Roles of novelty, generalization, and postingestive feedback in the recognition of foods by lambs

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ABSTRACT: Ruminants select foods higher in nutrients and lower in toxins than the average of what is available whether fed in confinement or foraging on pastures or wild lands. Our objective was to better understand how sheep learn to select the most nutritious foods when they concurrently ingest different foods. We hypothesized that novelty and generalization are two ways sheep discriminate among foods. The first experiment determined whether lambs offered two foods in a meal (one a novel-flavored food and the other a familiar food) acquired a preference for the novel-flavored food following an infusion of energy (starch) into the rumen. Lambs did not increase preference for the novel-flavored food when the amount of starch infused (150 g) was held constant (P > 0.05). However, when the amount of starch infused was made directly proportional to the amount of novel-flavored food ingested, lambs quickly formed a preference for the novel-flavored food (P < 0.001). The second experiment determined whether lambs generalized preferences from familiar to novel foods. Lambs fed coconut-flavored milo grain for 51 d subsequently preferred coconut-flavored straw to plain straw (P < 0.001). Conversely, lambs that were not fed coconut-flavored milo grain preferred plain to coconut-flavored straw (P < 0.001). Lambs infused with a source of energy (starch, 100 g/[lamb-d]) consumed more coconut-flavored straw and less plain straw than lambs that had no infusions or lambs infused with a toxin (LiCl, 100 mg/kg BW; P < 0.05). Lambs infused once with LiCl had the lowest preference for coconut-flavored straw (P < 0.05). Lambs conditioned with starch had the highest intakes of coconut-flavored straw, even after starch infusions were suspended (P < 0.1). When straw was replaced by an energy-dense food (wheat grain), all lambs equally preferred coconut-flavored grain to plain grain (P < 0.001). Collectively, our results suggest that lambs learned to prefer a novel-flavored food when the amount of energy reward was contingent on the amount of novel-flavored food ingested, and that they generalized from familiar to unfamiliar foods based on common flavor cues. Once generalization occurred, postingestive feedback from nutrients and toxins calibrated preference according to the food’s utility.

Key Words: Feeding Preferences, Flavor, Food Acceptability, Food Preferences, Novel Foods, Sheep

Introduction

Ruminants encounter a variety of foods with concentrations of nutrients and toxins that vary in time and space (Freeland and Janzen, 1974; Provenza et al., 1998). Despite this challenge, animals manage to select diets that are higher in nutrients and lower in toxins, indicating that food selection is not random (Newman et al., 1992; Illius and Gordon, 1993). However, it is not well known how ruminants identify the qualities of different foods.

Traditionally, food preferences have been attributed to the innate ability of animals to sense, through taste and smell, specific flavors, nutrients, and toxins in plants (e.g., Arnold and Dudzinski, 1978; Rhoades, 1979). Contemporary research suggests that food preferences are better understood as a learned process involving complex interrelationships between a food’s flavor and its postingestive effects (Provenza, 1995a,b; 1996). Evidence for the role of postingestive feedback on preference comes from studies in which animals are trained to consume a specific food, without the confounding effects of other foods, to facilitate the animals’ associating a specific food with its postingestive consequences. However, ruminants often eat several foods during a meal, which may interfere with their ability to recognize specific foods (van Wieren, 1996). Nevertheless, we suspect that novelty and generalization are
two ways in which ruminants discriminate among foods. Novelty enhances the association of unusual gastrointestinal events with previously ingested novel foods (Revsusky and Bedarf, 1967), and generalization transfers the effects of learning to novel foods with familiar flavors (Launchbaugh and Provenza, 1993).

Our objectives were to determine 1) whether lambs learned to prefer a novel-flavored food when its consumption was associated with the supply of energy (starch) in the rumen, 2) whether lambs generalized preferences from familiar to novel foods, and 3) whether intraruminal infusions of nutrients (starch) or toxins (LiCl) influenced generalization.

