EFFECTS OF INTRAGASTRIC LOADS OF XYLOSE, SODIUM CHLORIDE AND CORN OIL ON FEEDING BEHAVIOR OF PONIES

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Summary
This series of experiments was designed to investigate gastrointestinal (GI) stimuli that contribute to the normal control of feed intake in ponies. Osmotic stimuli were tested using intragastric (IG) infusion of .83 osmolar solutions of xylose (250 g) and NaCl (48 g) vs 2-liter water controls. Treatments were given 15 min before ponies were allowed ad libitum access to pelleted feed after a 4-h fast. Both hyperosmotic solutions delayed onset of the first meal (xylose: 72 ± 32 min, P<.05; NaCl: 71 ± 40 min, P<.1), resulting in an immediate reduction (P<.01) in feed intake. No effects were observed 3 to 18 h post-treatment and 24-h intake was not affected. The behavioral responses to the hyperosmotic solutions, however, were different. The xylose-treated ponies displayed normal sequences of satiety behaviors before eating their first meal, whereas the salt infusion caused moderate to severe colic in five of seven of the same animals. Nutrient stimuli were tested using infusions of corn oil (133 g) or mineral oil (133 g) administered 15 min before the ponies were fed after a 4-h fast. Corn oil did not alter the onset of feeding or the size or duration of the first meal relative to control values. The first intermeal interval, however, was prolonged (91 ± 27 vs 29 ± 4 min; P<.05) and feed intake 3 to 18 h post-treatment was reduced (1.00 ± .42 vs 2.01 ± .30 kg; P<.05) by corn oil relative to mineral oil. These results are comparable to those obtained in earlier experiments testing nutrient vs bulk solutions. It appears that nutrients in the gastrointestinal tract of ponies provide stimuli that affect subsequent feeding responses primarily by delaying onset of meals. Osmotic stimuli do not appear to play a major role in the satiety responses.
(Key Words: Pony, Feeding Behavior, Gastrointestinal Stimuli, Colic.)

Introduction
Intragastric (IG) administration of nutrients reduces feed intake in ponies (Ralston and Baile, 1982b), rats (Balagura and Coscina, 1969; Booth, 1972a,b), rabbits (Novin et al., 1974), pigs (Houpt et al., 1979), monkeys (McHugh, 1979) and humans (Stellar, 1967). The decreases in feeding have been attributed to: 1) nonnutrient stimuli such as osmotic pressure, which stimulate afferent nerves in the gastrointestinal tract (Jacobs, 1964; Ehman et al., 1971; Houpt et al., 1977; Anika et al., 1980), 2) the release of putative satiety hormones from the gastrointestinal tract in response to local nutrient stimuli (Smith and Gibbs, 1976) and 3) postabsorptive stimuli, which act through the liver (Russek, 1981) or other metabolic responses to absorbed nutrients (Bray and Campfield, 1975). The relative contribution of the above stimuli to the immediate control of food intake in ponies has been debated at length (Stellar, 1967; Bray and Campfield, 1975; Smith and Gibbs, 1976; Houpt et al., 1979; Russek, 1981). Nutrient and(or) osmotic stimuli may be responsible for the decrease in feed intake observed in ponies (Ralston and Baile, 1981) after IG administration of .83 osmolar (osM) glucose solution. The reductions in feeding were dose related, rapid (15 to 60 min post-treatment) and were not attributable to either the volume of the treatments (Ralston and

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Baile, 1982b) or the resultant increases in blood glucose and insulin (Ralston and Baile, 1982a).

The series of experiments described in this paper were designed to investigate gastrointestinal stimuli that contribute to the control of feed intake in ponies. On the basis of the results of IG glucose experiments (Ralston and Baile, 1981), we first explored the hypothesis that the glucose effect was due to osmotic rather than nutrient-related stimuli. Xylose is a 5-carbon sugar that is absorbed in the small intestine, but is not known to be a source of metabolizable energy (Roberts, 1974). We chose a .83 osM xylose solution as a nonnutrient pentose stimulus, which is otherwise similar to .83 osM solutions of the nutrient hexose (glucose). To further investigate osmotic stimuli, a .83 osM NaCl solution was tested. Sodium chloride is not similar to glucose in either structure or nutrient properties.

To test the hypothesis that ponies can regulate their feed intake on the basis of either pre- or postabsorptive nutrient stimuli, corn oil was chosen as a nutrient that is absorbed and metabolized by different pathways than are the carbohydrates, xylose and glucose; mineral oil was used as a nondigestible, nonmetabolizable control.

