

ASPECTS OF INGESTIVE BEHAVIOR IN CATTLE^{1,2}

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Summary

Ingestive behavior in cattle differs from other species because of physiological mechanisms developed *pari passu* with fermentative digestion. The secondary refection of rumination allows remastication and reinsalivation of the large bulk of vegetable food ingested. The need to buffer acid products of cellulose digestion demands continuous high secretion of alkaline saliva. Nervous and hormonal stimuli emanating from the gastrointestinal tract evoke centrally controlled behavior of hunger and satiety. The four primary taste receptors occur in cattle but thresholds are low. Because of the low Na level in plants, cattle have developed the behavior of seeking salt by taste and smell. During Na deficiency it can be shown that cattle readily learn and develop memory, providing a powerful behavioral dimension in the search for food.

(Key Words: Cattle, Feeding Behavior, Sodium.)

Introduction

In order to obtain food, the special senses and "drive" originating in the brain combine to activate the grazing animal to locate, then to make a choice from the available plant growth, and finally to initiate ingestion. When confronted with suitable food and water, herbivorous animals eat intermittently. The central nervous system (CNS) generates reaction between the animal and its environment by inaugurating somatomotor activity, which

when integrated with a great variety of repetitive stimuli activates eating behavior. Later cessation or reduction of these signals inhibits eating. These two levels of afferent stimuli to the nervous system, one activating and one inhibiting, are fundamental for the ingestion of food and have been incorporated into psychological terminology as hunger and satiety.

The success of cattle as a domesticated accessory to man is reflected in the ability displayed by ruminants to survive successfully in a wide range of disparate ecosystems extending over the whole land area of the globe from arctic to equatorial regions. Ruminants, however, pay a price for the ability to garner energy from plant material, because plants have a meager content of both Na and water, substances that are essential to buffer the acid products of fermentative digestion. A high output of alkaline saliva is necessary to provide the relatively large increase in extracellular fluid needed, not only to aid digestion, but to assist the ancillary process of rumination. The complex alimentary functions fundamental to ruminant digestion are probably also intimately linked to the patterns of behavior that develop in cattle with the ingestion of food.

Central Neural Control

There is evidence that regulation of food intake in ruminants may not directly involve the hypothalamus; for example, Holmes and Fraser (1965) failed to produce hyperphagia in sheep when they placed large lesions in the ventromedial hypothalamus. Furthermore when the ventromedial nuclei of the hypothalamus were destroyed with precision in sheep, no change in food or water intake occurred (Tarttelin and Bell, 1968). In other similar experiments variable results have been reported.

Rumination, an essential component of digestion in cattle, causes retardation of food ingestion because it precludes eating for about 8 h of the day. Rumination, however, must be regarded as a specialized act of ingestive behav-

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ior, this action ensuring that ingested food is subjected to a further prolonged period of remastication and reinsalivation. It could be argued that the primary ingestive intake of food provides a fairly rapid and optimal fill of the rumen, and that the second phase of passive refection is needed for cellulose digestion. Little is known about the factors that control the onset and cessation of rumination, but this stereotyped affective behavior may be a part of voluntary food intake. Rumination periodicity may not be affected by the type of food ingested, but the total time spent daily in rumination is dependent on the physical nature of the food. The fact that rumination occurs when ruminants are suckling their calves, and during recovery from anaesthesia, suggests control through the brain stem reticular formation as in sleep and wakefulness.

The rumen volume has been shown to be closely connected with the amount of food ingested (Campling, 1970). This effect on ingestion appears to be related to the factors arising from distension caused by rumen fill; but the nature of the food, the periodicity of feeding and, not least, the metabolic changes associated with milk yield are all concerned. Neural reflexes control the coordination of muscular movement in the rumen and abomasum to ensure continual transfer of ruminal digesta to the intestine, with the pyloric antrum of the abomasum providing the pump for this transfer. When the ruminal digesta become acidified either directly or from HCl secreted in the abomasum, hormones such as gastrin, secretin, motilin and somatostatin are released, and, by inhibiting muscular contractions, cause alimentary stasis, indirectly inhibiting food intake (Bell, 1980). Degraded elements of the gut hormones have been shown by radio-immunoassay to be present in the brain. Injection studies, either iv or intracerebroventricularly, suggest that some of these hormones, such as oxytocin or cholecystokinin, may have an effect on gut motility and even indirectly on food intake.

