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Food Aversion Conditioned in Anesthetized Sheep

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PROVENZA, F. D., J. J. LYNCH AND J. V. NOLAN. *Food aversion conditioned in anesthetized sheep*. *PHYSIOL BEHAV* 55(3) 429-432, 1994.—We discovered that a food aversion could be conditioned in anesthetized sheep. Sheep were allowed to eat a familiar food (alfalfa-grain pellets) for 30 min, and 90 min later they were given either an intraruminal (IR) injection of water (C), an IR injection of LiCl (L), anesthesia followed by an IR injection of water (A), or anesthesia followed by an IR injection of LiCl (A+L). Induction of anesthesia was by an intravenous injection of pentobarbitone sodium, and maintenance of deep anesthesia was by halothane. Sheep were maintained in deep anesthesia for 2 h to ensure that the effects of LiCl on the acquisition of a food aversion, which occur within about 1 h, were completed before they awakened. When tested 5 days later, sheep that received LiCl (treatments L and A+L) consumed less alfalfa-grain pellets than sheep that did not receive LiCl (treatments C and A) (241 g vs. 306 g; $p = 0.057$). Intake of sheep that were anesthetized (treatments A and A+L) did not differ from that of sheep that were not anesthetized (treatments C and L) (295 g vs. 252 g; $p = 0.183$). Nor was there an interaction between LiCl and anesthesia ($p = 0.423$). Thus, we conclude that changes in preferences for foods caused by postingestive feedback occur automatically every time food is ingested (i.e., they are noncognitive), and the kind and amount of feedback is a function of the match between the food's chemical characteristics and its ability to meet the animal's current demands for nutrients.

Food aversion Cognitive Noncognitive Ruminant Monogastric Sheep

RUMINANTS select nutritious diets from environments that contain a diverse array of plant species, growth stages, and plant parts that vary temporally and spatially in nutritional value and toxicity (4,24,28). There is growing evidence that conditioned responses, caused by postingestive feedback from nutrients and toxins, are responsible for the ruminant's ability to select a nutritious (nontoxic) diet (18,27,29,31). Certainly, several studies during the past decade have shown that postingestive feedback causes ruminants to decrease intake of foods that are nutritionally deficient or toxic and to increase intake of the foods as toxicity diminishes and nutritional value improves (7,12,13,23,25,34,36).

The mechanisms that cause animals to change their intake of foods that vary in nutritional value and toxicity evidently involve affective and cognitive processes (15). Taste [i.e., the gustatory system specifically, see (15)] plays a prominent role in both processes. Affective processes integrate the taste of food and its postingestive consequences, and changes in the intake of food items depend on the degree to which postingestive consequences are aversive or positive. Cognitive processes involve use of the senses of smell, sight, hearing, and higher cortical centers, and they enable animals to select foods that provide positive consequences and, thus, taste good, and to avoid foods that cause internal malaise and, thus, taste bad. These means of regulating the internal environment generally function in parallel: the taste of food is adjusted according to its effect on the

internal environment, and on that basis, animals use thalamic and cortical mechanisms to select foods that are nutritious and avoid those that are toxic (27,29).

Affective processes are a critical part of acquired food aversions in monogastric animals like rats, dogs, and humans (15). These animals decrease their intake of foods that contain toxins as a result of aversive feedback from the emetic system. This affective system coordinates incoming and outgoing information about toxicity that involves complex interactions between adjacent areas in the brain stem and other parts of the body (2,38). Afferent and efferent interactions involving the emetic system occur automatically, and as a result, do not entail any cognitive associations. Thus, food aversions have been conditioned in monogastrics even though they were deeply anesthetized (1,37), deeply tranquilized (14), and when their electrocortical activity was depressed (5,11).

