Regulation of Feed Intake in the Horse in Relation to Gastrointestinal Disease

Sarah L. Ralston, VMD, PhD, ACVN

Cook College, Rutgers University

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Introduction

Knowledge of the mechanisms of both normal and abnormal regulation of feed intake is important in the prevention of gastrointestinal diseases, especially in equine animals. Understanding why horses start and stop eating, what factors influence the size of a given meal and the neuroendocrine and biochemical controls of appetite is important in the prevention and management of feed-related diseases (Ralston, 1986). Unfortunately there is limited information with respect to these issues in equine animals. What little is known suggests that regulation of feed intake in horses and ponies may differ from what is known about other species. For example ponies are relatively resistant to the development of conditioned taste aversions to feeds associated with gastrointestinal malaise (Houpt et al., 1990). Though data obtained from studies on horses suggest that there are many similarities to reports on control of feed intake in ponies (Doreau, 1978), some differences may exist in the horse's ability to adapt to new diets and defend a constant body weight (Ralston, 1980, unpublished data). Abnormal eating activity also is of concern especially in clinically ill horses. Malnutrition secondary to anorexia adversely affects immune competence (Naylor and Kenyon, 1978, 1981; Ralston and Naylor, 1991). Horses with gastrointestinal disease may exhibit altered preferences for feeds, the "nutritional wisdom" of which has yet to be elucidated. Anorexia and alteration in feed preference secondary to gastrointestinal disease in horses have received little scientific attention, despite their clinical importance.

Known factors in the regulation of feed intake in horses will be discussed with respects to their significance in the prevention or management of gastrointestinal related disorders. Pertinant data from other species will be included to elucidate areas in need of investigation in equine animals.

Normal Regulation of Feeding

General patterns and weight regulation Horses and ponies engage in eating acitivity for 40 to 60 % of a 24 hour period (Doreau, 1978; Ralston, 1986). They

Summary

Control of feed intake (or lack thereof) in horses and ponies contributes to this species' susceptibility to gastrointestinal disorders. Unfortunately relatively few studies have focussed upon factors which influence feeding behavior in equine animals. What little is known, however, provides insight regarding causes of gastrointestinal disorders related to feeding behavior. For example, the ability of oropharyngeal stimuli to override gastrointestinal or metabolic cues within a single eating bout contributes to horses' susceptibility to colic and metabolic disorders secondary to gastrointestinal overload. Factors which influence the response of the animal include the degree of hunger experienced at the initiation of the meal, taste, texture and potentially odor of the feed and previous experience with the feed. Ponies adapted to free choice access to a single feed can regulate their caloric intakes almost as precisely as do rats over a 24 hour period, however preliminary experiments with horses suggest a lack of similar control.

Abnormal feeding behaviors such as anorexia and alteration in feed preference secondary to gastrointestinal disease in horses are poorly understood. Data from other species provide insight to areas of specific research needed for management of these phenomena in equine animals.

Regulation der Futteraufnahme bei Pferden in Abhängigkeit von Erkrankungen des Verdauungskanals

Die Regulationsmechanismen für die Futteraufnahme tragen bei Pferden und Ponys zu ihrer Disposition für gastrointestinale Störungen bei. Leider beschäftigen sich bisher nur relativ wenig Untersuchungen mit den Mechanismen, die das Freßverhalten von Pferden beeinflussen. Obwohl wenig bekannt ist, zeigt sich jedoch, daß das Auftreten gastrointestinaler Störungen mit dem Verhalten während der Futteraufnahme in Verbindung gebracht werden kann. Reize im Mund-Rachen-Bereich können während der Futteraufnahme gastrointestinale oder metabolische Signale überlagern, so daß die Disposition von Pferden zu Koliken und metabolischen Störungen steigt. Dies gilt auch bei Überladung im Magen-Darm-Trakt. Faktoren, die das Fressverhalten der Tiere beeinflussen, sind abhängig von dem Grad des Hungers bei der Futteraufnahme, dem Geschmack, der Beschaffenheit, möglicherweise dem Geruch des Futtermittels und der Gewöhnung an das Futter. Ponys, die an Ad-lib.-Fütterung gewöhnt sind, können die Energieaufnahme über 24 Stunden fast genauso gut regulieren wie Ratten. Vorläufige Untersuchungen weisen jedoch darauf hin, daß ein solcher Kontrollmechanismus bei Pferden nicht vorhanden ist. Inwieweit sich krankhaftes Freßverhalten wie Anorexie oder Abweichungen in der Präferenz für Futtermittel begünstigend auf Erkrankungen des Magen-Darm-Trakts bei Pferden auswirkt, ist noch wenig aufgeklärt. Beobachtungen bei anderen Tierarten geben Hinweise auf Forschungsschwerpunkte, die beim Pferd zur Lösung dieser Probleme beitragen könnten.