**Materials and Methods**

Eight mature ponies (seven castrated males and one female) of mixed breeding (body weight range = 100 to 227 kg) were maintained indoors in a temperature-controlled room under 24-h lights. Animals were maintained in individual free stalls that were equipped with a feeder and an automatic waterer. The stalls had concrete floors bedded with wood shavings and were separated by metal bars that allowed the ponies to interact with each other. The feeders were connected to a data acquisition system in an adjacent room (Ralston et al., 1979). The ponies were accustomed to a standard feeding-fasting schedule during which they had 19 h of ad libitum access to a complete, pelleted feed (Ralston and Baile, 1982a) for at least 1 mo before the initiation of the experiments.

In both experiments, treatments were given by nasogastric tube 15 min before the ponies were fed after the 4-h fast. The ponies accepted the tubing procedure with a minimum of manual restraint. The latency to eat, first meal size (at least 100 g of pellets) and duration (minimum of 10 min) and subsequent intermeal interval (minimum of 15 min without feeding activity before eating a criterion meal) were recorded for each pony. The meal criteria were established by observations on the same ponies (S. L. Ralston, unpublished data) and data collected previously from other animals (Ralston et al., 1979). Nonconsummatory activities such as social activities, resting behaviors (Ralston and Baile, 1982b) and signs of malaise (pawing, trembling, sweating, looking at flanks; Blood et al., 1979) were also recorded for the first 3 h post-treatment. Feed intakes were calculated for the prefasting meal (0800 to 0900 h), 0 to 3 h post-treatment (1300 to 1600 h) and 3 to 18 h post-treatment (1600 to 0700 h). Data were analyzed by two-way analysis of variance and Students t-test.

**Exp. 1: Osmotic Stimuli.** Seven ponies (six castrated males, one female) were used in this experiment. Both hyperosmotic solutions tested were assigned to the animals in a simple crossover design with control treatments of 2 liters of tap water. The hyperosmotic solutions (.83 osM) tested were: 1) D-xylose3, 250 g in 2 liters water and 2) NaCl3, 48 g in 2 liters tap water. Treatments were not adjusted according to body weight. The water treatments served as a control for volume and the two hyperosmotic treatments served as controls for each other, because all animals received each treatment at least once.

In a replicate run of the xylose crossover, three ponies (two males and one female) were equipped with indwelling catheters4 placed into the jugular vein during the 4-h fast. Blood samples were drawn at: 1) time (t) = −15 min, before treatments were given, 2) t = 0 min, just before the ponies were untied and allowed access to feed and 3) t = 15, 30, 60 and 90 min after the animals were permitted to feed. The samples were analyzed for concentrations of glucose (from NaF-treated tubes5 by an automated hexokinase assay6), xylose (from heparin-treated tubes6; Eberts et al., 1979) and immunoreactive insulin (from sodium ethylenediaminetetraacetate-treated tubes6 to which Tra-sylol7 had been added (Morgan and Lazarow, 1963)).

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4 Intracath, 19 gauge, Deseret Co., Sandy, UT.
5 Vacutainer tubes, Becton, Dickinson and Co., Rutherford, NJ.
6 Gemsae Centrifugal Analyzer, Electronucleonics, Fairfield, NJ.
7 Aprotinin, 100 µl, Mobay Chemicals, NY.
Exp. 2: Nutrient Stimuli. In the second experiment, five ponies (all castrated males) were used. The same treatment procedures and feeding-fasting schedules as described in Exp. 1 were used. The treatments consisted of: 1) corn oil (133 g), a vegetable oil that is digested, absorbed and utilized as a source of energy by ponies (Kane et al., 1979; Rich et al., 1981) and 2) mineral oil (133 g), a mixture of liquid hydrocarbons that is "indigestible, nonmetabolizable and absorbed only to a limited extent" (Phillips and Lewis, 1977). The dose of corn oil was chosen to be isocaloric to the dose of glucose (300 g; Ralston and Baile, 1981), which had significantly reduced subsequent feeding activity in previous experiments. Treatments were assigned randomly to each animal according to a simple crossover design. Data collection and analyses were the same as in Exp. 1.

Results

Exp. 1: Osmotic Stimuli. The feeding responses to intragastric loads of .83 osM solutions of xylose and NaCl vs equal volumes (2 liters) of water are presented in table 1. Both of the hyperosmotic treatments decreased (P<.01) feed intake immediately and to approximately the same degree; the ponies delayed onset of feeding 77 ± 32 min after xylose vs 71 ± 40 min after NaCl. There were dramatic differences, however, between the two treatments with respect to the animals' behavior during this latency to eat period (table 2). Xylose-treated ponies that did not eat for >15 min after being untied (six of seven subjects) performed normal sequences of satiety behavior (Ralston and Baile, 1982b) before initiating their first meal. This behavior included socializing with neighboring ponies, investigating the floor of the stall, self-grooming and eventually assuming a resting position. The seventh animal ate a small but criterion meal immediately. None of these animals displayed signs of colic (abdominal pain; Blood et al., 1979).

