

BRIEF COMMUNICATION

Relationship Between Feeding, Stereotypies, and Plasma Glucose Concentrations in Food-Restricted and Restrained Sows

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Received 31 August 1992

TERLOUW, E. M. C., A. B. LAWRENCE, J. M. KOOLHAAS AND M. COCKRAM. *Relationship between feeding, stereotypies, and plasma glucose concentrations in food-restricted and restrained sows* PHYSIOL BEHAV 54(1) 189–193, 1993.—Previous work has shown that stereotypies, such as chain manipulation and excessive drinking, only develop in food-restricted sows. Furthermore, once stereotypies have been developed, ingestion of a small meal specifically stimulates the performance of stereotypies. These results suggest that the occurrence of stereotypies may strongly depend on the individual's nutritional status. As glucose is one of the main metabolic fuels, the present experiment investigated whether individual differences and/or daily variations in levels of chain manipulation and excessive drinking are correlated to individual differences and/or daily variations in pre- or postfeeding glucose concentrations. Blood samples were taken at regular intervals prior to, during, and after feeding, from sows that had developed stereotypies to different degrees over a period of 110 days of restrictive housing and feeding conditions. Glucose concentrations were low prior to and high after feeding. Levels of stereotypies showed similar variations, suggesting that the performance of stereotypies is not related to low glucose concentrations. Furthermore, whilst sows differed consistently in glucose concentrations, no correlations were found between individual glucose concentrations and stereotypies. Similarly, no correlations were found between glucose concentrations and chain manipulation or drinking on a sample to sample basis. These data show that although performance of stereotypies is strongly dependent on feeding regime, it is not related to plasma glucose concentrations.

Sows	Pigs	Food restriction	Stereotypies	Chain manipulation	Excessive drinking	Polydipsia
Feeding	Glucose	Hypoglycemia	Individual differences			

STEREOTYPIC behaviour has been defined as the repeated performance of motor patterns that are relatively fixed in form and orientation and that serve no obvious function [(14,19); for a recent review see (18)]. Sows that are food restricted and kept individually confined or tethered to a stall often show a variety of stereotypies, such as oral manipulation of the tether chain, bar-biting, weaving, vacuum chewing, and excessive drinking (3,8,25).

Previous work on sows in restrictive environments has reported that stereotypies only developed in food-restricted sows, indicating that restrictive feeding is a necessary condition for

the development of stereotypies in sows (3,25). Furthermore, ingestion of a meal that is insufficient to induce satiation specifically stimulates the performance of stereotypies (29). These results suggest that the occurrence of stereotypies may depend on the individual's nutritional status. As even under similar conditions sows show large individual variation in the amount and type of stereotypy they perform (3,26,27), these individual differences may be partly related to differences in nutritional status before or after feeding time. Blood glucose is one of the major metabolic fuels [see (15) for a review] and plays a role in the regulation of feeding behaviour; for example, in ad lib- fed

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rats, meal initiation is preceded by hypoglycemia, and can be delayed by reversal of the hypoglycemic state by injection with glucose (7,16,21). The present study was carried out on a group of food-restricted sows, receiving one meal a day, and having established stereotypies, consisting mainly of chain manipulation and drinking (27). The aim was to investigate the possible role of nutritional status in the development of stereotypies by analyzing the relationship between the performance of these two activities and pre- and postfeeding glucose concentrations. In addition, to investigate whether the performance of chain manipulation affects glucose levels, the effect of chain removal on glucose levels was assessed.

METHOD

This study was part of a larger experiment that investigated the relationship between various blood parameters and chain manipulation and drinking. The relationship between plasma cortisol, chain manipulation, and drinking in this group of pigs has been described previously (27).

Animals and Housing

The subjects were fifteen 15-month-old primiparous sows (Large White \times Landrace; Cotswold Pig Development Co., Ltd., UK), weighing 200–240 kg. They had been food restricted and restrained by neck tethers in stalls in the experimental room for a total period of 110 days, after which the experiment started. Permanent indwelling jugular catheters (polyvinyl; o.d.: 2.0 mm, i.d.: 1.5 mm; company) were preplaced under general anaesthesia induced with a mixture of Azaperone (Janssen Pharm Ltd., Oxford, UK) and Metomidate (Janssen Pharm Ltd., Oxford, UK) 1 week prior to the experiment [for further details, see (27)].

