Effect of a long-term exposure to concentrated sucrose and maltodextrin solutions on the preference, appetence, feed intake and growth performance of post-weaned piglets

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Abstract

Commercial pigs display an innate attraction for sweet taste compounds. However, the impact of long-term availability to supplementary carbohydrate solutions on their general feeding behaviour has not been examined. In this work we assess the effect of 12-days exposure to 16% sucrose and 16% maltodextrin solutions on the feed intake and growth performance of piglets, and on their preference and appetence for sweet or protein solutions. The innate preference of piglets was assessed by an initial choice test between 2% sucrose and 2% animal plasma solutions for a period of three minutes. Piglets showed higher intake and preference for 2% sucrose than for 2% animal plasma. In Experiment 1, piglets were then free-offered a 16% sucrose solution as a supplement to the diet, showing a higher intake of it than water and a reduction in feed intake and weight gain. A similar situation occurred during the last days of free-exposure to a 16% maltodextrin solution in Experiment 2. The choice test between 2% sucrose and 2% animal plasma solution was repeated after the exposure to the concentrated solutions. In both experiments, a reduction in the initial preference for 2% sucrose was observed. Similarly, piglets that had previous access to the 16% sucrose and 16% maltodextrin solutions showed a decrease in the appetence for 2% sucrose in comparison with that for 2% animal plasma, as measured by a one-pan test at the end of the experiments. It is concluded that long-term exposure to concentrated sucrose and maltodextrin solutions reduces feed intake and growth in weanling piglets, and also reverses their innate preference and appetence for dilute sweet over protein solutions.

Keywords: Carbohydrate solution; Growth performance; Maltodextrin; Pig; Preference; Sucrose

1. Introduction

The omnivorous diet of the pig in wild conditions shares significant similarities with human dietary habits not seen in other omnivorous species, such as the rat or the mouse [1]. Dietary preferences are intimately linked to taste perception mechanisms, which are also shared and similar between pigs and humans [2]. Among the currently accepted basic tastes, sweet and umami compounds are strongly pleasurable for pigs. Sugars, including different types of carbohydrates, polyols and sweeteners, are recognized by the T1R2/T1R3 heterodimeric receptor into the oral cavity and gastrointestinal tract of pigs [3,4]. Pigs show an innate attraction and preference for solutions of sucrose, glucose, lactose and sodium saccharin when compared in short-term preference tests against water [5,6]. The attraction is similar to that showed by humans, reflecting a trait that has probably evolved through years to signal highly caloric carbohydrate-rich nutrients [7]. From Glaser et al. (2000), it is known that sucrose and fructose response intensities are identical in both species, sucrose being the most strongly preferred carbohydrate for pigs [8]. These compounds added in-feed at levels of around 50 g/kg also increased feed intake and weight gain of weanling animals [9]. However, there is no conclusive literature concerning how and in which intensity pigs sense other oligosaccharides or more complex carbohydrates, such as maltodextrin. In a recent study [10], Roura et al. (2013) showed that the hedonic intensity of maltodextrin solutions in pigs is lower than that reported for sucrose, because the preference threshold for maltodextrin (3%) was higher than that for sucrose (0.5% - 1%) when tested against plain water. This is potentially important because humans report far lower taste intensities for maltodextrin solutions than for sugar solutions [11]. This is in stark contrast to rats which show a preference for maltodextrin over sucrose-solutions at low concentrations and also detect maltodextrin at lower concentrations than sucrose [12].

Kennedy and Baldwin (1972) observed in a 12-hour choice test against water that young pigs showed increases in sucrose solution intake of concentrations of approximately 0.3% to 7.7% with concomitant decreases in water intake – but there was no assessment of sucrose availability on feed

