Effects of hindgut fermentation of non-starch polysaccharides on the stability of blood glucose and insulin levels and physical activity in empty sows

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Abstract

A fermentable non-starch polysaccharides (fNSP)-rich diet was previously shown to stabilise glucose and insulin levels and reduce physical activity in restricted-fed sows. Stable glucose levels may prevent interprandial hunger. Aim of the present study was to elucidate the specific role of fermentation in these traits.

Ten empty sows were either fed a low- (L-sows) or a high-fNSP diet (H-sows), twice daily. In three successive periods, sows received first no infusion and then, in different sequences, continuous fNSP infusion in the cecum or glucose infusion in the blood for 8 days each (GLU; energetic control). Infused energy was similar to the difference in energy derived from fNSP between diets. Blood samples, drawn between feeding times, were analysed for glucose and insulin levels and stability. Video-recordings were analysed for posture changes (physical activity).

GLU and fNSP infusions stabilised glucose levels in L-sows and reduced posture changes in both L- and H-sows (H-sows, tendency). Insulin stability was less affected by infusions. GLU and fNSP infusions prevented drops of glucose below basal levels. fNSP infusion in L-sows (cecum) had similar effects as GLU infusion in H-sows (oral fNSP intake).

Results imply that fermentation plays an important role in the effects of a fNSP-rich diet on the stability of glucose levels and physical activity in sows.

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Keywords: Dietary fibre; Satiety; Stress; Fermentation; Volatile fatty acids; Sows

1. Introduction

In practice, the feed intake of non-lactating sows is restricted in order to maintain stable body condition
and to prevent a reduction in reproductive performance. Although diets that sows receive provide sufficient amounts of nutrients for maintenance and reproduction on a daily basis, they often do not sufficiently satisfy the sows. As a result, sows have a high feeding motivation throughout the day, even just after feeding (Lawrence et al., 1988). This, in combination with a barren housing environment in which the expression of foraging behaviour is virtually impossible, results in increased activity and the development of stereotyped behaviour (Lawrence and Terlouw, 1993; Terlouw and Lawrence, 1993; Spoolder et al., 1995).

Several studies have shown that diets containing dietary fibre reduce both activity and stereotyped behaviour (Brouns et al., 1994; Ramonet et al., 1999; Danielsen and Vestergaard, 2001; Zonderland et al., 2004). Fermentation of dietary fibre by the microflora in the hindgut may play an important role in the prolongation of satiety between meals. Volatile fatty acids (VFA), as products of fermentation, are available as a source of energy at times when glucose supply from the gut lumen is decreasing (Bergman, 1990; Bach Knudsen and Hansen, 1991; Rérat, 1996). Therefore, VFA may spare glucose. As transient declines of blood glucose levels below basal levels have shown to precede meal initiation (rats; Louis-Sylvestre and Le Magnen, 1980; Campfield et al., 1985) or meal request (humans; Campfield et al., 1996), we hypothesized that stable glucose levels may reduce hunger, as well as the increase in activity that may result from it. Recently, we have shown that a fermentable non-starch polysaccharides (fNSP)-rich diet (sugarbeet pulp), indeed, reduced physical activity and stabilised blood glucose and insulin levels several hours after feeding compared with a starch-rich diet (De Leeuw et al., 2004). In this study, sows were fed twice daily, at 7:00 h and 19:00 h. Sows fed the starch-rich diet showed a drop of glucose below basal levels at 14:00 h and showed a large increase in physical activity after 14:00 h. We could, however, not exclude that besides fermentation, other properties or effects of sugarbeet pulp may have played a role. In order to be able to distinguish between the effects of fermentation in the distal part of the gut and other effects (like increased gut fill) in the proximal part of the gut, fermentation has to be experimentally separated from gut fill.