The experimental room was a 8×7 m climate controlled room ($21 \pm 2^\circ\text{C}$), containing two rows of nine 70 cm wide stalls with vertical bars, facing each other on either side of a passage. Each stall had a metal trough at the front with a nipple drinker at one corner. In one of the front corners of each pen an extra chain was hanging down with its lower end attached to the side of the pen, forming a loop of 10 cm. The pigs were tethered to a front corner of the stall with a neck tether and a 65 cm chain. They were kept on rubber mats.

At 0945 h each morning a stockworker came in to switch on the lights and to feed the pigs, delivering 2.5 kg of a standard pelleted sow food into each trough. Water was available continuously. No daylight could penetrate in the room. Lights went off automatically at 2100 h. Cleaning was carried out daily between 1300 and 1330 h.

Behavioural Recording

Time spent in chain manipulation and amount of water drunk were automatically recorded for each individual pig. The automatic recording system for chain manipulation and drinking has been described in detail by Terlouw et al. (27). Briefly, the extra chain was attached to a strip of piezo electric wire (Quantalec Ltd., Witney, Oxon, UK), which registered movements of the chain via electric pulses. These were stored by digital counters and read by a BBC Master microcomputer. The system was calibrated such that number of pulses produced by chain manipulation correlated with the time spent manipulating the chain. All pigs preferred manipulating the extra chain to manipulating the tether chain.

A water flow meter (Farnell, Electr. Comp., Leeds, UK) was fitted above each nipple drinker. Electric pulses generated from

the water flow meter by use of the drinker were stored and read as above. The amount of water recorded as taken from the drinker was corrected for the water remaining in the trough every 24-h period. With one exception, water left in the trough was generally low (<1.5 litre/day).

The BBC data logging system recorded time spent in chain activity (minutes) and amount of water drunk (ml) over 10-min intervals.

Experimental Procedure

Twenty minutes before blood sampling commenced, a 300 cm silastic extension (Rubber, Hilversum, The Netherlands; i.d. 1 mm, o.d. 3 mm) was fitted to each catheter, such that blood sampling could take place from behind the animal to reduce disturbance. Thirteen 5 ml samples were taken at 20-min intervals between 0840 (80 min before feeding) and 1200 h; two additional samples were taken at 1500 and 1800 h, respectively. Blood was collected in heparinized tubes; subsequent storage, spinning, and pipetting took place at 4°C . The plasma was stored at -20°C until assaying.

The experiment took place over a period of 19 days. Blood samples were taken on days 1, 2, 4, 5, 8, 12, 15, and 19. Glucose concentrations were assessed for all days except day 1. To assess the effect of performance of stereotypies on glucose concentrations, chains were removed from 0945 on day 4, until 0945 on day 5 (this period will be further referred to as day 4) and between 0945 h on day 7 until 1900 h on day 14. In addition, water was made unavailable from the drinkers between 0945 and 1900 h on day 4 and instead provided in the trough by hand, in order to prevent possible substitution of chain manipulation by drinker manipulation. Behavioural recordings were based on 24-h periods. Chain manipulation was recorded on all days that the chain was present. Similarly, drinking was recorded on all days, with the exception of day 4.

Blood glucose was measured by the ferricyanide method of Hoffman (Technicon autoanalyser TM II).

Statistical Analysis

The catheter of one sow became blocked, and another sow filled the trough without ingesting the water; these individuals were, therefore, excluded from the glucose analysis and the analysis of drinking levels, respectively. All analyses were based on square root transformations of the data. Linear correlation coefficients based on average daily, and prefeeding and postfeeding individual glucose concentrations were calculated in order to estimate consistency of individuals compared to other group members. The effect of chain removal was estimated separately for glucose concentrations before and after feeding using an analysis of variance for repeated measures with nested structures for pig, and for pig \times chain presence or absence (to assess the factor chain presence or absence). Day and sample effects were estimated separately for days with and without chain using an analysis of variance for repeated measures with nested structures pig, pig \times day (to assess factor day), pig \times sample (to assess factor sample), and pig \times day \times sample (to assess day \times sample interactions). Levels of chain manipulation and drinking preceding and following each blood sample were fitted as a covariate in this analysis, and assessed on the pig \times day \times sample level, to study the direct relationship between behaviour and glucose concentrations. The same analysis was repeated while fitting previously reported cortisol levels as a covariate [see (27)], to study whether glucose and cortisol levels were correlated. Where

