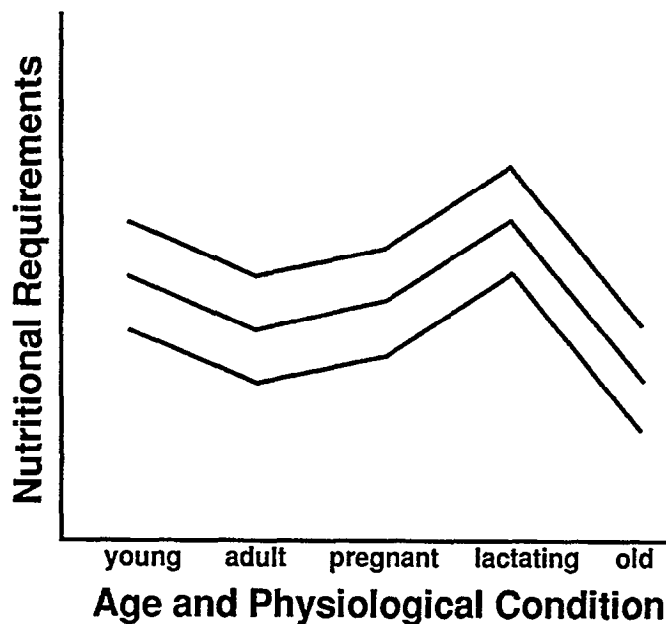
Fig. 2. Animals require various nutrients in amounts and proportions that vary with age, physiological condition, and environment. The ideal nutritional state (center line) occurs when all nutrients are obtained simultaneously. It is dynamic and multidimensional, with as many dimensions as there are functionally relevant nutrients (Emmans 1991, Simpson and Raubenheimer 1993). Nonetheless, ruminants need not maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that they can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins) (Booth 1985). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient (lower line) or of an excess of toxins or nutrients (upper line), to generate conditions (i.e., malaise) to correct the disorder (i.e., cause animals to change food selection). Malaise causes animals to increase diet breadth, to acquire preferences for foods that rectify states of malaise, and to exhibit state-dependent food selection.

they browsed blackbrush, a shrub low in nitrogen (0.67%) (Provenza 1977).

Digestibility and intake are positively correlated, and they are closely related to the energy requirements of ruminants (Baile and Forbes 1974, Anil and Forbes 1980, Anil et al. 1993). Animals do not prefer poorly digestible foods low in energy, whereas they generally select highly digestible foods that are a source of energy when offered alternatives. The postingestive basis for this is illustrated experimentally when lambs ingest flavored foods (e.g., onion- or oregano-flavored straw) or solutions (e.g., grape or orange) paired with (e.g., glucose or starch) or without (e.g., saccharin) a readily available source of energy. Following conditioning, lambs show a strong preference for the flavors paired with the energy source (Thorhallsdottir 1991, Burritt and Provenza 1992, Ralphs et al. 1995, Villalba and Provenza unpublished).

Deficits or imbalances of amino acids also cause decreases in intake and food aversions in liquid-fed (Rogers and Egan 1975) and solid-fed (Egan and Rogers 1978) lambs. Conversely, sheep increase intake of a protein-deficient diet following infusions of protein into the duodenum (Egan 1977). Rats acquire strong aversions to amino-acid-imbalanced diets, but if no alternative is available, they will eat an imbalanced diet for energy and adapt to ad libitum intake over 7 days (Gietzen 1993). Nonetheless, this does not reflect the extinction of an aversion to the food because rats strongly prefer a protein-free diet to an amino-acid-imbalanced diet (Rogers and Leung 1977). Several amino acids (e.g., sulfur containing amino acids, lysine, histidine, and possibly threonine, valine, and isoleucine) may be co-limiting in different foods ingested by ruminants (reviewed by Merchen and Titgemeyer 1992, Oldham 1993). When lambs are fed low-protein diets, compensatory effects (e.g., nitrogen recycling) increase abomasal nitrogen flow to a level similar to that of lambs fed diets containing up to 30% more protein; nevertheless, lambs fed low-protein diets have lower nitrogen retention, which may reflect changes in profile and absorption of amino acids (Sultan and Loerch 1992). The quantity and quality of protein that enters the small intestine of ruminants depends largely on the amino acid composition of microbial protein. Ruminally produced microbial protein may not meet the amino acid needs of the animal when microbial protein production is limited, when amino acid requirements are high, or when nitrogen comes primarily from non-protein nitrogen sources.

Intake also decreases when diets are deficient in minerals. For example, cattle, sheep, and goats eventually decrease their intake of phosphorus-deficient diets. The reduction in food intake depends on the severity of the deficiency (Ternouth 1991), and is exacerbated because animals no longer meet requirements for energy and protein. As mineral concentrations increase or as electrolyte balance (e.g., Na+K-Cl) improves, intake increases linearly but then declines as concentrations increase further or as balance changes (Ross et al. 1994). Sheep rectify mineral deficits (e.g., phosphorus, sulphur, selenium) by ingesting mineral supplements (White et al. 1992), and the pica exhibited by cattle foraging on heathlands is evidently a response to a phosphorus deficit (Wallis de Vries 1994). Although it is not known whether recovery from mineral deficiencies causes acquired preferences for foods, sheep apparently prefer food flavors associated with a mineral (i.e., phosphorus) which caused recovery from deficiency (Welch 1980).

Ruminants experiencing nutrient deficits sample new foods and increase intake of particular foods that can rectify deficits, including substances other well-fed animals avoid. For instance, cattle with mineral deficiencies eat rabbit flesh and bones, whereas non-deficient animals may sniff or lick the flesh, but never eat them, and they ignore the bones (Wallis de Vries 1992, 1994). Deer and other ungulates experiencing deficits eat antlers (Sutcliffe 1977). Angora goats foraging on nitrogen-deficient blackbrush pastures ingest woodrat houses high in nitrogen (Provenza 1977), and bighorn sheep use rodent middens as mineral licks (Coates et al. 1991). Ruminants experiencing deficiencies eat live and dead lemmings, rabbits, birds (caribou, red deer, sheep: Kelsall 1968, J.P. Bryant, personal communication, Furness 1988), ptarmigan eggs (caribou: D. Swanson, personal communication), arctic terns (sheep), and fish (white-tailed deer) (Bazely 1989). Cattle ingesting mineral-deficient forages lick urine patches of rabbits and man, chew wood, consume soil, eat fecal pellets of rabbits, and ingest non-food items such as plastic, feathers, bones, cinders, sacks, tins, and even dead rabbits (Green 1925, Wallis de Vries 1992, 1994).