Materials and Methods

Two experiments were conducted at the Green Canyon Ecology Center, located at Utah State University in Logan. Four different sets of lambs (Finn-Polypay-Suffolk crossbreds of both sexes) were used in the experiments (two sets per experiment). During each experiment, lambs were individually penned and had free access to mineral blocks and fresh water. Alfalfa pellets were the basal diet and provided approximately 80% of the daily digestible energy requirements (NRC, 1985).

Experiment 1

The objective of this experiment was to determine whether lambs learned to prefer a novel flavor added to a familiar low-quality food when consumption of the novel flavor was associated with an increased supply of energy (starch) in the rumen.

Experiment 1A

Twenty lambs (47 kg BW; 5 mo of age) were familiarized with a low-quality food, grape pomace (1.09 Mcal/kg DE, 1.6% DP; NRC, 1985), from 0800 to 0900 for 8 d. Refusals were collected and weighed, and at 1200 all animals received alfalfa pellets (1,650 g/lamb-d). Following the familiarization period, lambs were sorted by the amount of grape pomace ingested and pairs of lambs were randomly assigned to two groups (10 lambs/group) so that the intake of grape pomace was balanced between groups. The average intake of grape pomace during the 8-d familiarization period was 244 g/d (SEM = 17) and 247 g/d (SEM = 16) for lambs in Groups 1 and 2, respectively.

After familiarization, all lambs were offered grape pomace and grape pomace with a novel component: mountain big sagebrush (Artemisia tridentata subsp. vaseyana). Sagebrush was added at 20% to provide a strong novel flavor to the grape pomace. Mountain big sagebrush leaves and twig tips were chopped to a 5- to 10-mm particle size and stored in sealed plastic bags in a freezer until fed. The pomace-sagebrush diet was hand-mixed daily before feeding. The food was offered from 0800 to 0900 daily.

During Exp. 1A, Groups 1 and 2 had a choice between grape pomace and grape pomace plus sagebrush. Lambs from Group 1 were observed individually, and, when they began to eat the novel pomace-sagebrush mix, they received intraruminal infusions of starch by oral intubation. Thus, starch infusions where not predetermined but contingent on the ingestion of the novel food. The suspension was prepared by mixing 150 g of starch with 250 mL of tap water at room temperature. Lambs develop strong flavor preferences when ingestion of a specific flavor is associated with intraruminal infusions of 150 g of starch (Villalba and Provenza, 2000b). Animals were not infused on days when they did not eat the novel mixture (i.e., they ate only grape pomace). Lambs in Group 1 were offered the choice between grape pomace and the novel pomace-sagebrush mixture in the ensuing days until every lamb had consumed the novel mixture and received infusions of starch for 7 d. Lambs in Group 2 were also offered pomace and pomace-sagebrush for 1 h/d, but no starch was administered (control; Table 1). At 0900, refusals were collected and weighed. At 1200, all lambs received a basal diet of alfalfa pellets.

After conditioning, all lambs were offered the two foods for 15 min and intake of each food was measured. No intraruminal infusions of starch were given during the preference test (Table 1).

Experiment 1B

During Exp. 1B, we used a different test food and different flavors. We also increased exposure to the familiar food and infused starch after lambs ingested the foods. We allowed all lambs to experience the postigestive effects of starch after ingesting a novel flavor.

A new group of 18 lambs (32 kg BW; 4 mo of age) was randomly divided into two groups (nine lambs/group). Lambs in both groups were exposed to wheat straw (1.81 Mcal/kg DE, 3.5% DP; NRC, 1985) from 0800 to 1200 for 22 d. Lambs in Group 1 were offered onion-flavored straw (ground through a 1-mm screen) and those in Group 2 were offered maple-flavored straw. Onion (Pacific Foods, Kent, WA) and maple (Agrimexica, Northbrook, IL) flavors were mixed with straw at a concentration of 2% (wt/wt). At 1200, refusals were collected and weighed and all animals received alfalfa pellets (1,400 g/lamb-d). Lambs consumed 99 g/d (SEM = 5) of onion-flavored straw and 94 g/d (SEM = 6) of maple-flavored straw.