The main objective of the present study, therefore, was to elucidate whether fermentation plays an important role in the effects of a fNSP-rich diet on the stability of glucose and insulin levels and physical activity in sows several hours after feeding. In order to answer this question, two main hypotheses were tested. Firstly, it was tested whether a continuous fNSP infusion in the cecum stabilises blood glucose and insulin levels and reduces physical activity as effectively as a continuous iso-energetic glucose infusion in the blood (positive control), compared with no infusion. Secondly, it was tested whether intracecally received fNSP (sows fed a fNSP-poor diet and continuously infused with fNSP in the cecum) is at least as effective as orally ingested fNSP (sows fed a fNSP-rich diet and continuously infused with glucose in the blood).

2. Materials and methods

The protocol for this experiment was approved by the Ethical Review Committee of the Animal Sciences Group of Wageningen UR.

2.1. Animals and housing

Twelve empty first-parity sows (Topigs), bred at ‘de Waaiiboerhoeve’ in Lelystad, were used. The experiment took place in the ‘Metabolism Unit’ in Lelystad. Sows were housed individually in metabolism cages (180×80 cm). Metal funnels beneath the slatted floor of the cage allowed separate collection of excretions and spilled water. Cages were equipped with an automatic feeding system and a water reservoir, connected to a nipple next to the trough. The ambient condition was kept at a constant level and the temperature was set at 20.5 °C. Artificial lights were on from 06:00–20:00 h. Windows were blinded to prevent entrance of daylight. During the dark period, dimmed artificial lights were on.

2.2. Diets and feeding

Sows were either fed a diet with a high level of fNSP (H-diet; n=6) or a diet with a low level of fNSP (L-diet; high-starch diet; n=6). They received this diet throughout the whole experiment (about 60 days).
Sows were divided into two weight-classes (high and low). Within each class, animals were randomly assigned to one of the two diets. Siblings were assigned to different diets.

Diets were formulated according to the Dutch recommendations (CVB, 2002), except for the NSP content in the L-diet (at least 340 g/kg is compulsory). Diets were manufactured at a research feed mill (Arkervaart-Twente, Leusden, The Netherlands). The composition is given in Table 1. Diets were isoenergetic (net energy) and provided the same amount of ileal digestible amino acids and digestible phosphorus. The H-diet contained sugarbeet pulp (SBP) as main fNSP source at the expense of barley, wheat and maize starch. The latter are main sources of glucogenic energy in the L-diet. Representative samples of each diet, taken during production, were analysed for dry matter, ash, crude protein, crude fat, starch and sugar. NSP content was calculated by subtracting crude protein, crude fat, starch and sugar from the organic matter content, similar to others (Schrama et al., 1998; Rijnen et al., 2001; Van der Peet-Schwering et al., 2003). fNSP content was calculated by subtracting digestible crude protein, digestible crude fat, starch and sugar content from the digestible organic matter content (CVB, 2002). Sows automatically received 900 g of feed, twice daily at 07:00 h and 19:00 h. Water availability was restricted to maximally 12 L per day.

2.3. Surgery

After 18 days of adaptation to their new housing and diets, sows were surgically fitted with catheters in the jugular vein and in the carotid artery on four consecutive days (Mroz et al., 1993). These catheters could be used for blood sampling and infusion. Sows also received a SICV cannula in their cecum (Steered Ileo-Cecal Valve; Mroz et al., 1996). This cannula is designed to enable quantitative collection of ileal digesta. Ileal digesta were sampled for analyses outside the scope of the study reported in this paper. In this study the cannula was used for infusions. Anesthesia and pre- and post-operative care took place as previously described (De Leeuw et al., 2004). During the days after surgery the feed allowance was gradually increased towards a high level in order to allow good recovery and adaptation of the gut to the