intake [13]. Since that study, no other report has evaluated the possible effects of a long-term availability to a highly hedonic and more concentrated supplementary carbohydrate solution on the feeding behaviour of pigs. In humans, there is a general concern about the detrimental impact on public health of a long-term consumption of caloric drinks [14–16]. This phenomenon has been well studied in laboratory rodents. Thus, when offered a highly palatable 32% sucrose solution as a supplement to their nutritionally complete diet, adult rats overeat and gain excessive weight, which has been described as obesity by choice [17–19]. In the present work, in order to further explore the hedonic motivation of piglets we used a concentrated sucrose solution (16%, Experiment 1) to expose the animals with a highly hedonic sweet compound which also has considerable caloric post-ingestive effects. The aim was to assess whether a long-term exposure (12 days) might alter feed intake and growth of piglets, as well as modify their preference and appetence for sweet (2% sucrose) and protein (2% animal plasma) solutions. Subsequently, in order to discriminate between the influence of sweetness and the contribution of the caloric load on the response, a low dextrose equivalent 16% maltodextrin solution was used (Experiment 2). It was hypothesized that, similar to rodents, pigs may show a high-affinity pattern towards a palatable solution if it is freely offered as a supplement to the diet, based on their innate attraction with sweet taste compounds. In addition, the long-term exposure to solutions that are hedonically preferred to the growing feed may have a negative effect on the feed intake of the animals, and may also reduce their preference for less hedonically valuable low-concentration sweet solutions as compared to protein solutions.

2. Material and methods

All procedures described in this study were conducted at the animal research facilities of the Universitat Autònoma de Barcelona (UAB). Experimental procedures were approved by the Ethical Committee on Animal Experimentation of the UAB (CEAAH 1406).

2.1. Animals, diets and housing

In total, 108 male and female piglets (Pietrain × [Landrace × Large White]) from 14 to 35 days post-weaning were selected to be used in three experiments, with 36 piglets in each.

During lactation, piglets were supplemented with a milk replacer feed from 10 days of age until weaning in order to familiarize the animals with solid feed as early as possible. Then, piglets were weaned at 28 days of age. In Experiments 1 and 2, at the beginning of the starter period on Day 14 after weaning piglets were distributed according to their body weight and were further allocated into 12 pens of three piglets per pen. In Experiment 3, on Day 35 after weaning piglets were similarly allocated into 12 pens of three piglets per pen. In all experiments, piglets were fed a single, commercial starter diet (Table 1) formulated to provide a complete and equilibrated nutrient content in order to maximize growth potential of animals, according to NRC [20]. This diet was offered ad libitum in mash form.

The weaning room had automatic, forced ventilation and completely slatted flooring. Each pen (3.2 m^2 in floor area) was equipped with a feeder with three feeding spaces and an independent and automatic water supply to ensure ad libitum feeding and freshwater access.

2.2. Experimental designs

2.2.1. Experiments 1 and 2: Long-term solution exposure in piglets

These experiments were designed to evaluate the effect of a long-term free availability of an extra sucrose or maltodextrin solution on the preference and appetence of piglets for sweet and protein solutions, and also on their feed intake and growth performance. The experimental design included an initial choice test on Day 14 after weaning, an ad libitum solution exposure period from Days 14 to 26 during which feed intake and growth were recorded, a final choice test on Day 26, and one-pan test on Days 27 and 28 after weaning.

2.2.1.1. Initial and final choice test

During the first two weeks after weaning, piglets were familiarized to the weanling room and pre-trained with two pans containing 800 mL of tap-water in each pen for 30 minutes. The preference of piglets for sweet or protein water-based solutions was assessed at the beginning of the experimental period (Day 14 after weaning) by using a single choice test for 3 minutes. This test was also repeated at the end of the experimental period (Day 26 after weaning). The test was performed for the 3 piglets of each pen, with 2 pans placed in the front of the pens containing 800 mL of either 2% of porcine animal plasma (AP820, APC; Ankeny, USA) as protein solution (0.014 g crude protein, 0.324 kJ digestible energy/mL) or 2% of commercial sucrose as carbohydrate solution (0.335 kJ digestible energy/mL). The rationale was to study whether pigs may adapt their dietary preference for protein or carbohydrate solutions depending on the nutritional status, in this case, after the long-term exposure to the supplementary solutions. Porcine animal plasma is a high-quality protein source commonly used in swine diets (700 g crude protein, 16213 kJ digestible energy/kg), composed of albumin and globulin proteins. Its amino acid composition mainly contains a great amount of glutamic acid (10.5%) which is the main substance eliciting umami taste, in addition to aspartic acid (7.1%), leucine (7.0%), lysine (6.1%), valine (4.8%) and threonine (4.3%). To control for side preference during tests, solution position inside the pen was counterbalanced between pens, i.e., the protein solution was offered on the left side of the pen and the carbohydrate solution on the right side for half the pens and vice versa.