The study by Gordon et al. (1954), in which sheep and cattle apparently did not rectify phosphorus deficits, does not provide strong evidence that ruminants can not rectify deficits. In the study, 90 cattle and 500 sheep grazed on 5,500 acres that contained 8 groups of troughs (3 troughs per group), 2 containing calcium carbonate and 1 containing equal parts of calcium carbonate and dicalcium phosphate. It was not known how many animals visited the troughs, the consumption of the compounds by individuals that frequented the troughs, and the phosphorus status of animals that did and did not frequent the troughs. Animals ingested little of either substance throughout the year-long study (2.3 g/animal/day). Consumption may have reflected avoidance of unfamiliar substances by the animals (Distel and Provenza 1991, Provenza et al. 1994b), and the reluctance of sheep to ingest food offered in unfamiliar containers (Chapple et al. 1987).

Finally, ruminants need not maximize (optimize) intake of any particular nutrient or mix of nutrients within each meal or even on a daily basis, given that animals can withstand departures from the normal average intake of nutrients (i.e., energy-rich substances, nitrogen, various minerals, and vitamins) (Booth 1985). Rather, homeostatic regulation needs only some increasing tendency, as a result of a gradually worsening deficit of some nutrient or of an excess of toxins or nutrients, to generate behavior to correct the disorder (Figs. 1 and 2). Extreme states should cause herbivores to increase diet breadth and to acquire preferences for foods that rectify maladies. Nutrients required in the greatest amounts should have the most consistent and compelling influence on food selection. Energy is important because it is required in large amounts, but other nutritional needs may take precedence at times. For instance, young lambs and rats select diets that meet their protein requirements for growth (Kyriazakis and Oldham 1993), even when that means overingesting energy in the case of rats (Webster 1993). Nutrients like phosphorus, required in lower amounts, may often be ingested as a result of meeting other nutrient requirements. If not, animals search for foods to rectify the deficit (e.g., Wallis de Vries 1994).

Fermentation and Feedback

Feedback mechanisms let ruminants sense the consequences of food ingestion. Aversive feedback or a lack of positive feedback from the gut to the central nervous system (CNS) probably causes

animals to reduce intake if foods are too high or low in energy or nitrogen; the effect would be opposite if these nutrients were adequate (Fig. 1). Responses are probably mediated by a lack or an abundance of by-products of microbial fermentation (e.g., propionate, acetate, ammonia, amino acids). The microbes in the reticulo-rumen play an essential role in the nutrition of the ruminant. Nutrient deficiencies and toxins can adversely affect microbes (Owens 1988, Bryant et al. 1991), thereby reducing the production of byproducts of microbial fermentation and growth required by the ruminant. The same thing is probably true for other essential nutrients, and how they affect food selection will depend on nutrient requirements and availability in the forage (Emmans 1991).

Food nutritional quality and intake rate (i.e., bite size and bite rate) affect the rate of nutrient release in the gut (i.e., postingestive feedback). The preference for foods that can be eaten quickly (Kenney and Black 1984) probably reflects high rates of positive postingestive feedback, which in turn means it is important to define the relationship between intake rate and feedback from nutrient ingestion (Illius and Gordon 1990, Gross et al. 1993). Chewing facilitates feedback because it promotes the rapid release of nutrients (Beauchemin 1992). The speed and duration of nutrient release during microbial fermentation depend on the physical and chemical characteristics of the food. Feedback should be greater and more rapid from foods that are high in nutrients and highly digestible (e.g., soluble carbohydrates, protein), which can help to explain the well-known relationship between digestibility and intake. Animals should prefer meals of foods that rapidly provide positive feedback followed by a steady release of nutrients, which would quickly cause and subsequently maintain satiety. Sheep show a strong diurnal preference for clover (high rate of digestion) early in the day, after an overnight fast, and grass (slow but steady release of nutrients) later in the day, even though clover and grass have similar gross energy contents and ultimate digestibilities (Parsons et al. 1994).

Food selection and intake are not necessarily restricted by digesta load in the intestines or rumen or by rate of passage. Physical factors in the intestines do not limit intake of roughages because the intestines have a large excess capacity to transport bulk (Grovum 1987). Moreover, ruminants immediately increase intake to meet increased demands for nutrients during lactation (Ketelaars and Tolkamp 1992), and dramatic increases in forage intake and rumen fill postpartum are not limited by rumen capacity or distension (Stanley et al. 1993). Likewise, digesta load changes in response to energy deficit when sheep are fed a single roughage (Gherardi and Black 1989), such that the digestible energy consumed remains constant on a high- (i.e., 50% alfalfa pellets 50% corn) or a low-energy (100% fescue hay) diet (Quigley and Heitmann 1991). Rumen capacity remains relatively constant during the year, but digesta load increases with food intake in red deer (Francoise Domingue et al. 1992). In addition to changes in digesta load, rumen volume can increase to accommodate different forages when the rumen is distended for long periods (e.g., with water or air balloons, Mowat 1963). For instance, rumen tissue mass and volume are significantly greater when goats are reared on a poorly nutritious shrub (blackbrush) than when they are reared on a nutritious diet (alfalfa and calf-manna) (Distel and Provenza 1991). Increases in intake with increasing digestibility are commonly attributed to reductions in rumen fill and increases in rate of passage (Van Soest 1982). But

rumen fill increases until digestibility is about 70% and then declines, even though intake continues to increase (Ketelaars and Tolkamp 1992). Finally, crude protein concentrations below 6 to 8% decrease microbial fermentation rates thereby reducing intake, presumably by decreasing rate of passage. But ruminants quickly (< 1 hour) increase intake of nutritious foods when consuming poorly digestible foods low in nitrogen (Baumont et al. 1990, Distel and Provenza 1991). The range (2 to 35%) of crude protein concentrations over which intake can be stimulated far exceeds limitations on fermentation in the rumen (Ketelaars and Tolkamp 1992).