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>L</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>130.0</td>
<td>–</td>
</tr>
<tr>
<td>Tapioca (starch, 625–675 g/kg)</td>
<td>191.3</td>
<td>123.4</td>
</tr>
<tr>
<td>Soybean meal (extracted; CF, 50–70 g/kg; CP, &gt;440 g/kg)</td>
<td>80.0</td>
<td>80.0</td>
</tr>
<tr>
<td>Soybean hulls (CF,&lt;310 g/kg)</td>
<td>70.0</td>
<td>124.0</td>
</tr>
<tr>
<td>Peas (CP, &lt;220 g/kg)</td>
<td>70.0</td>
<td>70.0</td>
</tr>
<tr>
<td>Wheat middlings</td>
<td>150.0</td>
<td>–</td>
</tr>
<tr>
<td>Sunflower seed (extracted; CF, 160–200 g/kg)</td>
<td>60.0</td>
<td>37.4</td>
</tr>
<tr>
<td>Sugarbeet pulp (dehydrated; sugar, &lt;100 g/kg)</td>
<td>–</td>
<td>450.0</td>
</tr>
<tr>
<td>Molasses (cane; sugar, &gt;475 g/kg)</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Animal fat</td>
<td>22.2</td>
<td>26.1</td>
</tr>
<tr>
<td>Maize starch</td>
<td>150.0</td>
<td>20.0</td>
</tr>
<tr>
<td>Limestone</td>
<td>9.8</td>
<td>0.6</td>
</tr>
<tr>
<td>Salt</td>
<td>4.7</td>
<td>2.7</td>
</tr>
<tr>
<td>Cr2O3–maize starch mix (1:3)</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Monocalcium phosphate · H2O</td>
<td>4.8</td>
<td>7.2</td>
</tr>
<tr>
<td>Vitamins and trace elements mixα</td>
<td>5.0</td>
<td>5.0</td>
</tr>
<tr>
<td>DL-Methionine</td>
<td>0.8</td>
<td>1.4</td>
</tr>
<tr>
<td>L-Threonine</td>
<td>0.4</td>
<td>0.9</td>
</tr>
<tr>
<td>L-Tryptophan</td>
<td>–</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Analysed composition

| Dry matter | 858 | 866 |
| Ash        | 58  | 67  |
| Crude protein | 123 | 120 |
| Crude fat  | 36  | 36  |
| Starch     | 343 | 123 |
| Sugar      | 53  | 87  |

Net energy (MJ/kg)d

<table>
<thead>
<tr>
<th>L, low-fNSP diet; H, high-fNSP diet; CF, crude fibre; CP, crude protein.</th>
</tr>
</thead>
<tbody>
<tr>
<td>The vitamin–mineral premix supplied (per kg diet): Vitamin A, 10,000 IU; Vitamin D3, 2000 IU; Vitamin E, 25 IU; Vitamin K3, 1 mg; Vitamin B1, 0.75 mg; Vitamin B2, 4 mg; D-pantothenic acid, 13 mg; niacin, 15 mg; Vitamin B12, 0.015 mg; folic acid, 1.3 mg; Vitamin B6, 1 mg; Fe, 150 mg; Cu, 20 mg; Zn, 65 mg; Mn, 30 mg; Co, 0.15 mg; I, 1 mg; Se, 0.2 mg.</td>
</tr>
<tr>
<td>Non-starch polysaccharides β Non-starch polysaccharides γ 173 378</td>
</tr>
<tr>
<td>Fermentable non-starch polysaccharides e 246 436</td>
</tr>
<tr>
<td>Net energy (MJ/kg)d 8.9 8.9</td>
</tr>
</tbody>
</table>

L, low-fNSP diet; H, high-fNSP diet; CF, crude fibre; CP, crude protein.

α The vitamin–mineral premix supplied (per kg diet): Vitamin A, 10,000 IU; Vitamin D3, 2000 IU; Vitamin E, 25 IU; Vitamin K3, 1 mg; Vitamin B1, 0.75 mg; Vitamin B2, 4 mg; D-pantothenic acid, 13 mg; niacin, 15 mg; Vitamin B12, 0.015 mg; folic acid, 1.3 mg; Vitamin B6, 1 mg; Fe, 150 mg; Cu, 20 mg; Zn, 65 mg; Mn, 30 mg; Co, 0.15 mg; I, 1 mg; Se, 0.2 mg.

β Non-starch polysaccharides (NSP) were derived by subtracting the CP, crude fat, starch and sugar content from the organic matter content (CVB, 2002).