After familiarization, all lambs were offered 150 g each of onion- and maple-flavored straw simultaneously. Choices were conducted for 20 min/d for 8 d. Maple and onion were novel for Groups 1 and 2, respectively. After each exposure, refusals were collected and weighed. Lambs that consumed at least 5 g of straw with the novel flavors received 150 g of starch by intraruminal infusion as described for Exp. 1A (Table 1). At 1200, all lambs received a basal diet of alfalfa pellets.
After 8 d, all lambs continued to receive a simultaneous offering of 150 g of straw in the two flavors, but we made the amount of starch infused directly proportional (2\times) to the amount of novel (or less familiar) flavor consumed, with a maximum value set at 150 g of starch. Conditioning lasted 15 d (Table 1).

After the second conditioning period of 15 d, all lambs received a simultaneous offering of straw in the two flavors. No starch was administered (Table 1).

**Experiment 2**

Our first objective was to determine whether lambs generalized preferences from familiar to novel foods. Our second objective was to determine whether preference for a low-quality food was enhanced by nutrient reinforcement, and diminished by lack of nutrient reinforcement, or by the addition of a toxin.

**Experiment 2A**

Thirty lambs (1 mo of age) were reared as a group in a 0.12-ha pasture. Every day at 0800, lambs were fed as a group an average of 200 g of coconut-flavored milo/ (lamb-d). Coconut (Agrimerica, Northbrook, IL) was mixed with milo (1 to 2-mm particle size) at a concentration of 2% (wt/wt). Lambs were fed flavored milo daily for 24 d. Lambs had ad libitum access to alfalfa pellets throughout the familiarization period. Lambs were then penned individually and continued to receive coconut-flavored milo (300 g/[lamb-d]) and alfalfa pellets (ad libitum) for another 27 d.

After the familiarization period, lambs (22 kg BW) were given a choice of plain wheat straw and coconut-flavored wheat straw to determine whether they generalized preferences from milo to straw based on coconut flavor. Coconut was mixed with straw (1- to 2-cm particle size) at a concentration of 2% (wt/wt; Table 2). Lambs were tested from 0800 to 0820 for 8 d. At 0820, refusals were collected and weighed, and at 1200 all lambs received a restricted amount of alfalfa pellets (1,190 g/[lamb-d], 80% of their daily energy requirements; NRC, 1985). During the initial 20-min exposures, lambs were reluctant to eat straw, so on d 5 and 6, alfalfa pellets were restricted to 500 g/[lamb-d] to encourage the intake of straw.

Following the 8-d exposure to straw and coconut-flavored straw, lambs raised with coconut-flavored milo were sorted by preference for coconut-flavored straw (grams of coconut-flavored straw consumed ÷ total amount of straw consumed) as recorded on the last day (d 8) of the flavor generalization tests. Sets of three lambs were then randomly assigned to three groups (10 lambs/group) so that the groups were balanced according to preference for coconut.

Lambs in Group 1 received intraruminal infusions of starch by oral intubation (100 g/[lamb-d]) immediately before receiving a simultaneous offering of plain straw and coconut-flavored straw for 20 min. Lambs in Groups 2 and 3 were offered the same foods, but they did not receive infusions of starch. Immediately after the 20-min choice, lambs in Group 2 received intraruminal infusions of a mild dose (100 mg/kg BW) of LiCl, a toxin that conditions food aversions in ruminants (duToit et al., 1991). Lambs in Group 3 (control) did not receive infusions. Control animals were not infused with water because in experimental conditions similar to those in this study flavor preferences were neither enhanced nor depressed by water infusions (Villalba and Provenza, 1997a,b; 1999). Refusals of straw and coconut-flavored straw were collected and weighed, and at 1200 all lambs were fed alfalfa pellets (1,190 g/[lamb-d]) as their basal diet. During the 15 d of conditioning, lambs in Group 1 received infusions of starch immediately before receiving straw and coconut-flavored straw. Lambs in Group 2 received LiCl only on the 1st d of conditioning (Table 2).