Finally, changes in the rumen during a meal (e.g., distension, production of VFAs, changes in pH, osmolality) are likely integrated in the central nervous system to cause eating to stop. Satiety within a meal is presumably mediated by tension receptors, and stimulation of tension receptors in the reticulum (Grovum 1979, 1987, 1988) and in the rumen (Mbanya et al. 1993) can decrease intake. Nevertheless, feedback from tension receptors differs from feedback of nutrients and toxins. Ruminants that responded only to tension receptors could easily ingest poorly nutritious and toxic forages. Instead, ruminants are extremely selective among plant species and plant parts as well, even when foraging in monocultures (e.g., see Parsons et al. 1994 and references therein). Accordingly, feedback from nutrients and toxins is likely to be more important than stimulation of tension receptors in food selection and intake. Intraruminal infusions of acetate and propionate depress hay intake in cattle (Anil et al. 1993) and in sheep (Ternouth 1967, Baile and McLaughlin 1970, Bergen 1972), and a combination of acetate, propionate, and distension of the rumen increases satiety (Mbanya et al. 1993). Sheep respond more to propionate than to acetate (Farningham and Whyte 1993). The mechanisms underlying the response are not known, but it does not appear to involve osmotic pressure changes or insulin. As discussed below, byproducts of fermentation like propionate and neuropeptides like cholecystokinin (CCK) interact to cause satiety and to affect food selection (Farningham et al. 1993). CCK also enhances constriction of the pyloric sphincter, thereby slowing the rate of gastric emptying and increasing gastric distention (Baile et al. 1986). Thus, satiety is probably due to mildly aversive feedback from chemo-, osmo, and mechano-receptors in the body to the central nervous system (Mbanya et al. 1993, Anil et al. 1993).

Feedback Mechanisms that Relate Nutrition to Behavior

Affective and Cognitive Processes

Neurally mediated interactions between the senses (i.e., taste and smell) and postingestive feedback cause changes in preference (affective value), and changes in preference cause changes in food selection (Garcia 1989). Taste (the gustatory system specifically, Garcia 1989) plays a prominent role in both processes. Affective processes integrate the taste of food and its postingestive consequences, aversive or positive, thereby causing changes in incentive to eat particular foods; they involve neurally (i.e., primarily brain stem and limbic system) mediated interactions between the sense of taste and the body and they are noncognitive. (Fig. 3). Cognitive processes involve use of the senses of smell, sight, and hearing to select foods that cause satiety and to avoid foods that cause malaise; they involve interac-
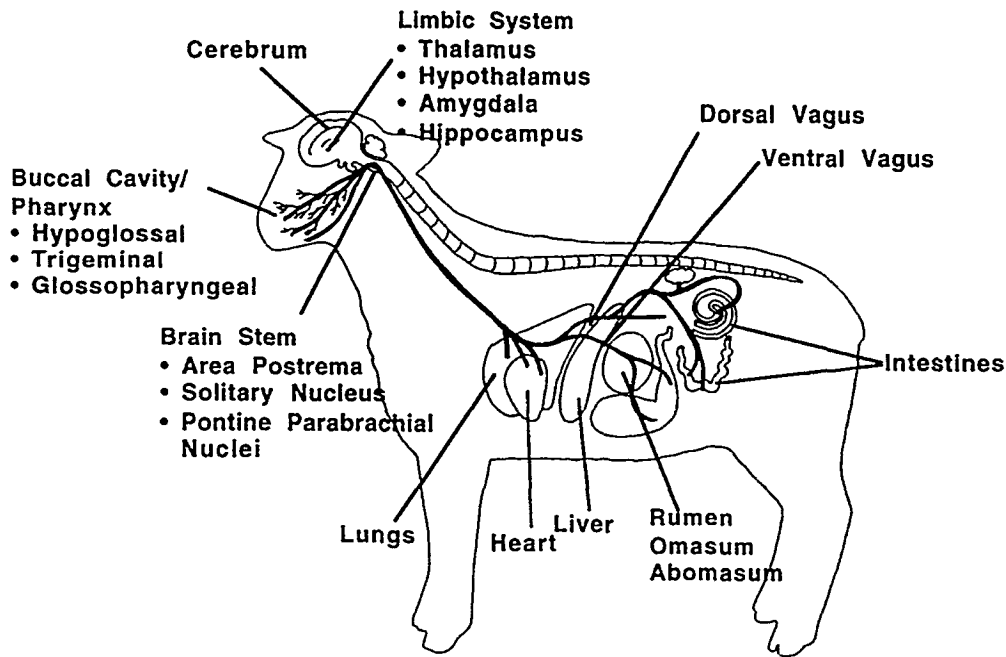
Fig. 3. The senses, visceral nerves, the brain stem, limbic system, and higher cortical centers interact through neuronal fibers that can facilitate or inhibit behavior. Gustatory and visceral afferent nerves that first synapse in the brain stem (involved with visceral, cardiac, and respiratory functions) proceed to the limbic system (concerned with emotional memory). Feedback from the gut to the brain stem and limbic system causes changes in preference for particular foods, which are non-cognitive and depend on the food's effect on the internal environment. On that basis, higher cortical centers (involved with declarative memory) interact with the limbic system to facilitate changes in food selection behavior.

tions between higher cortical centers, the limbic system and brain stem. Affective and cognitive processes are mediated by different brain systems, but they operate in parallel to regulate the internal environment. Thus, preference for food is adjusted according its effect on the internal environment, and on that basis animals select foods that are nutritious and avoid those that are toxic.