There are several reasons why affective processes may not be similar, in kind or in degree, in monogastrics and ruminants. First, their digestive systems differ considerably. Unlike monogastrics, where the ingested food is passed directly into the gastric stomach, the ruminant stomach consists not only of the abomasum, which is the portion of the stomach most similar to that of monogastrics, but also of the omasum, the reticulum, and the rumen. The rumen is a large vat between the mouth and the stomach in which foods are altered substantially by microbial

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fermentation (10). As a result of such adaptations, ruminants can ingest foods high in structural carbohydrates like cellulose that can only be digested by cellulosic microbes, and, thus, are of little or no nutritional value to monogastrics. Indeed, ruminants depend largely on the products of microbial fermentation and growth to supply the necessary energy and protein. In addition, ruminants differ from monogastrics in aspects of digestive physiology that include sites and modes of nutrient absorption (e.g., a large fraction of the energy substrate, volatile fatty acids, is absorbed from the rumen rather than from the intestines as in monogastrics), kinds of digestive enzymes, and tissue metabolism (10). Finally, given these differences in anatomy and digestive physiology, monogastrics and ruminants might also differ in the way postingestive feedback is processed, for instance, in the origins of afferent signals and in their ultimate destinations within the central nervous system.

Considering these differences between monogastrics and ruminants, we sought to learn if a food aversion could be conditioned in an anesthetized ruminant (sheep), as it can be conditioned in monogastrics. Our underlying consideration was whether there are pathways for processing postabsorptive stimuli that still operate in an anesthetized ruminant to condition an aversion. We reasoned that a finding that an aversion could be acquired in an anesthetized ruminant would strengthen contentions about the universal nature of the mechanisms that underlie acquired food aversions (17). Conversely, any evidence that ruminants and monogastrics differ in the mechanisms that underlie conditioned food aversions would have implications for further investigations of interspecific variation in food selection.

METHOD

Animals and Feeding

Twenty merino lambs (aged 6 months, average body weight 27 kg) were moved from grass pastures into two pens (10 lambs/pen), and fed alfalfa-grain pellets (AG) and oat chaff for 2 days. The lambs were then moved into individual pens, and for the next 10 days were fed AG pellets ad lib from 0800 h until 0830 h and oat chaff ad lib from about 0840 h until about 1600 h. They were without food from 1600 h until 0800 h the next day. Lambs had access to water ad lib.

Experimental Procedures

Lambs were fed AG pellets from about 0745 h until 0815 h and then transported about 500 m to the anesthesia room. Lambs then received one of four treatments: an intraruminal (IR) injection of water (40 ml) (C), an IR injection of LiCl (150 mg/kg b.wt. in 40 ml water) (L), anesthesia followed by an IR injection of water (40 ml) (A), or anesthesia followed by an IR injection of LiCl (150 mg/kg b.wt. in 40 ml water) (A+L). Lambs were anesthetized and received their injections of water or LiCl within 90 min of eating the AG pellets. The time between feeding and injection was equivalent for all groups, although the exact time varied a little from day to day. Four lambs, one from each of the four treatments, were included each day for the 5 days required to impose the treatments on all lambs.

We used a food (AG pellets) that lambs had eaten, because we wanted to ensure that the lambs would eat a substantial amount (i.e., >200 g) on the day the treatments were imposed; lambs are reluctant to consume novel foods (32). We also used a moderate dose of LiCl [150 mg/kg b.wt.; (12)], because at that dose the effects of LiCl on the acquisition of a food aversion occur within about 1 h (30). We were reluctant to anesthetize sheep for more than 2 h because we wanted to minimize any adverse effects caused by anesthesia (19).

Anesthesia was induced with an intravenous injection of pentobarbitone sodium (24 mg/kg b.wt.), and deep anesthesia was maintained by administration of 1% halothane given through an endotracheal tube. Lambs were brought to stage 3 anesthesia (characterized by total muscular relaxation, no eye-blink reflex, and a lack of reflex to pinching any digit), and then given the appropriate IR injection. They were maintained at stage 3 anesthesia for 2 h following the IR injection to ensure that the effects of LiCl occurred while they were anesthetized. The four lambs were returned to their pens at about 1400 h. We determined intake of oat chaff between 1400 h and 1700 h on the day of the IR injection, and from 0800 h until 1600 h daily for the next 5 days.

Testing

We waited 5 days before testing each group of lambs to ensure that they had fully recovered from any effects associated with the anesthesia, from the possible consequences of the restricted amount of time they were allowed to eat oat chaff on the day the treatments were imposed, and from the change in diet from AG pellets plus oat chaff to only oat chaff. During testing, lambs were offered AG pellets ad lib from 0800 h until 0830 h and oat chaff ad lib from 0840 h until about 1700 h daily for 5 days. We measured intake of AG pellets and oat chaff. Food was not available from 1700 h until 0800 h the next day.