Food and water intake in ruminants shows a number of cyclical variations of different periodicity. A long-term effect, unrelated to the nature of the food, is seen over a yearly cycle in sheep, with peak intake in July and lowest intake in January (Tarttelin, 1969). Depression in food and water intake occurs with oestrus in heifers (MacFarlane, 1967; Raun et al, 1967).

Taste Factors

Taste in cattle subserves a fundamental biological role in linking the animal with its environment, and aids in regulating intake of suitable and rejection of unsuitable food. The predominant need of cattle for nutrient material may induce the intake of metabolic poisons such as Mo, As, Se and F. Cattle have taste receptors on the tongue that respond to the four primary taste modalities of salt, sweet, sour and bitter (Bell and Kitchell, 1966). The strong movement of the tongue during prehension in cattle helps the presentation of these sapid substances to the gustatory receptors. Variation in the intensity of these recurring stimuli provides a constant input to central perception.

Two choice preference tests in cattle show them to have lower rejection and acceptance values than many other species, especially towards bitter substances. Cattle show no threshold for sweet substances (glucose), so that unlimited intake can occur, that may account for the use of molasses in diets. Preference tests in cattle also demonstrate that they can readily detect fecal contamination, but not by taste because anosmic cattle, following bilateral olfactory bulbectomy, ingested contaminated food (Bell and Sly, 1983). Thus smell rather than taste is the link that directs cattle to avoid fouled pasture and the consequent health hazards.

Sodium Appetite

Although grass is a good source of energy, its Na content is low and K is high.

There is anecdotal evidence that ruminants show bizarre behavior in order to obtain salt (Bell, 1963; Denton, 1967). The behavior of cattle to maintain Na homeostasis, especially the interplay between the special senses and locomotor activity, a feature of ingestion behavior, may be related to Na depletion. When a single parotid duct of a steer is fistulated, Na is lost from the body by continual secretion of parotid saliva. With Na depletion, a compensation process develops whereby reduction in salivary flow occurs as well as a reversal of the Na:K ratio in saliva from 145:5 to 5:130 mM (Bell and Williams, 1960). Nevertheless the parotid gland retains its reflex capability of increasing volume flow and varying Na composition during mastication and rumination. Similar but transient changes probably account

for the variation in salivary flow in cattle during feeding of foods with differing dry matter content. Salivary flow is dependent on reflex control initiated by chemoreceptors and osmoreceptors from the alimentary canal rather than hormonal mechanisms such as those that regulate the kidney. During the development of Na depletion, the volume of food and water intake gradually diminishes; and continuation of Na depletion for more than 8 d causes anorexia. These behavioral changes develop coincidentally with measurable changes in biochemical and physiological characteristics such as hypovolemia, hyposmolality and a reduction in plasma acidity to pH 7.2 (Bell and Sly, 1979).

Normal steers when hungry can readily be trained to press a plate for food rewards. Cattle find solutions of Na salts greater than isotonicity to be aversive, whereas Na depleted cattle will eat even powdered NaCl and bicarbonate. When Na depleted steers are allowed access to supplements of NaHCO₃, normal Na metabolism is restored and any abnormal behavior disappears.