The Senses and Feedback

Taste, smell, and sight help animals identify and discriminate among foods, but these senses play somewhat different roles in food preferences and food selection. When animals are made ill following audiovisual and taste cues, they show much stronger aversions to the taste than to the audiovisual stimuli. In contrast, if they receive foot-shock following the same cues, they show much stronger aversions to the audiovisual than to the taste cues (Garcia and Koelling 1966, Lett 1985). This phenomenon is illustrated experimentally with hawks (Brett et al., 1976). Hawks fed white mice, and occasionally given a black mouse followed by an injection of LiCl, do not eat either black or white mice, presumably because both mice taste the same. But when a distinctive taste is added to the black mice, hawks learn to avoid black mice on sight after a single black mouse-toxicosis event. The taste cue potentiates the color cue. As Garcia (1989) suggests, "taste is the most powerful arbiter of what is fit to eat, smell comes next."

Differences in neuroanatomy help explain the different functions of the senses. For instance, neurons associated with taste receptors converge with neurons from the viscera in the most primitive part of the brain (i.e., the solitary nucleus of the brain stem); these gustatory and visceral neurons then relay to other parts of the brain stem, limbic system, and cortex (Fig. 3).

Placement of the nose just above the mouth is beneficial in foraging, but olfaction has additional functions. For instance, olfactory receptors have direct and extensive connections with the part of the brain that affects emotion and motivation (i.e., the limbic system), and the part of the limbic system (i.e., the amygdala) which forms the basis for fear (Barinaga 1992, Davis 1992, LeDoux 1992, 1994). Thus, smell is involved in protecting animals from hazards like predation as well as noxious foods.

Taste and smell operate across different scales of time. Learning with long delays is characteristic of the taste-feedback system, which integrates information about food over a scale of minutes to hours; digestion and absorption are relatively slow processes (Garcia 1989). Thus, animals can acquire aversions even when feedback is delayed for many hours (Rozin 1976, Zahorik and Houpt 1981, Burritt and Provenza 1991). In contrast, a novel odor must be followed immediately by aversive postingestive feedback to produce strong aversion to the odor. In odor-taste-feedback conditioning, the odor-taste interval must be a matter of seconds or minutes. When odor is paired with taste, the conditioning of the odor is greatly enhanced. The ability of taste to enhance the conditioning associated with odor is called potentiation (Garcia 1989).

Cognitive and Non-cognitive Aspects of Food Selection

When nausea follows a meal, people often acquire aversions, and they generally rationalize why they no longer like particular foods (e.g., one of the foods made them sick in the past, they ate too much of a particular food, one of the foods was a novel, the food had a salient taste). In that sense, food aversions seem cognitive and rational. Nonetheless, affective processes involving

taste and postingestive feedback do not involve cognitive associations. For instance, many of us remember acquiring an aversion to a particular food, even though we know the illness was not related to food (e.g., flu, reaction to a vaccine, seasick, chemotherapy). This knowledge does not alter the newly acquired aversion to food. Thus, interactions between the senses and postingestive feedback are not readily changed by cognitive ruminations.

Nonruminants and ruminants evidently do not differ in the non-cognitive aspects of how feedback is processed, for instance, in the origins and destinations of afferent neural signals, even though they differ in the sites and modes of nutrient absorption, kinds of digestive enzymes, and tissue metabolism (Church 1988). For instance, sheep that ate a familiar food, and were then anesthetized and given an intraruminal injection of LiCl, subsequently acquired an aversion to the food (Provenza et al. 1994a). Likewise, food aversions have been conditioned in nonruminants when they were anesthetized (Roll and Smith 1972, Bermudez-Rattoni et al. 1988), deeply tranquilized (Forthman Quick 1984), and when their electrocortical activity was depressed (Davis and Bures 1972, Buresova and Bures 1973).

These results bring into focus cognitive and non-cognitive (affective) aspects of learning and memory. Memory is generally thought of as the process by which earlier conscious experiences are recalled (LeDoux, 1992). The original learning and remembering are both conscious events. Such declarative (cognitive) memory is mediated by the hippocampus and the cortex. In contrast, emotional (non-cognitive) memory is mediated by the thalamus, amygdala, and cortex, and in all likelihood operates independently of conscious awareness. Nevertheless, emotional information may be stored within declarative memory and retrieved in parallel, "their activities joined seamlessly in conscious experience" (LeDoux, 1994). The mechanisms of emotional and declarative memories thus provide an explanation for the fact that animals in deep anesthesia acquire food aversions. More generally, acquired preferences and aversions are part of emotional memory; postingestive feedback and memory of the event occur whether or not animals are conscious. The emotional memory is stored within declarative memory of specific foods and the context in which they were eaten.

Variables That Control Taste-Feedback Associations

The particular food(s) that come to be associated with malaise (or satiety) in nonruminants and ruminants depend on several factors that probably interact. For instance, the volume of each food eaten in a meal affects acquired aversions in both groups of animals (Bond and DiGuisto 1975): Following administration of LiCl, goats reduced consumption of the food previously consumed in the largest amount (Provenza et al. 1994c). The novelty of the food item also affects these associations (Revusky and Bedarf 1967): When sheep that consumed 4 familiar foods and one novel food in a meal subsequently received LiCl, they avoided only the novel food (Burritt and Provenza 1991). The strength of aversion also depends on how soon toxicosis occurs after a food is ingested (Garcia et al. 1974, Cannon et al. 1985): Sheep acquire an aversion to the food eaten just prior to toxicosis (Provenza et al. 1993b). The concentration of a compound also affects aversions (Kalat and Rozin 1970, Cannon et al. 1985): Sweet (sodium saccharin) or bitter (aluminum sulfate) flavors, regardless of concentration, did not affect lambs' consumption of

barley. But after a mild dose of LiCl, the lambs preferred the barley with the lowest concentration of either flavor (Launchbaugh et al. 1993). Goats had a similar response to blackbrush twigs (Provenza et al. 1994c). Finally, salient flavors affect the relationship (Kalat and Rozin 1970, 1971): For example, lambs with an aversion to cinnamon-flavored wheat also avoided cinnamon-flavored rice (Launchbaugh and Provenza 1993).