γ Fermentable NSP (INSP) were derived by subtracting the digestible CP, digestible crude fat, starch and sugar content from the digestible organic matter content (CVB, 2002).

d Calculated (CVB, 2002). A correction was made for the assumed energy saving effect by reduced physical activity. This correction is advised for diets for growing pigs containing up to 15% sugarbeet pulp (CVB, 2002). We assumed the same energy saving per unit of INSP derived from sugarbeet pulp in sows.
diets. Five days before measurements started, sows returned to the experimental feeding level. Catheters were flushed weekly with heparinised saline.

2.4. Experimental outline

The experiment consisted of three periods in which the same measurements took place. During the first period (16 days), sows did not receive any infusion. This period started approximately 1 month after surgery and was previously used to compare the H- and L-diet (De Leeuw et al., 2004). In the present experiment, it was used to compare the effects of no infusion with those of a fNSP or a glucose infusion. In the second period of the experiment (8 days), three sows per dietary treatment received a continuous infusion with fNSP in the cecum and a continuous saline infusion (0.9% sodium chloride) in the blood and the other three sows received a continuous saline infusion in the cecum and a continuous glucose infusion in the blood. In the third period (8 days) the infusion treatments were reversed. The amount of fNSP or glucose infused was such, that L-sows with a fNSP infusion and H-sows with a glucose infusion received similar amounts of total net energy and net energy derived from fNSP per day (Table 2). By doing so, possible effects of fNSP-rich ingredients in the proximal part of the gut, like increased gut fill, were excluded in L-sows, in contrast with H-sows. Before measurements started, sows were allowed to adapt to the infusions during 5 days in each period.

2.5. Infusions

Simultaneous infusions in the cecum and the blood (carotid artery) were administered by using two peristaltic pumps. For the blood-infusions, Watson-Marlow 202U pumps were used (Watson-Marlow Pumps BV, Rotterdam, The Netherlands). Several types of pumps were used for the cecum-infusions (205S, 502S and 504S; Watson-Marlow Pumps BV, Rotterdam, The Netherlands and WIZ; Isco Inc., Lincoln, NE, USA). All pumps were calibrated before the experiment started.

The fNSP-solution consisted of a mixture of 60 g/kg fructo-oligosaccharides (FOS; Nordos Netherlands, Putten, The Netherlands) and 60 g/kg sugar-beet pectin (RU301; Herbstreith and Fox, Germany) in saline. The solution was prepared in buckets and mixed thoroughly at least 1 day before use. Just before use, the solution was mixed again to dissolve possible lumps. For the calculation of the amount of fNSP to be infused, the net energy of FOS was set at 8.8 kJ/g (100% pure FOS; digestibility coefficient estimated at 93%) and the net energy of sugar-beet pectin was set at 7.7 kJ/g (95% pure pectin; digestibility coefficient estimated at 85%). These values are based on a net energy of fNSP of 9.5 kJ/g (CVB, 2002). Therefore, 3.7 kg of the fNSP-solution was infused per day at a constant rate (i.e. 3.7 MJ per day). During a blood-glucose infusion, saline (0.9% sodium chloride) was infused into the cecum (0.9% sodium chloride) was infused into the cecum (3.7 kg per day).

The amount of glucose (30%; AUV, Cuijk, The Netherlands) to be infused per day was 1002 ml (net energy content of glucose, 12.2 kJ/g; CVB, 2002). Three bottles of glucose solution (500 ml per bottle) were connected to each other in order to be able to infuse more than 1 L of glucose per day without changing the bottles during the day. During a cecum-fNSP infusion, saline (AUV, Cuijk, The Netherlands) was infused into the blood.

Each morning, buckets and bottles were changed and the remaining infusate was weighed. If necessary, the rate of the pumps was adjusted.