After 15 d of conditioning, lambs received a simultaneous offering of wheat grain and coconut-flavored wheat grain for 5 min. Thus, a nutritious food (wheat grain) replaced the low-quality roughage (wheat straw). The test lasted only 5 min to prevent overconsumption.
Food recognition by lambs

of grain and acidosis. Refusals were collected and weighed and at 1200 all lambs received alfalfa pellets. Exposure to wheat grain and coconut-flavored wheat grain was repeated for 15 d. Lambs were not infused with starch or LiCl (Table 2).

After exposure to grain and coconut-flavored grain, all lambs received a choice of straw and coconut-flavored straw, as described for conditioning, but during the 15 d of testing lambs did not receive infusions of starch or LiCl (Table 2).

**Experiment 2B**

To examine the responses of naive lambs to coconut flavor, a different group of 30 lambs (31 kg BW, 3 mo old), with no experience eating coconut-flavored straw, were offered wheat straw and coconut-flavored straw as described for the experienced lambs (Table 2). Preference tests were repeated for 3 d. All lambs received alfalfa pellets as their basal diet (1,400 g/[lamb/d], 80% of their daily energy requirements, NRC, 1985).

**Statistical Analyses**

Intake was analyzed as a split-plot design with lambs nested within groups. Group (1, 2 [Exp. 1]; 1, 2, 3 [Exp. 2]) was the between-lamb factor. Food (sagebrush-pomace, pomace [Exp. 1A]) and experience with the flavor (novel, familiar [Exp. 1B]) were the within-lamb factors in Exp. 1. Flavor (plain, coconut) was the within-lamb factor in Exp. 2. Day was the repeated measure. Means were compared using the LSD test.

**Results**

**Experiment 1**

The objective of this experiment was to determine whether lambs associated the ingestion of a novel-flavored food, given in a choice with a familiar food, with an increased supply of energy to the rumen.

**Table 2. Methods and procedures in the study, Exp. 2**

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**Experiment 1A**

Intake of the pomace-sagebrush mix (novel) was higher than intake of pomace (familiar) for lambs that did (Group 1) or did not (Group 2) receive starch during conditioning (169 vs 126 g; \( P < 0.01 \); SEM = 11). There were no interactions for group \( \times \) food or group \( \times \) food \( \times \) day \( (P > 0.05; \) Figure 1). Intake of pomace-sagebrush mix was 165 and 174 g for lambs treated (Group 1) or not (Group 2) with starch, and intake of grape pomace was 105 and 146 g for those groups. When the data were analyzed as proportions ([grams of novel food consumed \( \div \) total amount of food consumed] \( \times \) 100), starch marginally enhanced preference for the novel pomace-sagebrush mix (65 vs 54%; \( P < 0.1; \) SEM = 4).

Lambs in both groups ate more pomace:sagebrush than plain pomace (136 vs 77 g for Group 1; and 149 vs 80 g for Group 2) during the 15-min choice test, but the two groups did not differ in their preferences for the novel pomace-sagebrush mix (group \( \times \) food interaction \( P > 0.05; \) SEM = 26). Intake of pomace-sagebrush was higher than intake of pomace (169 vs 126 g; \( P < 0.01; \) SEM = 11).

**Experiment 1B**

When lambs received a constant amount of starch (150 g) after ingesting a novel or familiar flavored straw, they did not prefer the novel flavored straw (flavor experience \( \times \) group, \( P > 0.05; \) SEM = 8; flavor experience \( \times \) group \( \times \) day, \( P > 0.05; \) SEM = 3; Figure 2). Novel and familiar flavors were consumed in similar amounts (31 vs 25 g, respectively; \( P > 0.05; \) SEM = 6).