Preference and Feedback

Animals may express preferences for foods based on a change in liking for the flavor of the food or based on anticipated consequences from eating the food (Rozin and Zellner 1985). For instance, a human may avoid eating strawberries, because they cause hives, but still like their flavor. Conversely, the person is likely to acquire an aversion for the flavor of strawberries if their ingestion is followed by aversive postingestive feedback (i.e., nausea caused by a toxin). The same process occurs for acquired preferences. A person may ingest medicine, because of anticipated benefits (e.g., relief of a headache), but not like its flavor. On the other hand, the person is likely to acquire a liking for the flavor of the medicine if its ingestion is followed by positive postingestive feedback (e.g., satiety caused by calories).

Decreases in Preference

Lower- and upper-gastrointestinal distress evidently have different effects on preference. Lower intestinal discomfort (e.g., cramps, diarrhea, flatulence) may cause discerning animals to decrease intake of foods, but they evidently do not cause a decrease in liking for the food (Pelchat and Rozin 1982, Pelchat et al. 1983, Garcia et al. 1985, Garcia 1989). The same is true for respiratory distress, rashes, and allergies. Conversely, foods that cause upper-gastrointestinal distress (i.e., nausea from stimulation of the emetic system, Coil et al. 1978, Provenza et al. 1994d) cause negative hedonic shifts. Alternatively, upper gastrointestinal discomfort may simply cause more of a hedonic shift than lower gastrointestinal distress. The difference between hedonic shift and discomfort caused by distension may explain why livestock sometimes over-ingest nutritious foods that cause bloat (e.g., alfalfa). Positive feedback from nutrients may cause a strong liking for the food (i.e., a positive hedonic shift) that overrides any physical discomfort caused by stimulation of tension receptors in the reticulum and rumen.

Increases in Preference

Lambs acquire preferences for flavors paired with nutrients. For instance, when lambs consumed either grape- (group 1) or orange- (group 2) flavored glucose solutions on some days and orange- (group 1) or grape- (group 2) flavored saccharin solutions on alternate days, they subsequently preferred (96% to 4%) the flavor paired with glucose (Burritt and Provenza 1992). This acquired preference for a flavor reflected the nutritive properties of the solutions because lambs consumed the same amount of nutritive and non-nutritive solutions during conditioning and did not exhibit any preference when allowed to choose between unflavored solutions of glucose and saccharin in short-term tests (i.e., 5 min). Lambs exhibited similar preferences in experiments involving flavored straw paired with starch, propionate, or glucose (Thorhallsdottir 1991, Ralphs et al. 1995, Villalba and

Provenza, unpublished data).

The fact that lambs that are not deprived of nutrients exhibit a preference for certain flavors, even when the nutrient is no longer present suggests hedonic shifts are important (Villalba and Provenza, unpublished data). Rats also learn to like flavors paired with calories (i.e., they experience positive hedonic shifts), whether or not they initially like the flavor (Mehile 1991), and they acquire a strong preference (>95%) for bitter and sour tastes paired with nutritional consequences, even though these flavors were not preferred initially (Sclafani 1991c). These preferences persist for weeks in the absence of nutritional feedback, they occur whether or not rats are food deprived, and they are manifest in different environments, which suggests that rats acquire preferences for flavors on the basis of nutrient feedback.

Animals may also consume particular flavors because they anticipate the benefits, rather than because they prefer the flavors. For example, lambs evidently rectify acidosis by drinking a solution containing sodium bicarbonate (Phy and Provenza 1994 and unpublished data). But when lambs are given a choice between plain water and water with sodium bicarbonate, they prefer water. Thus, lambs drink the sodium bicarbonate solution (i.e., the medicine) because they anticipate its positive consequences (i.e., attenuate malaise caused by acidosis, Provenza et al. 1994d), not because they like the flavor. Likewise, rats prefer flavors associated with recovery from threonine deficiency (Gietzen et al. 1992), but only when they are deficient in threonine (Gietzen 1993).

Dependence on Internal State

Hedonic responses depend on the needs of the organism, positive if it ameliorates malaise and negative if it causes malaise. Sucrose or glucose tastes pleasant to fasted humans, but their tastes become unpleasant after they are consumed (Cabanac 1971). Non-ruminants can discriminate between foods, even when the differences in energy content are relatively small (Post 1993), and people given differently flavored medium- and low-carbohydrate snacks prefer the flavor paired with low-carbohydrate snacks when satiated but not when food deprived (Booth and Toase 1983). Flavor preferences conditioned using protein (Gibson and Booth 1986) or carbohydrates (Gibson and Booth 1989) also depend on the state of an animal.

State-dependent food selection generally has not been studied experimentally in ruminants, but their food selection changes within meals (Arnold and Dudzinski 1978), and there is no reason to believe they do not exhibit state-dependent foraging within and among meals (Jung and Koong 1985, Newman et al. 1994, Parsons et al. 1994). It is also likely that diet will vary with age, physiological condition, and environment (Fig. 2). For instance, the required protein:carbohydrate should decrease when animals cease growing, increase when animals are reproducing, and increase when energy requirements are high during winter.

Evolutionary Significance

Feedback is a process in which the factors that produce a result are themselves modified, corrected, and strengthened by that result. Accordingly, feedback adjusts hedonic value commensurate with the food's utility to the animal, and it enables animals to survive in an everchanging world. From an evolutionary standpoint, mechanisms that enable animals to experience feedback, sensations such as satiety and malaise, should be highly correlated with nutritional well being, toxicosis, and deficiencies. That is

different from saying that food ingestion is reinforcing because food tastes good or bad, or because postingestive feedback from food ingestion is aversive or positive (Skinner 1976). These hedonic sensations merely accompany the conditions responsible for food selection, the nutritional and physiological well being of the animal. Accordingly, behavior and nutrition are directly related through feedback mechanisms.