Table 2

<table>
<thead>
<tr>
<th>Infusion</th>
<th>Diet b</th>
<th>Infusion</th>
<th>Diet + Infusion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>fNSP</td>
<td>Other</td>
<td>fNSP d</td>
</tr>
<tr>
<td></td>
<td></td>
<td>GLU c</td>
<td>fNSP</td>
</tr>
<tr>
<td>H</td>
<td>NO</td>
<td>6.5</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
<td>GLU c</td>
<td>6.5</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
<td>fNSP d</td>
<td>6.5</td>
<td>9.5</td>
</tr>
<tr>
<td>L</td>
<td>NO</td>
<td>3.0</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td>GLU c</td>
<td>3.0</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td>fNSP d</td>
<td>3.0</td>
<td>13.1</td>
</tr>
</tbody>
</table>

NO, no infusion; GLU, glucose; fNSP, fermentable non-starch polysaccharides.

Data were rounded at one decimal after calculations.

Based on analysed digestibility (see footnotes in Table 1).

Glucose infusion into the blood and saline infusion into the cecum.

fNSP infusion into the cecum and saline infusion into the blood.
2.6. Blood sampling

Blood samples were taken in all periods on 1 day at 0.25 h before feeding-time and at 0.5, 1, 2, 3, 5, 7, 9 and 11 h after feeding-time. It was accounted for that none of the sows would be in oestrus on sampling days (this also counts for the video recordings, mentioned in the next section). Samples were taken with 9 ml syringes containing Lithium-heparin (Monovette®, Sarstedt BV, Etten-Leur, The Netherlands) via the catheter in the jugular vein, after flushing the catheter with saline. After sampling, the catheter was filled with heparinised saline again. Blood samples were immediately ice-chilled and centrifuged during 10 min at 800 \( \times \) g and 4 \( ^{\circ} \)C. Plasma was stored at \( ^{-20} \) C until analysis.

A preliminary blood sample (one h before feeding-time) was taken to allow sows to get used to the sampling procedure. This sample was not analysed. All other samples were analysed for glucose and insulin. Glucose was analysed by the Boehringer Mannheim hexokinase method (Roche Diagnostics Nederland BV, Almere, The Netherlands). Insuline was analysed using a time-resolved fluorimunoassay (AutoDELFIA® Insulin; Wallac Oy, Turku, Finland) with porcine standards.

Stability of glucose and insulin levels after the presumed post-prandial peak was determined by calculating the sum of absolute differences between levels in consecutive samples (SAD) after (and including) 10:00 h. The SAD appeared to be a good measure of stability in a previous study (De Leeuw et al., 2004). Glucose and insulin levels were expressed as a percentage of their basal level within sows as well. The basal level was defined as the average of the level in the first and the last sample (i.e. 15 min before morning feeding and 60 min before afternoon feeding, respectively).

2.7. Video recording

In all periods, behaviour of sows was recorded on videotape on 1 day during the light period, using a time-lapse video recorder. The number of posture changes in the periods 08:00–14:00 h and 14:00–19:00 h (excluding feeding time) was determined as a measure of physical activity. Postures were: Standing (body supported by all four legs), Lying (body not supported by any of the legs) and Sitting (body supported by both front legs only).

2.8. Data analysis

Data were statistically analysed by using non-parametric tests in StatXact (2001). Effects of glucose (GLU) and fNSP infusions were compared with those of no infusion (NO) within animal with a paired permutation test. In addition, effects of the fNSP infusion were compared with those of the GLU infusion. Dietary treatments were analysed separately as it was expected that effects of GLU and fNSP infusions would be present in sows fed the L-diet (L-

<table>
<thead>
<tr>
<th>Diet</th>
<th>Infusion</th>
<th>Glucose (mmol/L)</th>
<th>Insulin (pmol/L)</th>
<th>P-values (P&lt;0.1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO</td>
<td>GLU(^{a})</td>
<td>fNSP(^{b})</td>
<td>GLU-NO</td>
</tr>
<tr>
<td>Glucose</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>3.07±0.82</td>
<td>1.77±0.56</td>
<td>1.40±0.40</td>
<td>0.063</td>
</tr>
<tr>
<td>H</td>
<td>1.26±0.40</td>
<td>1.12±0.12(^{c})</td>
<td>1.28±0.31</td>
<td>–</td>
</tr>
<tr>
<td>Insulin</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>123.7±39.0</td>
<td>146.8±56.2</td>
<td>85.6±12.0</td>
<td>–</td>
</tr>
<tr>
<td>H</td>
<td>43.8±11.3</td>
<td>90.8±15.9(^{c})</td>
<td>61.8±6.8</td>
<td>–</td>
</tr>
</tbody>
</table>

SAD, sum of absolute differences between levels in consecutive samples; NO, no infusion; GLU, glucose; fNSP, fermentable non-starch polysaccharides.