When lambs received an amount of starch directly proportional (2×) to the amount of novel flavored straw consumed, they formed a strong preference for the novel flavor (\( P < 0.001; \) Figure 2). Novel flavors were consumed in higher amounts than familiar flavors by both groups of lambs (38 g of maple/novel vs 25 g of onion/familiar for Group 1; 42 g of onion/novel vs 16 g of maple/familiar for Group 2; \( P < 0.01; \) SEM = 5). Intake
Figure 1. Consumption of grape pomace (familiar food) and grape pomace-sagebrush (novel food cue) by two groups of lambs. Lambs in Group 1 received intraruminal infusions of starch (150 g/[lamb·d]) upon consumption of pomace-sagebrush. Lambs in Group 2 did not receive infusions of starch. There was no group by food × day interaction (P > 0.05). Values are means for 10 animals; standard errors are represented by vertical bars.

Figure 2. Consumption of flavored straw with familiar and novel flavors by lambs during three conditioning periods. In the first conditioning period, lambs received a constant amount of starch (150 g) after ingestion of straw containing familiar and novel flavors. The intake of novel and familiar flavors did not differ (P > 0.05). In the second conditioning period, lambs received an amount of starch that was directly proportional (2×) to the amount of novel flavor ingested. Lambs formed a preference for the novel flavor (P < 0.001). In the third conditioning period, starch was no longer administered (extinction). Lambs retained their preferences for the novel flavor (P < 0.05). Values are means for nine animals; standard errors are represented by vertical bars.

of onion-flavored straw increased by 41% (from 25 to 42 g) and intake of maple-flavored straw increased by 58% (from 16 to 38 g).

Lambs preferred the novel flavors even when starch was no longer administered (P < 0.05; Figure 2). Novel flavors were consumed in higher amounts than familiar flavors by both groups of lambs (49 g maple/novel vs 16 g of onion/familiar for Group 1; 47 g of onion/novel vs 14 g of maple/familiar for Group 2; P < 0.001; SEM = 4). Ingestion of onion-flavored straw increased by 66% (from 16 to 47 g) and intake of maple-flavored straw increased by 71% (from 14 to 49 g).

Experiment 2

The objectives of this experiment were to determine whether lambs generalized flavor preferences and
whether preferences for low-quality foods were enhanced by nutrients and depressed by lack of nutrients or by toxins.

Experiment 2A

Lambs previously exposed to coconut-flavored milo preferred coconut-flavored straw to plain straw ($P < 0.001$). On average, lambs consumed 12 g of coconut-flavored straw and 3 g of plain straw ($P < 0.001$; SEM = 2). Initial preference for coconut-flavored straw over plain straw did not differ among groups of lambs: 15 vs 2 g (Group 1); 10 vs 5 g (Group 2); 12 vs 4 g (Group 3), as reflected in nonsignificant group × flavor ($P > 0.05$; SEM = 3) and group × flavor × day ($P > 0.05$; SEM = 3) interactions.

When the consumption of straw was paired with starch, LiCl, or no feedback, lambs ate more coconut-flavored than plain straw (45 vs 8 g; $P < 0.001$; SEM = 3). Within this general pattern of preference, postingestive feedback modified the degree to which different groups of lambs ingested plain or coconut-flavored straw (Figure 3; group × flavor, $P < 0.05$; SEM = 6, and group × flavor × day, $P < 0.001$; SEM = 4).

Averaged across days, lambs in Group 1 (infusions of starch) consumed more coconut-flavored straw than lambs in Groups 2 (infusions of LiCl) and 3 (no infusions): 60 vs 34 and 40 g, respectively ($P < 0.05$; SEM = 6). Lambs conditioned with LiCl ate more plain straw than lambs conditioned with starch (12 vs 3 g; $P < 0.05$; SEM = 6).

Intake of plain or coconut-flavored straw did not differ among groups of lambs during the 1st d of conditioning ($P > 0.05$; Figure 3). However, after receiving infusions of LiCl on d 1, lambs in Group 2 ate less coconut-flavored straw than lambs in the starch (d 2 to 15) and control groups (d 2 to 5; $P < 0.05$; Figure 3). Conversely, lambs in the LiCl group ate more plain straw than lambs in the starch (on d 2 to 3, 7 to 8, and 10 to 14) and control groups (on d 2 to 3, 7, and 13; $P < 0.05$; Figure 3). Lambs conditioned with infusions of starch consumed more coconut-flavored straw (on d 5 to 15) and less plain straw (on d 2, and 11 to 12) than lambs in the control group ($P < 0.05$; Figure 3).