Aspects of the Neural Basis for Food Selection

Neural Convergence

Visceral afferents probably interact with gustatory and olfactory afferents to facilitate or inhibit food ingestion (Fig. 3). Although there is little evidence to support or refute this hypothesis, because of a lack of research, there are anatomical and physiological mechanisms that might underlie such interactions (Novin 1983, Norgren 1983). The neural pathways of gustatory and visceral afferents have been fairly well established (e.g., gustatory and visceral afferents that first synapse in the nucleus of the solitary tract project through the pontine parabrachial nuclei (PBN) to the area postrema, to the thalamic gustatory relay (which in turn projects to the neocortex), and to ventral forebrain structures including the hypothalamus, amygdala, and red nucleus of the stria terminalis, Glenn and Erickson 1976, Spector et al. 1992). Lesions at various points along the pathway (e.g., vagotomy Louis-Sylvestre et al. 1983, Anil and Forbes 1980, 1988; abdominal vagus, solitary nucleus, midbrain, paraventricular nucleus, Crawley et al. 1984; ventromedial hypothalamic lesions, Cox and Smith 1986; PBN, Spector et al. 1992) make it impossible for animals to integrate taste and visceral signals to appropriately modify food selection and ingestion. This illustrates that gut-brain-gustatory interactions allow nutrients and toxins to be sensed. In the following section, I explain how the brain may actually sense excesses and deficits, and in turn provide feedback which causes an animal to alter food selection.

Acquired Aversions

Animals may acquire aversions to excesses of toxins and nutrients when the emetic system is stimulated (Coil et al. 1978, Provenza et al. 1994d). The emetic system is very sensitive to low doses of most toxins (Davis et al. 1986), and involves complex interactions between several areas in the brain stem including the area postrema and the chemoreceptor trigger zone (Seynaeve et al. 1991, Mitchelson 1992; Fig. 3). The area postrema is a circumventricular organ lying outside the blood-brain barrier, and the chemoreceptor trigger zone is a chemosensitive region in the area postrema. These regions of the emetic system can be stimulated directly by toxins in the cardiovascular system and cerebrospinal fluid (Borison and Wang 1953), and through visceral afferents (i.e., neurons that carry sensory information to the brain), primarily vagal afferents, and to a lesser extent, splanchnic afferents (Borison, 1986; Davis et al., 1986; Grahame-Smith, 1986; Kosten and Contreras, 1989). Efferent impulses (i.e., neurons that provide motor input to innervated structures) from the emetic system to effector organs travel through the hypoglossal, glossopharyngeal, and trigeminal nerves (innervating the buccal cavity and pharynx), through the vagal nerve (innervating the pharynx, respiratory and gastrointestinal tracts), from the respiratory center to the phrenic and intercostal nerves, and through some sympathetic efferents in the gastroin-

testinal tract (Seynaeve et al., 1991). These pathways to and from the emetic system clearly show how ingestion of an excess of a toxin or nutrients can cause upper gastrointestinal malaise, thereby causing the animal to decrease (intake), and how impulses from the emetic system to the gastrointestinal tract can cause a decrease in gut motility and rate of absorption of toxins (Stricker and Verbalis 1990, Bernstein et al. 1992) or nutrients (Baile et al. 1986).

Little research has concerned the role of the emetic system in food selection and intake of ruminants. In one study, antiemetic drugs (diphenhydramine, metoclopramide, dexamethasone) attenuated LiCl-induced aversions in sheep (Provenza et al. 1994d). Moreover, mild aversive feedback apparently caused sheep to limit their intake of grain. In another study, ergopeptide alkaloids (primarily ergovaline), produced by the endophytic fungus *Acremonium coenophialum*, reduced the intake of tall fescue by sheep (Aldrich et al. 1993). Daily dosages of an antiemetic drug (metoclopramide, which acts on serotonin ($5HT_3$) receptors) significantly increased intake of endophyte-infected tall fescue, but not intake of endophyte-free fescue. The ability of antiemetic drugs to increase intake of foods that cause aversive feedback is consistent with the hypothesis that antiemetic drugs cause intake to increase primarily by attenuating food aversions, not by increasing the rate of passage of food from the gut (Mitchelson 1992).

Lambs acquire aversions to foods that they eat when they experience imbalances in many essential amino acids (Rogers and Egan 1975, Egan and Rogers 1978). The neural mechanisms that enable ruminants to recognize an amino acid imbalance have not been identified. Neural mechanisms let rats recognize an imbalance as soon as 28 min. after ingesting a deficient diet (Gietzen et al. 1986), and similar mechanisms probably operate in ruminants. Rats avoid foods that are imbalanced in amino acid content when there is a decrease in the concentration of the limiting amino acid in the prepyriform cortex, as well as decreases in norepinephrine and cyclic AMP, and altered protein synthesis (Gietzen and Beverly 1992, Gietzen 1993). Rats then acquire an aversion to the diet, which is mediated by undetermined structures in the central nervous system and the neurotransmitter serotonin ($5HT_3$) (Hammer et al. 1990, Gietzen et al. 1991b). Blocking of $5HT_3$ receptors (by ICS 205-930) attenuated the aversive response of rats to an amino acid imbalanced-food (Gietzen 1993), and to LiCl (Gietzen et al. 1991a). Blocking $5HT_3$ receptors also attenuates chemotherapy-induced vomiting in humans (Costall et al. 1988).

Acquired Preferences

Much of the research concerning conditioned food preferences has involved rats. Rats eat more foods or non-nutritive flavors (foods) paired with calories (Messier and White 1984, Booth 1985, Mehiel and Bolles 1984, 1988, Simbayi et al. 1986, Mehile 1991, Sclafani 1991a,b), during recovery from nutritional deficiencies (Garcia et al. 1967, Zahorik et al. 1974), and during recovery from postingestive distress (Green and Garcia 1971, Sherman et al. 1983). Many mechanisms are likely to be involved in acquired preferences, as is the case with acquired food aversions (Grahame-Smith 1986) and with the control of food intake (deJong 1985). Accordingly, a single nutrient, compound, hormone, or organ is not apt to have a dominant role in the acquisition of food preferences, considering the variety of nutrients needed by animals. Nonetheless, all are likely to operate on a continuum, as outlined below for calories.

Acquired preferences caused by calories may be mediated by neuropeptides like CCK. Rats acquire preferences for flavors of noncaloric solutions when their ingestion is followed by intraperitoneal injections of CCK. Likewise, when exogenously administered CCK is given along with a calorie-paired flavor, CCK further increases rats' preference for the flavor (Mehile 1991). Conversely, high doses of CCK can condition food aversions (Deutsch and Gonzalez 1978, Stricker and Verbalis 1990, Perez and Sclafani 1991). These seemingly contradictory findings suggest there is a fine line between satiety (satisfied to the full) and surfeit (filled to nauseating or disgusting excess), which is to be expected if preferences and aversions to energy and nutrients are points along a continuum.