\(^{a}\) Glucose infusion into the blood and saline infusion into the cecum.
\(^{b}\) fNSP infusion into the cecum and saline infusion into the blood.
\(^{c}\) \(n=3\); no blood samples could be drawn from two H-sows during the GLU infusion, although after section catheters appeared to have been perfectly placed.
sows), whereas the effect of these infusions would be absent or less pronounced in sows fed the H-diet (H-sows). Moreover, animals were their own controls, concerning the infusions.

Results of L-sows receiving a fNSP infusion were compared with those of H-sows receiving a GLU infusion with an unpaired permutation test. Differences were considered significant at \( P < 0.05 \). Results are presented as means ± S.E.M.

3. Results

3.1. General

Two sows (one from each dietary treatment) were excluded from analysis. One of these sows severely damaged the cannula shortly after surgery. In the other sow the cannula was not perfectly placed, as became apparent after section.

The net energy and fNSP contents of the diets (Table 1) were derived from determined digestibility coefficients of nutrients (not shown). The total daily intake of net energy was equal for sows on both L- and H-diets during fNSP or GLU infusions (Table 2). The daily intake of total net energy and net energy derived from fNSP (originating from diet or infusion) was equal for L-sows receiving a fNSP infusion and H-sows receiving a GLU infusion.

3.2. Glucose and insulin

A large variation was observed in stability of glucose and insulin levels (SAD) between sows within the same treatment.

In L-sows, both the GLU and the fNSP infusion tended to reduce the glucose SAD in comparison with NO infusion (Table 3). The fNSP infusion was as effective as the GLU infusion. In H-sows the infusions did not affect glucose SAD. Compared with the GLU infusion, the fNSP infusion caused a slightly higher glucose SAD in H-sows (not significant).

No large effects of either the GLU or fNSP infusion were found on insulin SAD. The GLU infusion increased the insulin SAD to a certain extent in both L- and H-sows (not significant). The fNSP infusion tended to increase the insulin SAD in H-sows and non-significantly reduced the insulin SAD in L-sows in comparison with NO infusion. Compared with the GLU infusion, the fNSP infusion caused a slightly lower insulin SAD in both L- and H-sows (not significant). There was no difference between L-sows receiving the fNSP infusion and H-sows receiving the GLU infusion, concerning both their glucose and insulin SAD.

In both L- and H-sows, glucose levels were continuously above or equal to basal levels during both the GLU and the fNSP infusions (Fig. 1). With NO infusion, glucose levels of L-sows dropped below basal levels at 14:00 h. In L-sows, insulin levels were continuously above or equal to basal levels during both the GLU and the fNSP infusions (Fig. 1).

![Fig. 1. Blood glucose levels of sows fed either a low-fNSP diet (L; panel A) or a high-fNSP diet (H; panel B) with or without infusion, relative to their basal levels (mean ± S.E.M.). NO, no infusion; GLU, blood glucose infusion (saline into the cecum); fNSP, cecum fermentable non-starch polysaccharides infusion (saline into the blood); \( n = 3 \), *NO differs from its basal level, 1GLU differs from its basal level, 2fNSP differs from its basal level (underlined, \( P < 0.05 \); not underlined, \( P < 0.1 \)). Arrows represent feeding times.](image-url)
continuously above or equal to basal levels during the GLU and fNSP infusions as well as during NO infusion (Fig. 2). In H-sows, insulin levels were slightly below basal levels at 14:00 h, during the fNSP infusion.