After NaCl treatments, however, five of seven of the same animals showed signs of colic, though only four delayed onset of feeding for a mean of 165 ± 44 min. The ponies performed behaviors associated with moderate to severe abdominal pain (Blood et al., 1979), which included rolling repeatedly, kicking and looking at their abdomens, trembling, sweating and moving about their stalls in an agitated manner. These signs of malaise appeared immediately after NaCl treatments.
TABLE 2. NONFEEDING RESPONSE OF PONIES TO INTRAGASTRIC LOADS OF .83 OSM XYLOSE (250 G) OR NaCl (48 G) SOLUTIONS VERSUS NORMAL POSTPRANDIAL BEHAVIOR

<table>
<thead>
<tr>
<th>Item</th>
<th>No.</th>
<th>No. ponies delaying onset of feeding &gt;15 min</th>
<th>Latency to eat next mealabc, min</th>
<th>No. ponies resting before eating</th>
<th>Latency to resting positionabc, min</th>
<th>No. ponies exhibiting signs of colic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xylose</td>
<td>7</td>
<td>6</td>
<td>85 ± 28c</td>
<td>3c</td>
<td>19 ± 9</td>
<td>0</td>
</tr>
<tr>
<td>NaCl</td>
<td>7</td>
<td>4</td>
<td>165 ± 34c</td>
<td>4c</td>
<td>21 ± 5</td>
<td>5</td>
</tr>
<tr>
<td>Postprandial controlc</td>
<td>14</td>
<td>0</td>
<td>67 ± 8d</td>
<td>13</td>
<td>30 ± 4</td>
<td>0</td>
</tr>
</tbody>
</table>

*a* Means ± SE.

*b* Time between either refeeding (xylose, NaCl) or last bite of first meal (control) and the assumption of a resting position (Ralston and Baile, 1981).

*c* Values represent only those animals that delayed onset of feeding 15 min (meal 1 size and duration = 0).

*c* Represents interval between first and second meals.

*c* Behavior observed after last bite of first meal after water (control) treatments.

Figure 1. The effect of intragastric xylose (250 g), control treatments (2 liters of water) and subsequent feeding on blood xylose concentrations in ponies (n = 3) fasted for 4 h. Treatments (Tx) were given by nasogastric tube 15 min before feeding ponies after the fast. Xylose-treated ponies delayed 77 ± 32 min before consuming only .08 ± .06 kg of feed during the sampling period. Water-treated ponies ate .46 ± .10 kg of feed during the first 38 ± 6 min after being fed. *Different from control, ANOVA (P<.05); ** different from control, ANOVA (P<.01); + different from baseline within treatment by Duncan's multiple range test (P<.05).

Exp. 2: Corn vs Mineral Oil. The feeding responses of the ponies to corn vs mineral oil treatments are presented in table 3. The animals given corn oil reduced (P<.05) their total feed intake by prolonging (P<.05) their intermeal periods and were not correlated with the absorption of xylose from the gastrointestinal tract.
Figure 2. The effect of intragastric xylose (250 g), control treatments (2 liters of water) and subsequent feeding on blood glucose concentrations in ponies (n = 3) fasted for 4 h. Treatments were given by nasogastric tube 15 min before ponies were fed. Xylose-treated ponies delayed 77 ± 32 min before eating whereas water-treated ponies ate .46 ± .10 kg of feed during the first 38 ± 6 min. *Different from control, ANOVA (P<.05) and +different from baseline within treatment by Duncan's multiple range test (P<.05).

Figure 3. The effect of intragastric xylose (250 g), control treatments (2 liters of water) and subsequent feeding on immunoreactive insulin concentrations in ponies (n = 3) fasted for 4 h. Treatments (Tx) were given by nasogastric tube 15 min before the ponies were fed. Xylose-treated ponies delayed 77 ± 32 min before eating whereas water-treated ponies ate .46 ± .10 kg of feed during the first 38 ± 6 min.