Behavioral observations also suggest a fine distinction between satiety and malaise, and that malaise operates in subtle ways to control food selection. For instance, when a person eats a food to satiety, the pleasantness of the flavor of the food is reduced more than other foods that were not eaten, which enhances intake of different foods offered later (Rolls et al. 1981, 1984). The more subsequent foods differ in taste, smell, appearance, texture, and nutrient content, the more intake of these foods is likely to increase (Rolls et al. 1984). Thus, a person can apparently acquire mild aversions to the flavors of particular foods, which eventually extends to all foods eaten during a meal. Such an aversion may last well beyond the end of the meal. When sheep on a pelleted diet are infused with propionate, their consumption of pellets over a 24 hour- period decreases as the dose of propionate increases (Farningham and Whyte 1993). Furthermore, sheep given low or moderate doses of propionate during a meal, acquire a strong preference for the food (Villalba and Provenza unpublished data), whereas sheep given a high dose of propionate during a meal, acquire a persistent aversion to the food (Ralphs et al. 1994). All of these observations are consistent with the hypothesis that preference and aversion are points along a broad and sensitive continuum.

Acquired preferences and aversions may involve many of the same mechanisms, which respond in a dosage-dependent fashion to nutrients and toxins alike. These may involve several brain regions (e.g., solitary nucleus, PBN, area postrema, and hypothalamus) and neurotransmitters. For instance, the area postrema, which is thought to be involved in acquired preferences and aversions, has receptors or binding sites for neurotransmitters (i.e., histamine, dopamine, serotonin ($5HT_3$), norepinephrine, CCK, enkephalins, and acetylcholine) that play roles in satiety (Baile 1974) and malaise (Seynaeve et al. 1991, Mitchelson 1992). Also, peptides involved in satiety and malaise mediate interactions between snakes and toxic frogs: Peptides in the frog's mucous produce satiety at low doses and toxicosis at higher doses in snakes. As Garcia (1989) suggests, "That may be the way chemical protection gradually evolves; those organisms which can quickly induce satiety in foragers stand a better chance of having their kind survive. Perhaps it is no accident that many phytochemicals such as caffeine, nicotine and digitalis cause a loss of appetite in vertebrates including humans, thus providing an excellent protection against continued munching by foragers."

In ruminants, visceral afferents probably interact with gustatory and olfactory afferents, and these effects are likely modulated through byproducts of microbial fermentation and by neurotrans-

mitters within the CNS. For instance, the VFA propionate is a major source of energy in ruminants, and its role may be similar to that of hepatic glucose in the control of food intake in non-ruminants. Portal flow of propionate can control food intake in ruminants (Farningham and Whyte 1993). Food intake during spontaneous meals was decreased by about 40% in goats and sheep by injections of propionate into the ruminal vein, but not decreased by infusions into the jugular vein (Baile 1971). Intraportal administration of propionate depresses food intake in sheep only if the vagal or splanchnic nerve supply from the liver to the central nervous system is intact (Anil and Forbes 1988). Afferent nerve signals from the liver to the central nervous system may cause the release of peptides like CCK, which cause satiety in a dose-dependent fashion when administered within the central nervous system in sheep (Della-Fera and Baile 1979, 1981, Grovum 1981). Low doses of propionate or CCK do not affect food intake in sheep, but they interact and decrease intake by 44% over a 2- hour period (Farningham et al. 1993). These data suggest that byproducts of fermentation like propionate and neuropeptides like CCK interact to cause satiety and affect food selection.

There are 2 types of receptors for CCK in the area postrema, one for CCK in cerebrospinal fluid and one for axonally transported CCK (Moran et al. 1986). CCK receptors on vagal axons innervating the liver proceed rostrally to the area postrema, a circumventricular organ that receives input from both blood and synaptic transmission (Sankaran et al. 1979, Zarbin et al. 1981). The CCK pathway runs from the area postrema through the midbrain to at least three nuclei of the hypothalamus: the paraventricular nucleus, the ventromedial nucleus, and the dorsomedial nucleus (nuclei in the amygdala are also involved). Within the hypothalamus, CCK may modulate endorphins and norepinephrine (Baile et al. 1986), thereby affecting preferences for flavors paired with calories.

Varied Diets

Some believe animals ingest an assortment of foods to increase the likelihood of ingesting the necessary nutrients (Westoby 1978), whereas others believe they do so to reduce the potential of overingesting toxins (Freeland and Janzen 1974). Both factors are important. Plants contain a bewildering array of secondary metabolites, many (perhaps most) of them toxic (Cheeke and Shull 1985, Bryant et al. 1991). Secondary metabolites cause ruminants to limit intake of even the most nourishing foods, which in turn causes ruminants to ingest a diverse array of plants to minimize toxicosis. Energy and primary nutrients such as nitrogen and phosphorus often co-vary in their availability and they are often concentrated in young plant parts. Nonetheless, it may be difficult for animals to meet requirements when energy and nutrients are not equally distributed among resources. This can occur when habitats vary in soil fertility (Wallis de Vries 1994), or with an imbalance in nutrient contents, such as an excess of protein in young growth (Prins and Beekman 1989). Thus, varied diets also reflect availability of nutrients in plants and nutritional requirements of animals.