In L-sows, both basal glucose and insulin levels were lower during a fNSP infusion (4.57±0.10 mmol/L and 18.65±3.95 pmol/L, respectively) than with NO infusion (4.93±0.15 mmol/L and 34.88±7.25 pmol/L, respectively; \( P<0.05 \)). In H-sows, the fNSP infusion did not affect basal glucose and insulin levels (4.82±0.22 mmol/L and 33.89±6.73 pmol/L, respectively), compared with NO infusion (4.75±0.13 mmol/L and 31.87±1.84 pmol/L, respectively). The GLU infusion did not affect basal glucose and insulin levels in both L- and H-sows. L-sows receiving the fNSP infusion had lower basal insulin levels than H-sows receiving the GLU infusion (\( P<0.05 \)).

3.3. Posture changes

Before 14:00 h, neither the GLU nor the fNSP infusion affected the number of posture changes in both L- and H-sows in comparison with NO infusion (Table 4). In the same period, the fNSP infusion tended to reduce the number of posture changes in comparison with the GLU infusion in L-sows. After 14:00 h, both infusions reduced the number of posture changes in L-sows. In H-sows, only the GLU infusion tended to reduce the number of posture changes. In L-sows, the fNSP infusion reduced the number of posture changes after 14:00 h somewhat more effectively than a glucose infusion (not significant). There was no difference between the number of posture changes shown by L-sows receiving a fNSP infusion and the number of posture changes shown by H-sows receiving a glucose infusion.

4. Discussion

In a previous study it was found that H-sows had more stable blood glucose and insulin levels and a reduced physical activity in comparison with L-sows (De Leeuw et al., 2004). Objective of the present study was to elucidate whether fermentation of fNSP plays a major role in these effects. VFA, that are produced during fermentation, may also provide energy at times when glucose, available for absorption from the intestine is reducing in the interprandial period (Rérat, 1996). Therefore, VFA may spare glucose and prevent interprandial feelings of hunger, as well as the increase in activity that may result from it.

4.1. Cecum-fNSP infusion compared with blood-glucose infusion

One of the hypotheses was that a continuous fNSP infusion in the cecum stabilises blood glucose and insulin levels and reduces physical activity as effectively as a continuous iso-energetic glucose infusion in
the blood. It was assumed that a continuous GLU infusion stabilises glucose and insulin levels and reduces physical activity, as it results in a constant availability of the body’s main energy source. Therefore, the GLU infusion was assumed to be useful as a positive control for the effects of an iso-energetic fNSP infusion. Thus, within animal the effects of energy derived from fNSP (VFA) could be compared with the effects of energy derived from glucose.

Indeed, the GLU infusion did stabilise blood glucose levels (tendency), prevent declines of glucose below basal levels and reduce physical activity in L-sows, compared with NO infusion. The GLU infusion did not stabilise insulin levels in L-sows. This is due to the fact that with NO infusion no drop of insulin below basal levels was observed, in contrast with glucose. With a GLU infusion (tendency), as well as with NO infusion, a raise of insulin levels was observed at 12:00 h. This raise was due to an elevated glucose level at that time.

The fNSP infusion in L-sows was as effective as the GLU infusion, or even somewhat more effective than the GLU infusion in stabilising glucose levels and reducing physical activity (not significant). This may be due to effects of VFA, other than their utilisation for energy. For example, it is known that VFA (mainly acetate), present in the ileum due to colo-ileal reflux, can reduce gastric emptying rate, potentially mediated by peptide tyrosine–tyrosine (PYY; Cuche and Malbert, 1999; Cuche et al., 2000). Therefore, glucose may be available for absorption somewhat more spread over time. Moreover, PYY in humans was shown to reduce appetite (Batterham et al., 2002) and may, therefore, have reduced physical activity.