rarely fast voluntarily for more than 3 to 4 hours. When feed is restricted, especially if in the form of a low fiber pellet, alternate feeding acitivities are frequently reported, such as wood chewing, consumption of bedding or mouthing of metal bars or other objects (Ralston, pers. obs; Johnson and Hart, 1974; Laut et al., 1985; Ralston, 1986). These actitivities may contribute to the development of colic, especially if sand, dirt or foreign objects are ingested. Though provision of long stem roughage and/or small frequent feedings often are recommended to reduce the incidence of aberrant eating activity in horses, (Ralston, 1986) more studies are needed.

Ponies accurately regulate their body weight if given free access to a single feed (Ralston and Baile, 1982a). However, body weights maintained voluntarily corresponded to fat to moderately obese (Ralston, 1980, unpublished data). If fed a calorically dilute ration, ponies respond by eating larger meals more frequently to maintain caloric intake and body weight (Laut et al., 1985). However, it takes ponies 2 to 14 days to stabilize daily intakes of pellets of different caloric densities (Laut et al., 1985), where rats and monkeys can compensate for similar dietary dilutions in less than 24 hours (Gibbs and Smith, 1978). If given an intragastric load of glucose, corn oil or cellulose, ponies reduce subsequent intakes to compensate accurately for the additional energy intake in less than 24 hours if offered the pelleted feed to which they were accustomed (Ralston and Baile, 1982b, 1983a).

In an aborted trial with horse mares, feed intakes and body weights did not stabilize for over 5 weeks of an attempt to obtain free choice feeding of a pelleted ration utilized in the pony experiments (Ralston, unpublished data; Ralston and Baile, 1983a). The mares continued to gain weight and consume all feed presented in less than 24 hours for over three weeks. The trial was terminated when the mares attained a level of obesity considered by co-investigators to be detrimental to health. In other species, females differ from castrated males in their responsiveness to feeding cues and responses (Henry et al., 1992). Ponies used in the previous studies were all castrated males (Ralston and Baile, 1982a, b, 1983a, b) therefore the apparent differences may have been due to sex, not breed. Experiments on regulation of feed intake and body weight need to be done to compare the relative responsiveness of male and female horses.

Based on pony data, postabsorptive metabolic feed back cues as yet unidentified permit accurate and relatively rapid regulation of energy intake over a 24 hour period if a single feed of uniform caloric density is offered free choice. Determination of the amount of feed consumed within a given meal, however, is based primarily on the oropharyngeal stimuli generated by the prehension, chewing and swallowing and the sensory qualities of the feed. Unlike rats and monkeys (Koopmans, 1985; Gibbs and Smith, 1978), horses or ponies fasted 4 hours or less consume normal size meals even when ingested feed is diverted out of an esophageal fistula (sham feeding) (Ralston, 1986). If ponies are fasted for 24 hours, the first meal upon re-introduction of even a familiar feed is larger than if the pony were fasted for only 4 hours. This meal is even larger if the ponies are sham fed (Ralston, 1986). This suggests that when ponies are abnormally hungry after a prolonged fast, gastrointestinal stimuli will act in conjunction with oropharyngeal cues to regulate the size of a given meal, probably due to gastric distension stimuli (Laut et al., 1985). Even under these circumstances, however, oropharyngeal stimuli alone are sufficient for generation of normal satiety behavior, which is unlike other species used in sham feeding experiments.