Mild aversions caused by excesses of nutrients and toxins and by nutrient deficits cause animals to eat different foods. Moreover, eating to the point of satiety is likely to be mildly to strongly aversive. Accordingly, malaise is probably an important

reason why ruminants eat varied diets (Provenza 1994b). Several factors likely act synergistically to cause animals to acquire mild aversions to foods within and among meals. Aversions are acquired on the basis of interactions between sensory receptors (taste and odor of particular foods) and postingestive feedback (e.g., amount and frequency of malaise) which depends on the nutritional and toxicological characteristics of the diet. The more foods differ in taste, smell, appearance, texture, and nutrient content, the more each food is likely to contribute to the diet. The more closely a food matches the nutritional requirements of the animal, the more likely the food will be a staple in the diet. Nevertheless, ingestion of any food to satiety is likely to cause animals to temporarily decrease their preference for the food. For instance, sheep show a strong preference for clover early in the day and for grass later in the day (Parsons et al. 1994), which may reflect mild aversions to both clover and grass (Provenza 1994b). The time required for the onset of an aversion, the degree to which the aversion is manifest, and the duration over which a particular food is avoided will depend on the flavor of the food and the amount and frequency of malaise. Accordingly, aversions produced by satiety are likely a result of interactions between the senses and postingestive feedback, and not simply a result of sensory-specific satiety.

Sensory-specific satiety is the decrease in preference for a food as it is eaten within a meal and over longer periods (Rolls 1986). Such decreases in preference occur in ruminants (e.g., Baumont et al. 1990, Ramos and Tennessen 1993, Newman et al. 1992, 1994, Parsons et al. 1994) and nonruminants (Rolls 1986). The phenomenon has been attributed to sensory properties of foods, rather than to postingestive feedback, because the preference for ingested food tends to decrease soon after a meal (i.e., 2 to 20 min) and then gradually increases during the next hour (Rolls et al. 1981, 1984). Satiety occurs whether flavors are nutritive or non-nutritive (Wooley et al. 1972) and in foods of varying nutritional value (Birch and Deysher 1986). Other evidence that suggests the response is mediated by taste and smell is the fact that pleasantness of the sweetest sodas, containing the most calories and potentially the most satiating, declines even when they are tasted and not swallowed (Drewnowski et al. 1982).

Nonetheless, these changes in preference as a result of consumption do not rule out interactions between the senses (taste and smell) and postingestive feedback. Postingestive effects (e.g., release of saliva and digestive enzymes, release of most gastrointestinal and pancreatic hormones, release of neurotransmitters involved in satiety) occur upon initiation of a meal and can begin upon experiencing the flavor of a familiar food (i.e., they are Pavlovian processes). For instance, after a flavor is paired with a caloric solution, the flavor alone elicits the release of CCK, a peptide that moderates hedonics within a meal (Fedorchak and Bolles 1988, Mehile 1991). In addition, feedback from nutrients and toxins can begin rapidly following initiation of a meal, as discussed previously. Finally, when an animal only tastes a food or ingests a food of low nutrient density, the lack of a positive postingestive effect may be aversive. For example, the cephalic-phase responses to sweet substances can, if followed by ingestion of noncaloric solutions, reduce preference for the taste (Tordoff and Friedman 1989). Thus, it is more reasonable to assume that the senses and postingestive feedback interact during foraging to constantly modulate the hedonics of food ingestion, within a meal and from meal to meal. Eating a variety of foods has several benefits, such as obtaining a more balanced diet, reducing consump-

tion of toxic foods, sampling of foods, and maintaining a diverse microflora in the rumen. But malaise, rather than benefits, is the cause of varied diets.

Opportunities for Research

Ruminants discriminate among foods with their senses and sense the consequences of food selection through feedback mechanisms, both of which are integrated within the central nervous system. Several facets of this interaction merit further study. Studies of ruminants have focused on the effects of VFAs like propionate and peptides like CCK on suppression of feeding. These compounds probably mediate acquired preferences and aversions, and should be studied to determine how they affect the acquisition of preferences and aversions in ruminants. Administration of high concentrations of propionate to sheep not only caused satiety, but they also conditioned strong food aversions (Ralphs et al. 1995).

Calories cause positive hedonic shifts and toxins cause negative shifts, but it is not clear if the same is true for foods or flavors paired with other nutrients (e.g., nitrogen, phosphorus), with recovery from nutrient deficits, or with recovery from excesses of nutrients or toxins. It would also be interesting to know if ruminants sense the effects of toxins in the same way, and by the same mechanisms, as they sense states like acidosis (Ortega-Reyes et al. 1992), amino acid imbalances (Egan and Rogers 1978), and deficits of phosphorus (Ternouth 1991). Do ruminants sense all diet-related maladies in the same manner and by the same physiological mechanisms (Grant 1987, Galef 1991), or do they differ in how they sense satiety caused by carbohydrates (Miner 1992), amino acids (Egan and Rogers 1978), and other nutrients? If ruminants can distinguish among maladies (satieties), can they also learn to ingest substances that rectify different internal states? If so, this information would be valuable in preventing toxicosis and in rectifying nutritional deficits.

Positive and negative hedonic shifts occur as a result of experiences early in life, but it is not clear how experiences early in life cause hedonic shifts. Ruminants acquire strong preferences for foods consumed early in life, and prefer those foods as adults, whereas they are reluctant to eat foods they have not experienced (e.g., Distel and Provenza 1991, Ramos and Tennessen 1992, Walker et al. 1992, Biquand and Biquand-Guyot 1992). Mother and peers influence the dietary habits of young ruminants (Provenza 1994a, Provenza and Balph 1987, 1988, Provenza 1994a,c), and experiences with mother appear to be especially influential (e.g., Thorhallsdottir et al. 1990, Mirza and Provenza 1990, 1992, 1994, Nolte et al. 1990). It is not known if hedonic shifts simply reflect flavor-feedback conditioning over a long period, or if there are additive effects resulting from interactions between age of exposure, mother, and postingestive feedback.

Finally, it is important to determine how ruminants acquire dietary habits and the basis for varied diets within and among meals. Goats first introduced to blackbrush-dominated rangelands sample all foods in the area during the first few hours, including potentially toxic plants like *Juniperus osteosperma* (bark and green leaves), *Gutierrezia microcephala* (a forb), and *Marrubium vulgare* (a forb), as well as non-toxic shrubs like *Prunus fasciculata* and *Purshia tridentata*. They also sample both CSG and OG from blackbrush. Goats evidently eat small amounts of each food,

and during the next few days they limit intake of the potentially toxic foods and ingest meals composed primarily of blackbrush OG and *Prunus fasciculata*. It is important to understand how ruminants acquire aversions and preferences in such a complex environment.

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