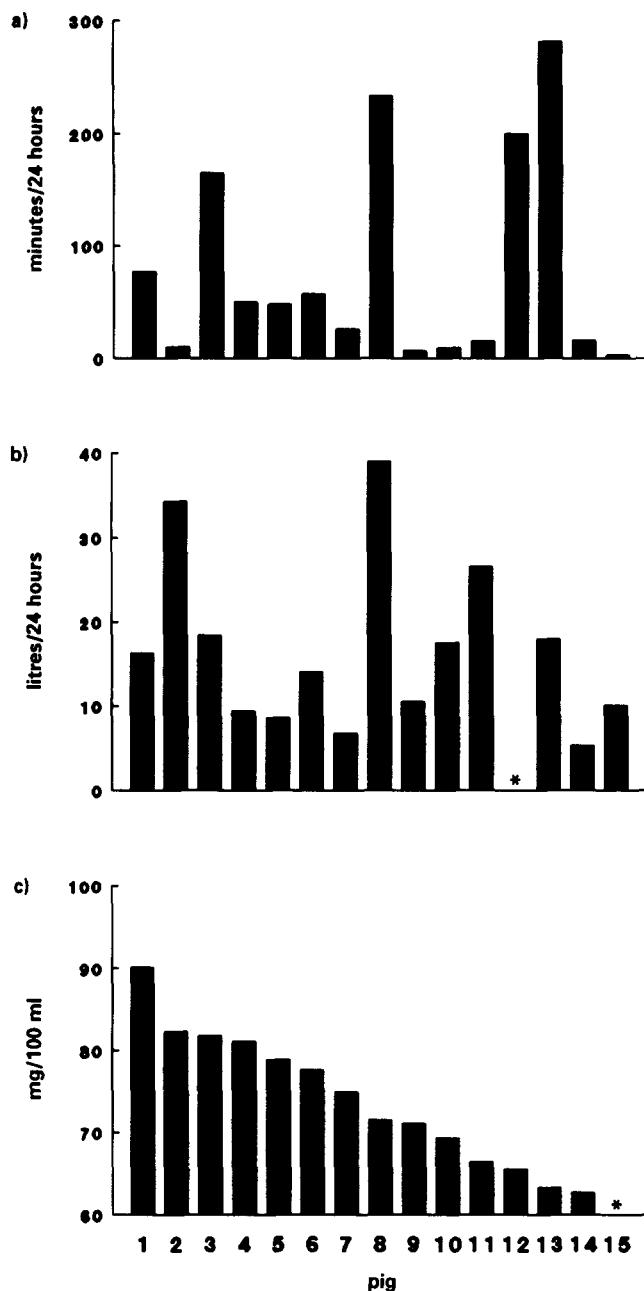


FIG. 1. Individual levels of total time spent in: (a) chain manipulation; (b) total amount drunk; and (c) average glucose concentration ($n = 15$ samples/pig), on day 2.

significant effects were found the least significant difference test was carried out to study where differences were largest.

Finally, linear correlations between total (square root transformed) postfeeding drinking and chain manipulation, and the absolute and relative increase in glucose after the meal were calculated. Postfeeding drinking and chain manipulation were based on levels between 1000 and 1600 h. Average glucose concentrations between 0845 and 1020 h (prefeeding low), and between 1020 h and 1050 h (postfeeding high) were used to calculate the absolute and relative increase in glucose concentrations.

RESULTS

Behaviour

The pigs finished their meal in approximately 10 min. Chain manipulation and drinking were generally low before the meal, but showed a significant increase after the meal [see (27)]. There were large individual differences in chain manipulation and drinking (see Fig. 1), but individuals were consistent relative to other group members, as shown by positive correlations between days (e.g., day 1 vs. day 2: $r = 0.85$; $p < 0.01$ and $r = 0.996$; $p < 0.01$ for chain manipulation and drinking respectively).

Glucose

Average glucose concentrations also varied across individuals, but these individual differences were not related to individual differences in behaviour (Fig. 1). Again, individual differences were consistent across days, as average individual levels were positively correlated to each other across days (e.g., first vs. last day: $r = 0.85$; $p < 0.01$), as well as within days (e.g., average prefeeding (sample 1–6) vs. postfeeding (sample 7–9) levels: $r = 0.78$; $p < 0.01$).