Statistical Analysis

The factorial design, with two levels of anesthesia and two levels of LiCl, was analyzed by repeated measures analysis of variance (40). Five lambs were nested within each treatment. The intake of AG pellets was adjusted for a covariate ($p < 0.001$), which was the intake of alfalfa-grain pellets on the day the treatments were imposed. We also compared the intake of oat chaff by lambs in the various treatments on the day the treatments were imposed (from 1400 h to 1700 h) and during the 5 days of testing. The means for the intake of oat chaff during testing were adjusted for a covariate ($p = 0.001$), which was the average intake for the 3 days preceding the IR injection.

RESULTS

All lambs consumed oat chaff when they returned to the pens on the day the treatments were imposed, but lambs that had been anesthetized ate less than the controls on that day and for the next 4 days (Table 1). The intake of oat chaff by all lambs increased steadily from the day the treatments were imposed and for the next 4 days ($p = 0.020$). On day 5, intake of oat chaff did not differ between treatments, so the tests to determine if the lambs had acquired an aversion to AG pellets were started on day 6. Intake of oat chaff did not differ among treatments during testing ($p > 0.419$).

TABLE 1
INTAKE OF OAT CHAFF BY LAMBS

Treatment	Day of Anesthesia	Days After Anesthesia				
		1	2	3	4	5
Anesthesia	324*	391*	500*	528*	623*	535*
No anesthesia	406†	515†	605†	667†	709†	611*

*† Means within a column differ (for day of anesthesia, $p = 0.092$, SEM = 32; for days after anesthesia; $p = 0.016$, SEM = 30; for day 5 after anesthesia, $p = 0.419$, SEM = 51).

Lambs that received LiCl (treatments L and A+L) ate less AG pellets than lambs that did not receive LiCl (treatments C and A) on the first day of the test (241 vs. 306 g; $p = 0.057$; Fig. 1), but there were no differences between groups on the second day (217 g vs. 258 g; $p = 0.389$) or on subsequent days. The conditioning parameters we used were likely the reason that the differences were not more highly significant ($p = 0.057$ and 0.389) (see the Discussion section). Anesthetized (treatments A and A+L) and nonanesthetized (treatments C and L) lambs did not differ in their intake of AG pellets on the day when the treatments were imposed (270 g vs. 266 g; $p = 0.909$), or on the first day (252 g vs. 295 g; $p = 0.183$) or the second day (238 g vs. 237 g; $p = 0.984$) of testing. Day did not interact with LiCl ($p = 0.974$) or with anesthesia ($p = 0.463$).

It is important to recognize that there was no interaction between LiCl and anesthesia on the first day ($p = 0.423$) or on the second day ($p = 0.840$) of testing. The interaction means for treatments C, L, A, and A+L on the first day of testing were 341, 250, 271, and 232 g, respectively. The significant difference in intake of AG pellets on the first day of testing indicates that both anesthetized (treatment A+L) and nonanesthetized (treatment L) lambs acquired an aversion to AG pellets. The lack of a significant difference between lambs that either did (treatments A and A+L) or did not (treatments C and L) receive anesthesia indicates that the anesthesia did not cause the lambs to acquire an aversion to the pellets. Accordingly, the statistical analysis supports the hypothesis that both anesthetized (treatment A+L) and nonanesthetized (treatment L) lambs acquired an aversion to AG pellets, and that anesthesia neither strengthened nor diminished the response (i.e., there was no interaction between LiCl and anesthesia).

DISCUSSION

Lambs that received LiCl ate less of a familiar food when tested 5 days later, whether or not they were deeply anesthetized when LiCl was exerting its influence. The aversive effects of LiCl given directly into the rumen of sheep had earlier been shown to occur primarily during the first hour following its administration (30). We found no evidence for attenuation or potentiation of the aversion as a result of an interaction between the anesthetics and LiCl. Accordingly, these data are consistent with the hypothesis that ruminants, like monogastrics, acquire aversions to toxic foods under anesthesia (17,29).