Lambs ate more coconut-flavored wheat grain than plain wheat grain (124 vs 63 g; $P < 0.001$; SEM = 5). However, this pattern was not affected by the lambs’ previous conditioning history (group × flavor, $P > 0.05$; SEM = 8; group × flavor × day, $P > 0.05$; SEM = 12; Figure 4).

Intake of coconut-flavored straw continued to be higher than intake of plain straw even after 15 d of exposure and testing with grain (54 vs 8 g; $P < 0.001$; SEM = 4). Averaged across the 15 d of testing, lambs in the group conditioned with starch (Group 1) ate more coconut-flavored straw than lambs in the LiCl (Group 2) or Control (Group 3) groups (71 vs 47 and 43 g; $P < 0.01$; SEM = 7). Intake of plain straw did not differ for Groups 1, 2, and 3 (7, 12, and 7, respectively; $P > 0.05$; SEM = 7). This pattern did not change across days (group × flavor × day interaction, $P > 0.05$; SEM = 5; Figure 5).

Experiment 2B

The group of lambs naive to coconut flavor preferred plain straw to coconut-flavored straw (26 vs 12 g; $P < 0.001$; SEM = 2). Intake was higher for plain than for coconut-flavored straw during the first 2 d of testing (30 vs 9 g; 28 vs 10 g; $P < 0.001$). During the last day of testing (d 3), intake of plain straw did not differ from intake of coconut-flavored straw (19 vs 18 g; $P > 0.05$), which caused a flavor × day interaction ($P = 0.02$; SEM = 4).
Figure 4. Consumption of plain and coconut-flavored wheat grain by three groups of lambs with previous experience eating coconut-flavored milo. No infusions were given during testing. During conditioning, lambs in Group 1 received intraruminal infusions of starch (100 g/[lamb·d]), lambs in Group 2 received intraruminal infusions of LiCl (100 mg/kg BW), and lambs in Group 3 (control) did not receive infusions. There was no group by flavor × day interaction (P > 0.05). Values are means for 10 animals; standard errors are represented by vertical bars.

Discussion

Association of a Novel Flavor with an Increase in Calories

We hypothesized that lambs would associate a novel postingestive event (supply of energy from starch) with a novel-flavored food and increase their preference for the novel-flavored food. When the amount of starch supplied to the rumen was not contingent on the amount of novel food eaten, lambs did not develop a preference for the novel-flavored food. However, when the amount of starch infused into the rumen was made contingent on the amount of the novel-flavored food ingested, lambs quickly developed a strong preference for the novel-flavored food, which was retained even when starch was no longer administered. Thus, lambs discriminated between flavors and associated the amount of the novel-flavored food ingested with the amount of starch entering the rumen. Our results suggest lambs make quantitative associations between food cues and postigestive feedback. Lambs exposed to low or high concentrations of added flavors also learn to prefer the concentration (low or high) associated with the highest amount of starch infused (Villalba and Provenza, 2000a). Sheep also learn associations between plant visual cues and the nutritional quality of food rewards (Edwards et al., 1997). Differential conditioning of concurrently presented flavors by postigestonal consequences also has been demonstrated in rats (Baker and Booth, 1989).

Figure 5. Consumption of plain and coconut-flavored straw by three groups of lambs with previous experience eating coconut-flavored milo. No infusions were given during this period (extinction). During conditioning, lambs in Group 1 received intraruminal infusions of starch (100 g/[lamb·d]), lambs in Group 2 received intraruminal infusions of LiCl (100 mg/kg BW), and lambs in Group 3 (control) did not receive infusions. There was no group × flavor × day interaction (P > 0.001). Values are means for 10 animals; standard errors are represented by vertical bars.
Sagebrush has negative effects on intake and digestibility (Ngugi et al., 1995), and it was added at low concentrations (20%) to provide only a distinctive flavor. Intake of pomace-sagebrush was higher than intake of pomace, which suggests that sagebrush did not promote negative postigestive effects. On the contrary, it is likely that the additional nutrients supplied by sagebrush to the low-quality grape pomace enhanced lambs’ preferences for the mix.