2.2.1.2. Ad libitum solution exposure

Pens were randomly assigned to a control or experimental group after the initial choice test, and each one was provided with an extra container with a total capacity of 5 L placed on the middle of the pen as a supplement to the diet and normal water supply. As stated before, each pen was equipped with an automatic supply that provided ad libitum freshwater access to the animals. Thus, the control group (six pens) was provided with an extra supply of tap-water, while the experimental group (six pens) was provided with one of the carbohydrate solutions used for 12 consecutive days.

During this period, containers were regularly checked and refilled at least daily in order to provide an ad libitum exposure to the additional solutions.

In Experiment 1, 16% of commercial sucrose was offered to the piglets in order to expose them to a highly hedonic sweet solution which also provides considerable caloric post-ingestive effects (2.678 kJ digestible energy/mL). The same concentration, 16%, of spray-dried maltodextrin (C*Dry MD 01910, Cargill Inc.; Minneapolis, USA) was supplied to the animals in experimental group in Experiment 2. The maltodextrin product used had a low dextrose equivalent value (12 to 16), providing similar caloric effects than those of the 16% sucrose solution (2.678 kJ digestible energy /mL) without the same hedonic effects of the sweet taste of a similarly concentrated sucrose solution. Therefore, maltodextrin solution focuses on the post-ingestive effects of that solution.

Animals were individually weighed in each experiment on Days 14, 21 and 26 after weaning, and the depletion from the feeders was also monitored on the same days in order to calculate the average daily feed intake, average daily gain and energy:gain ratio of piglets during these experimental periods. It was not possible to have a measure of the group water consumption from the normal supply in each pen.

2.2.1.3. One-pan test

The appetence of piglets for the sweet and protein solutions was assessed after the ad libitum period, and the final preference test, in the control and experimental group of each experiment by using a one-pan test, over two consecutive days. A single pan containing 800 mL of the 2% animal plasma or the 2% sucrose solutions was offered to the piglets for 3 minutes each day. The order of testing first the protein or carbohydrate solutions on Days 27 or 28 after weaning was counterbalanced across pens of each group.

2.2.2. Experiment 3: Piglets innate preference for carbohydrate solutions

Experiment 3 was conducted in order to better understand the innate preference values of piglets for the solutions used in Experiments 1 and 2 (16% sucrose and 16% maltodextrin) when tested against 2% sucrose solution as reference.

Naive piglets were fed the same commercial starter diet than in prior experiments and had no previous contact with any additional solution or related flavour all across the nursery period in this experiment. On Day 35 after weaning, the three piglets of each pen were offered two pans placed in the front of the pens containing 800 mL of the solutions tested for three minutes, in a single choice test procedure as described for the previous experiments. Two comparisons were conducted, with six randomly assigned pens for each: (i) 16% sucrose vs. 2% sucrose, and (ii) 16% maltodextrin vs. 2% sucrose. Piglets were individually weighed after finishing the choice test.

2.3. Calculations and statistical analysis

Solution intakes measured for each pen during the choice and one-pan test were averaged for the number of piglets that performed each test (3 piglets), and were standardized to the different weights of the animals in each group and experiment by dividing by the registered body weight on the test days. The standardization aimed to make the solution intake registered for animals with different body weight comparable; therefore, it diminishes differences in consumption due to different ingestive capacities of the animals.

Choice-test data were analyzed for the initial and final tests separately with a two-way ANOVA by using the GLM procedure of SAS (version 9.2, SAS Institute; Cary, USA), taking into account a within-subject factor of solution (2% animal plasma vs. 2% sucrose), a between-subject manipulation of solution exposure (control, water vs. experimental, 16% sucrose/16% maltodextrin), and their interaction as main factors (only included when significant). The pen of three piglets was considered the experimental unit. The same statistical model was used for the analysis of one-pan test data. Preference values for the protein solution in the initial and final choice test of Experiments 1 and 2; and for 16% sucrose and 16% maltodextrin solutions in Experiment 3

were measured as the percentage that each target solution comprised of the total fluid intake and were compared between each treatment and test (Experiments 1 and 2) and to the neutral value of 50% of preference (Experiment 3) by using a Student's *t*-test.