In the normal Na-replete state, trained steers continue to move quickly to the operant stand but show no motivation to press the panel to obtain NaHCO₃ rewards. When Na depletion is allowed to develop, the amount of panel pressing increases until a peak is reached in about 8 d. At the same time the steers show increasing awareness of the operant sessions, run from their home pens to the stand and begin immediately to press the panel vigorously. Intragroup behavior is expressed by display of intense interest in the movement of other steers and to the sounds from the apparatus. Motivation to work for NaHCO₃ reinforcements increases as the salivary Na decreases, thus providing an easy monitor of Na depletion.

This technique was used to demonstrate a clear specific taste for Na cations, and to show that the anion was not important. Other metabolic ions (Ca, Mg, K, NH₄) produced poorer responses to the operant procedures, but LiCl and LiSO₄ were also very effective.

Increased motivation developed in a T-maze with the onset of Na deficit; success in finding the reinforcement led to the steers finding the reward more quickly. The steers even jumped a barrier to obtain the NaHCO₃. Steers learned immediately the arm of the T-maze where they first encountered a Na reward, and thereafter moved to this arm first, indicating that their

first reaction now was a recollection, and only if frustrated did they then discriminate between the randomly placed NaHCO₃ and water by olfaction. This directional memory could still be demonstrated after a lapse of 6 wk and persisted when the calves were Na repleted. It is possible that the well-known behavior patterns of cattle towards salt pans and mineral licks may be a natural manifestation of the procedure shown experimentally.

We have examined the role of smell in the ingestion of liquids using a cafeteria system, where cattle display ability to select a Na salt from a single bucket in a range of 12, the others having water only (Bell and Sly, 1983). Care was taken to ensure random placements and to avoid all cues such as contamination that might invalidate the investigation. The cafeteria showed that Na depleted steers developed the ability to detect sodium salts by smell and that this olfactory sense, like taste, was also specific for Na and Li salts. A change in olfactory detection threshold in Na depletion parallels the very low detection thresholds noted for taste. The retention of taste responses in anosmic, Na-depleted cattle shows that the two forms of chemoreceptive receptors are distinct entities, with separate afferent channels to the brain, that impinge upon the same areas of the CNS. The enhancement of motivation to seek Na rewards demonstrated in the cafeteria seems to be the same manifestation of behavior seen in the T-maze. In both situations, once the first success towards the goal is achieved, with ingestion of the reinforcement, the behavioral pattern then becomes established as a conditioned reflex or some comparable learned process. With successful repetition the learning is consolidated into memory, so that locomotory action ensues, directed by smell, towards the point of acquisition of Na salts so that Na deficiency is alleviated.

This complex pattern of behavior in cattle, shown experimentally to occur in Na-depleted cattle, fulfills the criteria demanded by Young (1967) for the assessment of salt appetite. It remains difficult, however, to explain the stimulation of olfactory bulb receptors by nonvolatilizing Na salts.

Deranged metabolism caused by Na depletion can, of course, produce peripheral signals from visceral sites such as the rumen, or from the vascular bed. That this may be so is shown when the calculated Na deficit is replaced, either directly by allowing the depleted calves

to drink it, or indirectly via the rumen (Bell et al. 1981). Changes in plasma aldosterone did not appear to be related directly to the ionic changes, but increase in plasma renin may be involved, arising from changes in plasma volume, to produce a rise in plasma angiotensin. Salt appetite was rapidly inhibited when deficient calves consumed the calculated deficit by mouth, but the effect was of short duration, suggesting a short sensory effect from buccal receptors. Slower inhibition occurred when the mouth was bypassed by placing the ionic solution directly into the rumen, where visceral receptors in the gut or the portal vein reacted slowly and inhibition developed only after some hours.

These experimental findings related to ingestive behavior in cattle lean towards a central metabolic control modulated by visceral afferent impulses and hormonal changes from the rumen and cardiovascular system. There is no doubt that, as a result of Na deficiency, central nervous function can be altered so that "memory" is generated that can activate behavior whereby earlier locations of Na salts can be revisited. Such behavior must have survival value and may account for the behavioral activities frequently reported in the migration of wild ruminant herbivores to salt sources (Bell, 1972).

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