If a horse or pony is unfamiliar with a feed, however, regulation of energy intake may be less precise than suggested above. Preliminary studies revealed that normal satiety can be overcome merely by the presentation of a novel or fresh feed in animals adapted to free access to a single pelleted ration (Ralston, unpublished data). This may explain why stimulation of increased energy intake in horses unable or unwilling to consume adequate amounts of their regular feed may be accomplished by the presentation of fresh or novel feeds at frequent intervals. Taste, particle size and texture of feed all apparently influence the rate and amount of feed consumed (Hawkes et al., 1985; Ralston, 1986; McCann and Hoveland, 1991) but more work is needed on the relative importance of these factors on feed intake in horses and ponies. How long it takes for a horse or pony to accurately regulate caloric intake of a novel feed or the ability to regulate intake of a varied diet of familiar feeds has yet to be determined.

Overall, the reliance on oropharyngeal stimuli, lack of attention to gastrointestinal or metabolic feedback during the course of a meal in conjunction with relatively slow adaptation to changes in caloric density of feed make horses prone to excessive intake (gastrointestinal overload) when suddenly presented feeds of high caloric density.

Neuroendocrinology and biochemistry of feeding behavior Neuroendocrine and biochemical controls of feeding in other species have been the subject of extensive investigation for over 40 years (Stricker, 1984). Plasma and brain concentrations of serotonin and catecholamines such as dopamine and epinephrine and amino acid precursors (tryptophan, phenylalanine and tyrosine) influence feeding activity in other species (Chaftez, 1990; Schwartz and Hoebel, 1988; Bray, 1991; Henry et al., 1992). Relative concentrations of tryptophan, large neutral amino acids (methionine, phenylalanine and tyrosine) and short branch chain amino acids (leucine, isoleucine and valine) in the compete for the same transport mechanism across the blood brain barrier. The ratios of the amino acids therefore determine the rate of synthesis of serotonin and catecholamines in the brain (Fernstrom and Wurtman, 1971, Henry et al., 1992). Infusion of short branch chain amino acids (leucine, isoleucine and valine) in humans suffering hepatitis induced coma not only reversed the neurologic symptoms but resulted in a reported feeling of extreme hunger (Rossi-Fanelli and Cangiano, 1991). Johnson and Hart (1974) reported a dramatic increase in short branch chain amino acids in the plasma of horses fasted for over 24 hours relative to the other essential amino acids. This increase was also associated with an increase in wood chewing activity. Tryptophan unfortunately was not measured but both histidine (a precursor of histamine, also thought to affect appetite) and phenylalanine remained below baseline the second 24 hours of the fast. Diet can dramatically alter plasma tryptophan and serotonin in horses (Ralston, 1992; unpublished data) but the effects such changes have on appetite or feeding activity in this species is unknown. Rate of gastric emptying has long been thought to influence feeding activity in rats, monkeys and dogs (Stricker, 1984; Gibbs and Smith, 1978). Gastric emptying under normal conditions is regulated primarily by the fatty acid, amino acid and carbohydrate content of ingesta. However, the effects of these nutrients on gastric or cecal emptying

rates in horses has not been determined. Ponies receiving an intragastric load of corn oil immediately before being offered a familiar feed after a four hour fast consumed normal meals during the first 30 to 60 minutes but reduced subsequent intake by tripling the normal intermeal interval. Whether this was due to reduced gastric emptying of the meal or caused by post absorptive metabolic cues generated by the fat is unknown. If cellulose or glucose are given under similar circumstances, reductions in intake occur at times synchronous with the post absorptive phase (10 to 15 minutes for glucose, 4 to 6 hours for cellulose), apparently independent of gastric emptying rate effects. Intragastric infusion of acetic acid theoretically increases the rate of gastric emptying. Ponies receiving intragastric infusions of acetic acid increased their intake of feed by reducing the duration of the intermeal interval, as did ponies receiving intracecal propionate (Ralston et al., 1983). Diet is known to significantly affect fermentation, production and absorption of volatile fatty acids in ponies. The effects of intravenous infusions of volatile fatty acids on feeding behavior in equine animals is unknown at this time.

Cafeteria feeding (free choice selection of a variety of feeds) also alters rates of passage of ingesta in rats (Dameto et al., 1991) and as does stress of transportation (Diop et al., 1991). Stress-induced diarrhea is common in horses but has received little, if any, scientific attention. The effects of cafeteria feeding on weight regulation and feeding behavior of horses has not been reported.