Solution intakes from the extra container during the 12-day ad libitum period were monitored daily in order to establish a net balance of energy intake per kg of body weight. Intake values were averaged for the number of piglets that consumed them, and their contribution on the daily energy intake of piglets was considered. These data, as well as feed intake and growth performance data (body weight, weight gain and energy:gain ratio) were analyzed with a one-way ANOVA considering the exposure to water or the experimental solutions as the main factor, by using the GLM procedure of SAS. For all of the analysis, average values were compared by least-squares means with the Tukey adjustment for multiple comparisons. The alpha level used for the determination of significance was 0.05, and tendencies for $0.05<P<0.1$ are also presented.

3. Results

3.1. Experiments 1 and 2

3.1.1. Ad libitum solution exposure

The effect of a 12-day free availability of an extra 16% sucrose (Experiment 1) and 16% maltodextrin (Experiment 2) solution on the solution intake, feed intake and growth performance of piglets in periods Days 1 to 7 and Days 7 to 12 is shown in Tables 2 and 3, respectively. Piglets with free access to the 16% sucrose solution showed a higher intake of it in comparison with water intake of piglets in the control group during the period Days 1 to 7 [$F(1,10)=7.74$, $P=0.019$]. A lower feed intake and body weight was registered in piglets with access to the 16% sucrose solution during the periods Days 1 to 7 [$F(1,10)=19.01$, $P=0.001$ and $F(1,34)=8.19$, $P=0.007$ for feed intake and body weight, respectively] and Days 7 to 12 [$F(1,10)=15.06$, $P=0.003$ and $F(1,34)=8.03$, $P=0.008$ for feed intake and body weight, respectively]. Accordingly, a lower weight gain was observed in this group of animals during the period Days 1 to 7 [$F(1,34)=19.79$, $P<0.001$]. When

considering the total of energy ingested by both feed and solution, piglets supplemented with the carbohydrate solution showed a less efficient conversion of energy into body weight as observed by a higher energy:gain ratio in period Days 1 to 7 [$F(1,9)=31.48$, $P<0.001$] and a trend to a higher ratio in Days 7 to 12 [$F(1,10)=4.87$, $P=0.052$], as compared than those of control pigs.

Piglets with free access to the 16% maltodextrin solution showed no significantly higher intake of this solution in comparison with water intake of piglets in the control group during periods Days 1 to 7 [$F(1,10)=0.26$, $P=0.624$] and Days 7 to 12 [$F(1,10)=1.11$, $P=0.317$]. Nevertheless, a numerical increase of 25% in maltodextrin solution consumption was observed during the period Days 7 to 12. A lower feed intake [$F(1,10)=10.65$, $P=0.009$] and energy intake due to feed consumption [$F(1,10)=10.65$, $P=0.009$] was registered in those animals supplemented with the carbohydrate solution during the period Days 7 to 12, without significant differences in the body weight between both groups of piglets after the solution exposure, all over the experiment [$F(1,34)=0.85$, $P>0.364$]. Nonetheless, the weight gain of maltodextrin piglets was lower than that of control piglets during the period Days 7 to 12 [$F(1,34)=7.23$, $P=0.011$], affecting the way that animals convert energy into weight gain as observed by a higher energy:gain ratio in this period [$F(1,10)=11.36$, $P=0.007$].