In contrast with L-sows, in H-sows neither the GLU nor the fNSP infusion affected glucose stability. This could be expected, as glucose levels were already quite stable with NO infusion (De Leeuw et al., 2004; present study). It is remarkable that the fNSP infusion caused an increase in insulin SAD, compared with NO infusion (tendency). Numerically, this was also the case for the GLU infusion, but this was not significant due to a large variation. During the fNSP infusion, a small drop of insulin below basal levels was observed in H-sows at 14:00 h. At the same time, however, the glucose level was significantly higher than the basal level. It is not likely that low insulin levels cause hunger, when glucose levels are high. Both the GLU and the fNSP infusion tended to reduce physical activity (total period), even though glucose and insulin levels were not further stabilised, compared with NO infusion. This indicates that the reduction of physical activity is partly due to an increased energy availability (19.6 MJ per day with infusion versus 15.9 MJ per day without infusion).

4.2. Cecum-fNSP infusion compared with oral fNSP ingestion

In order to separate the effects of fermentation in the distal part of the gut from other possible effects of
fNSP-rich ingredients in the proximal part of the gut (e.g. increased gut fill), L-sows receiving a fNSP infusion were compared with H-sows (orally ingested fNSP) receiving a GLU infusion. We succeeded to infuse amounts of energy (fNSP or GLU), similar to the difference in energy derived from fNSP between the two diets. This was confirmed after fNSP determination in both diets. Therefore, L-sows receiving a fNSP infusion and H-sows receiving a GLU infusion had equal intake of total net energy and energy derived from fNSP.

No differences were observed in stability of glucose and insulin levels and physical activity between L-sows receiving a fNSP infusion and H-sows receiving a GLU infusion. The fNSP infusion in L-sows stabilised glucose levels and reduced physical activity as well as orally ingested fNSP (H-sows). This means that fermentation by itself has the same effect as orally ingested fNSP. This is in agreement with a study of Schrama and Bakker (1999), in which it was shown that physical activity reducing effects of dietary fibre in growing pigs (Schrama et al., 1998) were likely to be due to fermentation and not to bulkiness.

4.3. Basal glucose and insulin levels

In L-sows, the fNSP infusion caused a reduced basal level of glucose, and especially insulin. This is remarkable, especially since in H-sows the fNSP infusion did not reduce basal glucose and insulin levels. The effects of a fNSP infusion, therefore, are quite variable and seem to depend on the source of energy in the diet. Low pre-prandial glucose levels in L-sows during a fNSP infusion may cause hunger. In comparison with the basal level with NO infusion, the basal level during a fNSP infusion was 7% lower in L-sows. In rats and humans, initiation or request of a meal was preceded by a 6–8% (rats; Louis-Sylvestre and Le Magnen, 1980) or 10% (humans; Campfield et al., 1996) decline in glucose level, compared with basal levels. However, the more than 50% pre-prandial (14:00–19:00 h) reduction in the number of posture changes of L-sows during a fNSP infusion may indicate that sows had a reduced feeding motivation in comparison with NO infusion. The availability of energy from VFA may have sufficiently tempered pre-prandial feeding motivation. A feeding motivation test during continuous glucose monitoring may provide more insight into the effect of glucose levels on feeding motivation in sows fed low- or high-fNSP diets.

5. Conclusion

In general, a large variation of results was observed within treatments, which caused differences between treatments not to be highly significant.

The fNSP infusion was as effective, or even somewhat more effective than the GLU infusion in stabilising blood glucose levels in L-sows and reducing physical activity in both L- and H-sows. Insulin stability was less affected by the infusions. Both the GLU and the fNSP infusions prevented the 15% interprandial decline of glucose below basal levels, which was observed in L-sows with NO infusion. Basal levels themselves, however, in L-sows with a fNSP infusion were reduced by 7% in comparison with NO infusion. This lower level did not seem to cause a higher pre-prandial feeding motivation.

As no differences were found in physical activity and stability of glucose levels between L-sows receiving a fNSP infusion and H-sows receiving a GLU infusion, it can be concluded that fermentation (intracceally received fNSP) can achieve the same effect as fermentation plus gut fill (orally ingested fNSP).

Results imply that fermentation does play an important role in the effects of a fNSP-rich diet on physical activity and the stability of glucose levels. In order to confirm the observed results, the study may be repeated with more animals.

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