There was a sample effect on days with and without chain [e.g., days with chain: $F(14, 700) = 33.59$, $p < 0.001$], with in both situations lowest levels occurring before the meal (e.g., glucose concentration at 60 min prefeeding vs. 2 h postfeeding: LSD: $p < 0.001$ for days with chain present; see Fig. 2), whilst highest daily levels were reached between 30 and 60 min after food delivery (e.g., glucose concentration at 40 min vs. 5 h postfeeding LSD: $p < 0.001$ for days with chain present; Fig. 2).

Average glucose levels did not differ between days with the chain present, $F(4, 37) = 1.12$, NS; average value: 74.5 mg/100 ml. This was in contrast to days that the chain was removed, $F(2, 26) = 5.18$, $p < 0.05$, owing to significantly higher levels on day 8 (74.5, 79.2, and 76.1 mg/100 ml for days 4, 8, and 12, respectively; LSD: $p < 0.05$). Both pre- and postmeal glucose concentrations tended to be slightly higher on days without the chain [premeal: 70.3 vs. 74.0 mg/100 ml: $F(1, 13) = 10.8$, $p < 0.01$; and postmeal: 75.4 vs. 77.8 mg/100 ml: $F(1, 13) = 4.32$, $p = 0.06$]. Fitting chain manipulation or drinking as covariates in the analysis revealed, however, no significant correlations be-

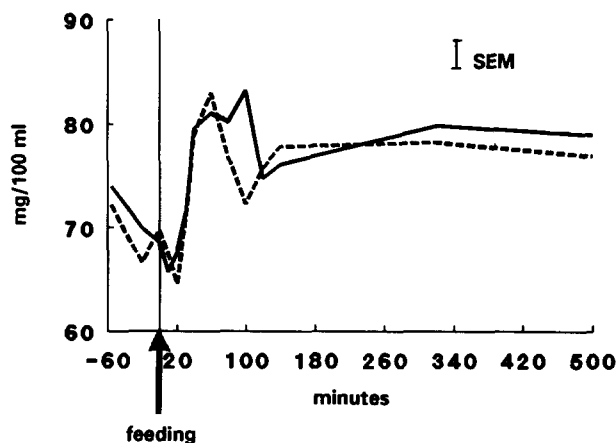


FIG. 2. Mean variation in glucose concentrations before and after feeding for pigs with levels of chain manipulation below (—; $n = 7$), and above (----; $n = 7$) the group median, on days with a chain present. No significant correlations were found between level of chain manipulation and plasma glucose concentrations.

tween postfeeding glucose concentrations and amount of chain manipulation preceding or following the blood sample [e.g., on a sample to sample level. $F(1, 383) = 2.44$, NS and $F(1, 383) = 2.48$, NS, for chain manipulation preceding and following the blood sample, respectively]. A similar lack of correlation was found in the prefeeding period [e.g., chain manipulation following the blood sample: $F(1, 143) = 0.85$, NS]. Similarly, no correlations were found between drinking and postfeeding glucose concentrations [e.g., drinking following the blood sample: $F(1, 383) = 2.40$, NS] or prefeeding glucose concentrations [e.g., drinking following the blood sample: $F(1, 143) = 0.03$, NS]. Finally, the absolute or relative increases in glucose concentrations after ingestion of the meal were also not correlated to subsequent chain manipulation and drinking on any day (e.g., day 2: $r = 0.08$, NS and $r = 0.14$, NS for chain manipulation vs. the absolute and relative increase in glucose concentrations, respectively).

Individuals' average glucose concentrations were also not correlated to individuals' average cortisol concentrations [e.g., for days with chains present: $F(1, 12) = 2.09$, NS]. No significant correlations between glucose and cortisol were found on a sample to sample level [e.g., days that the chain was present: $F(1, 699) = 2.04$, NS].

DISCUSSION

Previous work found that food-restricted sows kept under similar conditions show large individual differences in level and type of stereotypy (3,26,27). Furthermore, the ingestion of a meal that is insufficient to induce satiation stimulates the performance of stereotypies in food-restricted sows (29). The present study aimed to investigate whether performance of stereotypies is related to plasma glucose concentrations.