Generalization of Preference for a Familiar Flavor

Lambs generalized from familiar to unfamiliar foods based on a common flavor. Generalization of cues associated with nutritious foods likely enables animals to quickly recognize nutritious foods and thus facilitate the selection process. Within a short time period of being introduced to pastures, naive cattle select among forage species in ways similar to experienced animals (Ganskopp and Cruz, 1999). Cattle, sheep, and goats prefer forages of higher quality harvested in the afternoon to those harvested in the morning (Fisher et al., 1999), and they display this pattern of preference when they first encounter the foods (H. F. Mayland, personal communication). Once the novel (or less familiar) food is ingested, postigestive feedback calibrates preference according to the food’s biochemical characteristics.

Flavor generalization increases the acceptance of novel foods (Launchbaugh et al., 1997; Van Tien et al., 1999). Sheep and goats prefer hays sprayed with organic solvent extracts from herbage and energy concentrates (Dohi et al., 1996; Dohi et al., 1997; Dohi and Yamada, 1997). This generalization could be due to an innate recognition of the extracts or a learned response acquired through postigestive reinforcement. Our study and previous work (Edwards et al., 1997; Launchbaugh et al., 1997) suggest that flavor generalization is a learned process acquired through flavor-postigestive feedback interactions.

Generalization of Preference and Postigestive Feedback

Postigestive feedback affected the degree to which generalized preferences for straw were manifest. Feedback calibrated generalization when consequences were beneficial (starch) or aversive (LiCl). Lambs that received infusions of starch had the highest intakes of coconut-flavored straw during testing and extinction. Lambs that received a mild dose of LiCl had a low preference for coconut-flavored straw and the highest intake of plain straw, but this depression in preference was transient. Sampling quickly extinguishes aversions to nutritious foods (Provenza et al., 1992; Ralphs and Olsen, 1990), and the inherently dynamic and adaptive nature of flavor-feedback interactions means that aversions are not likely to be sustained if the toxic component is removed (Provenza et al., 2000).

Lambs continued to prefer coconut-flavored straw, even when preferences were not reinforced with calo-
ries. Thus, generalized preferences can be retained for some time. Further research is needed to clarify the degree to which nutritional state, increased daily exposure to the low-quality food, and availability of alternative foods can modify generalized responses to low-quality foods. In our study, animals were kept in the same nutritional state across experiments (energy-deprived) to enhance their responses to the supplemental energy provided by starch (Villalba and Provenza, 1997a).

When lambs were offered a nutritious food (wheat grain), they preferred wheat with the familiar flavor (coconut), but differences among groups due to starch administration disappeared. This suggests that postigestive feedback affected the pattern of generalization. When the food containing the common flavor was of high quality (grain), intake of the flavored food was similar for all groups. However, when the food containing the common flavor was of low-quality (straw), lambs that received infusions of starch had higher intakes of the flavored food than lambs that did not receive the infusions.

Implications

Our results suggest two means by which sheep recognize the nutritional value of foods and incorporate nutritious, novel foods into their diets. They discriminate between novel and familiar foods and associate the magnitude of a new postigestive event with the amount of novel food ingested. Generalization over familiar flavor cues in nutritious foods also facilitates the ingestion of novel food items. Postigestive feedback calibrates preference in accord with a food’s biochemical utility and thus influences the amount of a novel food that is incorporated into the diet. This information is relevant to livestock production. Animals in feedlots, dairies, or at weaning time are often exposed to unfamiliar foods. Adding familiar flavors from nutritious foods to novel foods can encourage animals to eat novel foods. Postigestive feedback from nutritious novel foods subsequently encourages livestock to continue to eat those foods.

Literature Cited