3.1.2. Initial and final choice test

Figure 1 shows a summary of consumption in the preference tests before and after the free access to the additional solutions in Experiments 1 and 2. In these, a higher intake and preference for the 2% sucrose solution in comparison with the 2% animal plasma solution was observed in the initial choice test conducted at the beginning of the experimental period [$F(2,21)=5.05$, $P=0.005$ in Experiment 1; and $F(2,15)=7.05$, $P=0.016$ in Experiment 2]. Subsequently, after receiving an extra supply of water for 12 days, piglets in control groups, in general, maintained their solution selection pattern despite the fact that no significantly different intakes were observed in the final choice test at the end of the experimental period in these animals. Importantly, the preference values observed for the 2% animal plasma solution were not significantly different with those observed at the onset

of the experiments in the initial choice test, i.e., 37% vs. 27% in Experiment 1 [t=1.07, df=16, P=0.299], and 37% vs. 29% in Experiment 2 [t=0.72, df=13, P=0.483].

In Experiment 1 (Figure 1(a)), a significant interaction among the within-subject factor of test solution type and the between-subject factor of solution exposure was observed [F(3,20)=2.69, P=0.019]. Piglets offered the 16% sucrose solution for 12 consecutive days showed a significant higher intake of 2% animal plasma solution in comparison with animals in control group previously exposed to water [F(1,10)=5.22, P=0.046]. The intake of the protein solution also tended to be higher than the intake of 2% sucrose solution in the final choice test of piglets pre-offered the highly concentrated carbohydrate solution [F(1,10)=3.60, P=0.087]. In addition, the 2% animal plasma preference of 64% was significantly different from the 37% of protein preference showed by the animals in the control group [t=-2.27, df=10, P=0.047] and the 27% of preference displayed in the initial choice test [t=3.47, df=16, P=0.003].

In Experiment 2 (Figure 1(b)), a similar interaction than that in Experiment 1 between test solution type and solution exposure was observed [F(3,18)=2.23, P=0.030]. A tendency towards a higher intake of 2% animal plasma solution was observed in piglets which had previously been offered free access to the 16% maltodextrin solution, in comparison with piglets in control group [F(1,9)=3.34, P=0.101]. The protein solution consumption in the final choice test of maltodextrin piglets was also significantly higher than that of 2% sucrose solution [F(1,8)=5.85, P=0.042]. The preference for the protein solution was 68% in this case and was significantly different from the 37% of protein preference showed by piglets in the control group [t=-2.27, df=9, P=0.050] and the 29% of preference in the initial choice test [t=3.43, df=12, P=0.005].

3.1.3. One-pan test

The appetence of piglets for 2% animal plasma and 2% sucrose solutions in the control and experimental groups in both experiments is shown in Figure 2. After receiving only the extra supply of water, piglets in the control groups in Experiments 1 and 2 exhibited a higher appetence for the

2% sucrose than for the 2% animal plasma solution, as measured by the one-pan access during two alternate days [$F(1,34)=6.52$, $P=0.015$]. In contrast, no significant differences in appetence for the protein or carbohydrate sources were observed in the experimental groups after the 12-day exposure to their respective experimental solutions [$F(1,10)=2.90$, $P>0.120$]. However, it is important to note that a significant interaction [$F(3,20)=1.85$, $P=0.033$] and a tendency to the same interaction [$F(3,20)=0.99$, $P=0.107$] between test solution type and solution exposure were observed in Experiments 1 and 2, respectively. Thus, piglets long-term offered 16% sucrose and 16% maltodextrin solutions numerically reversed the consumption pattern observed in control groups. In fact, a tendency to a higher appetence for 2% animal plasma solution was observed after the exposure to 16% sucrose when compared with the protein appetence of piglets in control groups [$F(7,64)=2.40$, $P=0.051$].

3.2. Experiment 3

Figure 3 shows the results of the two comparisons conducted in this experiment. In the first, naive piglets showed a higher intake of 16% sucrose than of 2% sucrose solution [$F(1,8)=8.06$, $P=0.022$; Figure 3(a)]. Indeed, the 66% preference observed for 16% sucrose solution was significantly higher than the neutral value of 50% [$t=3.79$, $df=4$, $P=0.019$]. In the second comparison, a statistical tendency towards higher intake of 2% sucrose was observed when it was tested against 16% maltodextrin solution [$F(1,10)=4.07$, $P=0.071$; Figure 3(b)]. The 27% preference for 16% maltodextrin displays no evidence that concentrated maltodextrin has a more preferred taste to 2% sucrose, indeed there was a trend for the ratio to be below the neutral value of 50% [$t=-2.52$, $df=5$, $P=0.054$].