Insulin release in response to both glucose and volatile fatty acid absorption in free feeding goats also has been proposed as a factor regulating normal meal size in free feeding animals (deJong, 1981). Similar data are not available for horses, but blood glucose concentrations alone do not alter feeding activity in ponies, whereas glucose entry into cells, as influenced by phloridizin or endogenously released insulin, does alter feeding responses in the same animals (Ralston and Baile, 1982a, 1983b).

Gastrointestinal hormones also contribute to the regulation of feeding activity as well as influencing post ingestive digestion and metabolism in most animals investigated to date. Data on this aspect of regulation of feeding in horses is lacking in the literature at this time. Insulin, gastrin and cholecystokinin are released by the mere anticipation of feeding or non-nutritive suckling in infants (Uvnas-Moberg, 1990) and cholecystokinin and insulin are well documented regulators of feeding activity in other species (Stricker, 1984). Data are needed on the effect of anticipation of feeding on hormonal release and gastrointestinal function in horses.

Abnormal Regulation

Feeding acitivity is normally based on regulation of energy intake. However feeding activity of horses which are clinically ill, especially those suffering gastrointestinal related disorders, rarely reflect their on-going caloric needs (Ralston and Naylor, 1991). Non-caloric controls of feeding exist which contribute to the anorexia or reduced intake

associated with disease. Stricker and Verbalis (1991) identified four such factors, three of which are pertinant to horses suffering gastrointestinal disease: toxin absorption, dehydration and gastric distension. Little is known regarding toxin or dehydration induced anorexia in horses other than the fact that reduced intake of feed is a common sequela to these problems. Gastric distension usually is associated with clinical signs of colic in horses and may be due to feed impaction, gas or fluid accumulation in the stomach.

Abdominal malaise induced by lithium chloride or apomorphine injections also is a potent inhibitor of feeding activity unrelated to the caloric needs of the animal (Zahorik and Houpt, 1981). Novel or, in some species, even familiar flavors paired with lithium chloride injections are avoided in future trials (conditioned taste aversion) (Zahorik and Houpt, 1981). Conditioned taste aversions are associated with increased acitivity at serotonin (5-HT) receptors and are facillitated by increased plasma tryptophan in relation to short branch chain or large neutral amino acids (Rossi-Fanelli and Cangiano, 1991; West et al., 1991). Ponies will develop conditioned taste aversions to novel feeds or alfalfa pellets when apomorphine is given within minutes of the meal but not if the drug was injected 30 minutes after feed consumption (Houpt et al., 1990). They fail, however, to avoid familiar feeds such as corn even when apomorphine was given immediately after feeding. This failure to avoid feeds that may cause gastrointestinal distress increases the risk of gastrointestinal disease.

On the other hand, horses frequently "go off feed" during rigorous training or when being fed high grain diets (Ralston, 1992, unpublished data). Usually the animals will readily consume hay or pasture forage but refuse to consume grain or concentrates. Some horses are reported to reduce their hay intake under periods of stress. Protein deficiency has been reported to decrease intake of the deficient feed to less than maintenance energy intakes in ponies, horse foals and donkeys (Ralston, 1986; Pearson et al., 1991). Causes of these altered feed preferences are unknown at this time but may be due to a form of conditioned taste aversion secondary to gastrointestinal or generalized malaise caused by the stress of training or altered amino acid/neurotransmittor availability, which may influence taste aversion learning (Chaftez, 1984, Bray, 1991, Wellman and Davies, 1991). More information is needed on the ability of horses to develop conditioned taste aversions and mechanisms of anorexia in this species.

In Conclusion

While factors influencing the control of feed intake in ponies have been investigated, relatively little is known concerning the neurobiochemistry of feeding in equine animals. Due to the apparent lack of normal regulation of meal size documented in other species, ponies and horses are extremely susceptible to over consumption of palatable feeds in a single meal, especially if hungry at the initiation of the meal. There may be distinct differences between horses and ponies in the responsiveness to various cues regulating feed intake. Anorexia and altered feed preferences frequently are reported not only in clinically ill horses but also those in rigorous training or fed high carbohydrate diets. These problems may be related to altered amino acid/neurotransmittor availability and/or conditioned taste aversions caused by malaise.

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Dr. Sarah L. Ralston Department of Animal: Sciences Bartlett Hall, Cook College P.O. Box 231 New Brunswick, N.J., 08903 USA