The results show that in long term (4 months) food-restricted and confined sows, prior to, and during feeding glucose concentrations were low, whilst the highest glucose concentrations were reached between 20 and 50 min after finishing the meal. A delayed postfeeding rise in blood glucose concentrations has similarly been found in studies on pigs and other species [e.g., (4,30)]. Levels of stereotypies showed, similar to glucose concentrations, low levels before and high levels after the meal, suggesting that performance of stereotypies was not related to hypoglycemia. Analysis at an interindividual level also showed that the sows showed consistent differences in both glucose concentrations and level of chain manipulation and drinking. These differences were, however, not related (see also Fig. 1); for example, individual differences in relative or absolute changes in plasma glucose concentrations due to food intake were not correlated to individual differences in behaviour. Furthermore, at an intraindividual level, chain manipulation and drinking, whether preceding or following the blood sample, were not related to glucose concentrations. This confirms that glucose concentrations did not affect performance of these activities, and that vice versa, performance of these behaviours did not affect glucose concentrations, despite the finding that pre- and postmeal glucose concentrations were slightly higher during chain removal.

The lack of correlation between glucose concentrations and postfeeding stereotypies may indicate that other effects of food intake are related to stereotypies. These may be metabolic effects, such as changes in plasma amino acid concentrations (20), or changes in endocrine factors, such as insulin and glucagon [see (12) for a review]. Although there is ample evidence that changes in plasma parameters, including glucose, can alter neuronal ac-

tivity [e.g., (23)], there is also evidence that feeding behaviour itself directly changes neuronal activity, for example, feeding, sham feeding, and feeding-related cues specifically increase dopaminergic and noradrenergic activity in various brain areas such as the hypothalamus, the nucleus accumbens, and the striatum (6,13,17,22). As these areas may also be involved in stereotypies (2,9,11,24,28), direct feeding-induced neuronal changes may explain the stimulatory effects of the ingestion of food on stereotypies (29).

The present work found sows to differ consistently within and across days in plasma glucose concentrations, in contrast to their cortisol concentrations (27). Accordingly, glucose concentrations were not correlated to cortisol concentrations. In a previous report on pigs it was suggested that cortisol concentrations affect those of glucose (5). However there was little evidence in this work to suggest that these two effects were causally related, as it was only found that restrictive housing was accompanied by increased concentrations of both glucose and cortisol concentrations, and no within-housing system correlational analysis was reported. Other factors that influence glucose levels (12), such as insulin and glucagon must, therefore, be related to the consistent individual differences in glucose levels.

Plasma glucose concentrations were low prior to the meal. It is often suggested that meal-fed rats show a prefeeding anticipatory hypoglycemic response [e.g., (15)], mainly based on the observation that in rats gustatory and olfactory stimuli, previously paired with intragastric glucose infusions, can become conditioned stimuli for a hypoglycemic response (10). To our knowledge, however, there is only indirect evidence to suggest that nonfood-related stimuli (e.g., auditory cues) can be conditioned to evoke a premeal hypoglycemic response; although nonfood-related stimuli have been found to induce a premeal anticipatory increase in insulin, glucose concentrations have not been reported (32–34). The present finding that the lowest daily glucose levels were found prior to the meal does suggest, however, that an anticipatory hypoglycemic response may take place in meal-fed sows, starting as early as 1 h before the meal. This is further supported by another study, where pigs receiving a meal in the morning and in the afternoon also showed significantly lower levels before each meal than at other times of day (1). Whilst in our study fitting of the extensions to the catheters may have formed a cue related to food delivery, an anticipatory hypoglycemic response before food delivery may be a general phenomenon in meal-fed sows; for example auditory cues may become the conditioned stimulus for imminent food delivery. It is further possible that time of day can become a conditioned stimulus for the hypoglycemic response, as was found for the anticipatory insulin response in schedule-fed rats (34).

Summarizing, although development of stereotypies in sows is critically dependent on food restriction (3,25), and feeding specifically stimulates stereotypies (29), performance of stereotypies is not related to plasma glucose concentrations. Further research is needed to investigate the physiological mechanisms underlying the stimulatory effects of feeding on the performance of stereotypies, and the premeal hypoglycemia found in the present study.

ACKNOWLEDGEMENTS

The authors wish to express their thanks to A. MacAndrew for taking care of the animals, B. Nielsen, and J. Whittemore for helping to collect the data, J. Bruggink and G. Bouws for assaying the plasma samples, Dr. G. Horgan for statistical advice, and Drs. J. S. Strubbe and I. Kyziazakis for comments on an earlier version of this manuscript.

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