4. Discussion

In humans, the widespread availability of tasty, inexpensive, energy-dense foods, typically rich in fat and sugar, is thought to contribute to the increasing prevalence of eating disorders [15]. The present work illustrates for the first time the feeding behaviour of post-weaned piglets when they

offered long-term access to highly hedonic and/or caloric compounds in their diet. Similar to the response observed in adult rats [17–19], weanling piglets exhibited a high-affinity pattern towards a concentrated sweet and caloric 16% sucrose solution when it was freely offered as a supplement to the nutritionally complete diet (Experiment 1). Piglets did not initially show the same ingestive behaviour when offered an almost tasteless (to humans) but densely caloric 16% maltodextrin solution, although an increase in maltodextrin solution consumption was observed during the later exposure days (Experiment 2).

Previous studies conducted by Kennedy and Baldwin (1972) [13] and Glaser et al. (2000) [8] in naive pigs have reported preferences for sweet solutions when they are tested against water in short- (2 minutes) or mid-term (12 hours) preference tests. These findings, together with those obtained by Kare et al. (1965) [21] and McLaughlin et al. (1983) [22], have supported the concept that pigs have an innate preference for sweet taste compounds. Here, we tested a sweet solution (2% sucrose) against a protein solution (2% animal plasma) in the initial choice tests for Experiments 1 and 2. In both experiments we observed a higher intake and preference for sweet when animals had no previous contact with the solutions. These results are in line with our previous observations in which, without a previous learning period, growing pigs preferred sucrose solutions over protein sources even under conditions of protein-deficiency [23,24]. The innate sweet preference of piglets observed in the 3-minute choice test set the starting point to investigate the effect of the long-term exposure to concentrated carbohydrate solutions.

In Experiment 1, giving piglets ad libitum access to the additional 16% sucrose solution reduced feed intake and weight of the animals at Days 7 and 12 of exposure, in comparison with piglets supplied only with additional water. The effects on growth were severe, with a 38% of weight gain reduction in the animals supplemented with carbohydrate. In contrast to adult rats, which become obese when offered free access to additional sucrose [17–19], weanling piglets did not increase their total energy intake but consumed, on average, 44% of their calories from the additional solution. This response is similar to that observed in newly weaned rats, which ingested nearly 50% of their

energy from a supplementary 40% sucrose solution [25]. The absence of additional calorie consumption suggests that piglets regulated their feed consumption in response to the calories ingested from the solution in order to avoid excessive energy intake. Although the situation is a complex one, these results are consistent with the theory of energy control of feed intake described in previous studies in pigs [26,27].

In Experiment 2, we observed a 25% of increase in 16% maltodextrin solution consumption during Days 7 to 12 of the exposure period. The mechanisms underlying maltodextrin perception in pigs are not yet known: In rats, maltodextrin is perceived as a palatable taste and can be detected at very low concentrations [12,28,29], while for humans it produces taste sensations of only a weak intensity even at the relatively high concentrations of 10% [11]. Pigs do prefer maltodextrin solutions above the concentration of 6% - 7% when tested against water [10], but it is not clear if the preference is due to a specific taste sensation or the physicochemical properties of the solution – although it is noteworthy that the preference thresholds for sweet sucrose solutions are far lower [8,13]. In the current Experiment 3 a concentrated 16% maltodextrin solution was not preferred to a much less concentrated 2% sucrose solution. In Experiment 2, an increment observed in maltodextrin consumption was observed later in the exposure phase which generated a reduction on the feed intake of the animals, and thus a reduction on their weight gain, presumably due to the caloric load provided by the solution. Based on this consumption pattern, it could be suggested that the low dextrose equivalent maltodextrin solution was not initially hedonically positive to the piglets but that the animals increased the intake once they have learned about the positive post-ingestive consequences of the consumption (caloric intake).