The difference in intake between animals that received LiCl and controls was not large and did not persist, likely because of the conditioning parameters we used. First, we used familiar food (AG pellets); a novel food would have resulted in a stronger aversion (6,32,35). Second, AG pellets were a highly nutritious food offered after 15 h of food deprivation; even sheep that have acquired an aversion to a food will eat substantial quantities of that food after 15 h of food deprivation (30). Third, we used a moderate rather than a high dose of LiCl; a high dose of LiCl would have caused a much stronger aversion (12). Finally, there was a delay of about 90 min between the time that lambs ingested AG pellets and the time they would have experienced the aversive effects of LiCl; the aversion would likely have been stronger had the delay been shorter (6,16). Despite these moderations, there was a significant decrease in intake of AG pellets by lambs that received LiCl, even though they were in deep anesthesia when the main effects of LiCl would have occurred. This highlights the sensitivity of the mechanisms that underlie acquired food aversions, apparently even for ruminants in which foods are metabolized in a large fermentation vat following ingestion.

All lambs increased intake of oat chaff during the 5-day period prior to testing, probably because they were deprived of the AG

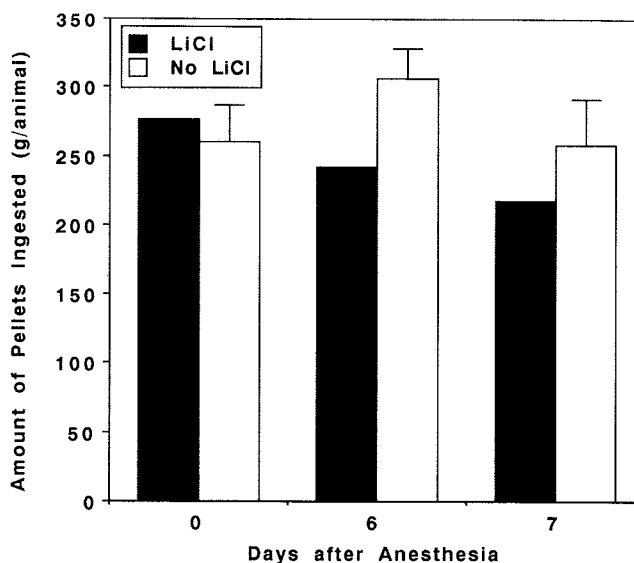


FIG. 1. Intake of alfalfa-grain pellets by sheep that either did (black bar) or did not (white bar) receive LiCl (lines above bars represent standard errors). On day 0, sheep ate a familiar food (alfalfa-grain pellets) for 30 min, and 90 min later they were given either an intraruminal (IR) injection of water (C), an IR injection of LiCl (L), anesthesia followed by an IR injection of water (A), or anesthesia followed by an IR injection of LiCl (A+L). When tested 6 days later, sheep that received LiCl (treatments L and A+L) consumed less alfalfa-grain pellets than sheep that did not receive LiCl (treatments C and A) ($p = 0.057$). Treatment means do not differ for day 0 ($p = 0.672$) or for day 7 ($p = 0.389$). There was no interaction between LiCl and anesthesia ($p = 0.423$).

pellets that had previously been fed in conjunction with oat chaff. In addition, lambs that had been anesthetized ate less oat chaff than controls during the period prior to testing. This may have been caused by a depression of the central nervous system, by gut stasis that can occur after administration of a barbiturate such as nembutal, or by loss of saliva and changes in rumen conditions (decreased pH, altered microbial flora) (19).

CONCLUSIONS

In spite of vast differences in anatomy and digestive physiology, species as seemingly diverse as rats (order Rodentia), cats, and dogs (order Carnivora), ruminants (order Artiodactyla), baboons, and humans (order Primates) show striking similarities in the mechanisms that underlie food selection. Affective processes that integrate taste and postingestive feedback are an indispensable part of those mechanisms. As a result of affective processes, feedback occurs automatically every time food is ingested, as does the release of digestive enzymes during different stages of the process of digestion, and the kind and amount of feedback is a function of the match between the food's chemical characteristics and its ability to meet the animal's current demand for nutrients, evidently regardless of the species of animal.

It is, thus, not surprising that the environmental variables that control affective processes are remarkably similar in monogastrics and ruminants. For instance, acquired aversions in both groups of animals have been shown to be dependent: a) on temporal contiguity between food ingestion and toxicosis (9,16,30), b) on food novelty (6,35), c) on the intensity of a particular flavor

(9,23), d) on the volume of food ingested (3,33), e) on prior experience with illness (8,23), and f) on prior experience with a salient flavor (20–23,33). These and other similarities between monogastrics and ruminants [e.g., the importance of social learning: (26,39,41)] add to growing evidence of the universal nature of the mechanisms that underlie food selection in animals (17).

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