Discussion

Corn oil (133 g), xylose (250 g) and NaCl (48 g) given IG to ponies fasted for 4 h decreased subsequent feed intakes. The NaCl solutions, however, caused obvious signs of colic and malaise for up to 20 min postadministration. Malaise is a common cause of anorexia and is not considered to be a normal factor in the control of feed intake (Deutsch, 1980). Xylose and corn oil, however, did not cause abnormal behavior. The corn oil- and xylose-treated animals performed normal sequences of satiety behavior (Ralston and Baile, 1982b) either before eating their first meal after a 4-h fast (xylose) or after a normal first meal (corn oil). Xylose is a 5-carbon sugar, polymers of which are present in corncobs and wood (Ensminger and Olentine, 1978). It is absorbed passively from the small intestine, but also can be actively transported in limited amounts by the same carrier as glucose (Hele, 1953; Sols, 1956; Annegers, 1968; Levitt et al., 1969; Bolton et al., 1976). Although there are no reports of the utilization of xylose as a direct energy source, the 5-carbon sugar can be fermented by intestinal bacteria into utilizable volatile fatty acids (Pazur et al., 1958; Church, 1976). If some of the xylose reached the hindgut of the ponies, it may have undergone a similar transformation because the fermentation processes in the equine cecum are similar to those of the rumen in the ruminant (Kern et al., 1974; Koller et al., 1978; Argenzio, 1981). The lack of insulin response to elevated blood xylose concentrations suggests that the 5-carbon sugar is not utilized by the same mechanism as glucose. Based on our results, however, xylose apparently generates satiety cues similar to those of glucose, possibly through changes in the firing rate of ileal mesenteric nerves that are sensitive to actively transported sugars (Hardcastle et al., 1978).

Vegetable oils, such as corn oil, are known to be of nutrient value to horses and ponies (Kane et al., 1979; Rich et al., 1981). The satiety cues generated by IG administration of corn oil were not, however, as rapid as those generated by IG glucose (Ralston and Baile, 1981) or xylose; reduction in feeding appeared only after the termination of the first meal (60 min post-treatment). In most animals, including horses, fats and oils must be emulsified with
bile salts before being absorbed into the lymphatic system (Church and Pond, 1974), whereas glucose and xylose are absorbed unchanged and transported via the mesenteric veins (Church and Pond, 1974; Roberts, 1975). The observed delay in corn oil effect, therefore, would appear to reflect the slower digestion and absorption of fat relative to simple carbohydrates. Mineral oil is indigestible and non-metabolizable (Phillips and Lewis, 1977) and the small amount (133 g) given to the ponies did not measurably alter their feeding behaviors.

The malaise the ponies experienced following NaCl treatment apparently was not due to the osmolarity of the solution (.83 osM), but rather to the concentration of Na and(or) Cl ions. Vagal afferent fibers in the stomach of cats are excited differentially by salt vs glucose solutions, suggesting that dissimilar somatosensory inputs were generated by the two solutions (Sudahov and Roga-Cheva, 1963). If the colic observed had been in response to the osmotic pressure stimuli alone, one would expect to see similar behaviors following intragastric administration of equiosmolar solutions of other substances. This was not observed in these or previous (Ralston and Baile, 1982b) experiments.

We conclude from these experiments that nutrients delivered to the gastrointestinal tract of ponies provide stimuli that affect the subsequent feeding responses of the animals by generating cues related to normal postprandial satiety. Osmotic pressure does not appear to play a major role in the satiety responses because the animals demonstrated normal satiety behaviors when treated with nutrient (corn oil, glucose) or nutrient-like (xylose) substances, regardless of the osmotic content of the solutions. A nonnutrient solution (NaCl) that was iso-osmotic to the glucose and xylose nutrient solutions, however, cause clear signs of colic. The nutrients apparently must at least be available for absorption before contributing to satiety, based on the delay in effect of cellulose (Ralston and Baile, 1981) and corn oil relative to the rapidly absorbed simple carbohydrates, glucose (Ralston and Baile, 1981) and xylose. Whether the effective nutrient stimuli are pre- or postabsorptive remains to be determined.

**Literature Cited**


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**Table 3. Feeding responses of ponies (N = 5) to intragastric loads of 133 g mineral oil**

<table>
<thead>
<tr>
<th>Item</th>
<th>Corn oil</th>
<th>Mineral oil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latency to est, min 1</td>
<td>3 ± 1</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>Initial meal size, kg</td>
<td>47 ± 18</td>
<td>57 ± 20</td>
</tr>
<tr>
<td>Initial meal duration, min</td>
<td>46 ± 12</td>
<td>56 ± 7</td>
</tr>
<tr>
<td>Interval between first and second meals eaten, min</td>
<td>46 ± 12</td>
<td>56 ± 7</td>
</tr>
<tr>
<td>All treatments given 15 min before feeding after a 4-h fast.</td>
<td>46 ± 12</td>
<td>56 ± 7</td>
</tr>
</tbody>
</table>

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*Different from mineral oil control, ANOVA (P < 0.05).*

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*Interval between meals, 1 and 2, min.*

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*Total intake, kg.*

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*Intake 3 to 18 h post-treatment, kg.*