Piglets provided with the extra supply of water maintained their innate sweet preference for 2% sucrose over 2% animal plasma in the final choice test at the end of the experiments. In contrast, long-term exposure to 16% sucrose or 16% maltodextrin solutions reversed this initial preference. One possible explanation of this change could be by an enhancing of the value of the protein solution. As discussed, 16% sucrose and 16% maltodextrin intakes generated a reduction in the feed

intake of the animals. While piglets reached and covered their energy needs with the caloric load provided by the solution consumption, the intake of other nutrients, such as amino acids, were not fully covered meaning that the animals self-generated a protein-deficiency status. We have previously investigated this topic by submitting piglets to a protein-deficiency condition through varying diet composition, either by lowering the total crude protein content or increasing the digestible energy content of the diet (by increasing the fat content). It was observed that piglets were unable to select and prefer a protein source based exclusively on its intrinsic flavour, and that in order to perform an appropriate selection pattern a learning process in which the sensory properties of the source solution is associated with the post-ingestive consequences of its consumption is needed [23,24]. In the current experiments, the simultaneous short-term offer of 2% sucrose and 2% animal plasma solutions during the initial choice test did probably not generate this learning memory in the piglets. Therefore, although 16% sucrose and 16% maltodextrin exposure probably did produce a protein deficiency, the rejection of 2% sucrose in the subsequent choice tests is unlikely to be exclusively due to an increase in the value of the alternative protein plasma solution.

Given that the choice behaviour of pigs exposed to concentrated sucrose or maltodextrin was presumably not only due to an increase in the value of the protein solution, it must instead be also due to a decline in the value of the 2% sucrose solution after the long-term 16% sucrose or 16% maltodextrin solution exposure. Critically, the response to a particular stimulus is not a fixed function of that stimulus, but instead is partially governed by previous and current exposure to other similar stimuli [30]. In this way, the reduction in the 2% sucrose preference in the final choice test might be due to a successive negative contrast effect in which this solution seemed less valuable to the piglets than 16% sucrose after the 12 days exposure, and as a result the consumption of 2% sucrose was reduced. This hypothesis is supported by the results of Experiment 3, where, as expected, a higher intake and preference for 16% sucrose than for 2% sucrose solution was observed. The importance of taste similarity is consistent with previous results where, despite a

protein deficiency generated by the incorporation of soybean oil in the diet (60 g/kg), piglets preferred 2% sucrose solution over a protein solution in a 3-minute choice test [23]. In this case, the nutritional imbalance was not produced by a compound with the same basic taste as that tested (soybean oil vs. sucrose, i.e., fatty vs. sweet), and so the value of 2% sucrose was not reduced in the subsequent choice test. Moreover, simultaneous negative contrast could also have contributed to the reduction in feed consumption observed when piglets had concurrent access to a more palatable sucrose solution. In the case of 16% maltodextrin, it was less preferred than 2% sucrose in Experiment 3, supporting the idea that naive piglets do not show an innate preference for maltodextrin if it is tested against an innately preferred solution such as sucrose. However, when increasing maltodextrin solution concentrations were tested against water, concentrations higher than 6% - 7% were significantly preferred [10]. The hedonic value of 16% maltodextrin might have been enhanced during the long-term exposure once the animals become familiar with the solution, and its post-ingestive consequences. Once this higher hedonic value for maltodextrin is established by experience it could then have reduced the attractiveness for 2% sucrose due to a contrast effect after the long-term exposure.

Results obtained in the appetence tests were, in general, in line with those from the preference tests. That is, we observed significantly higher appetence for 2% sucrose than for 2% animal plasma solution in control piglets, a difference which was not present, and partially reversed, in animals with access to the 16% sucrose and 16% maltodextrin solutions. In fact, a tendency to a higher appetence for the protein source was observed in piglets with long-term access to the 16% sucrose solution when compared with the appetence for protein in animals in control groups.

5. Conclusion

The feeding behaviour of post-weaned piglets is affected by long-term exposure to concentrated carbohydrate solutions, either 16% sucrose or 16% maltodextrin. The effects include reductions in feed intake and growth performance when the solutions are freely offered as a supplement to the

growing diet. In addition, the exposure reduces the innate preference and appetence of the animals for sweet over protein solutions. These data speak against the practicality of highly caloric solution supplementation in pig nutrition, and suggest that piglets may represent an alternative animal model for the study of carbohydrate appetite in young mammals.

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Table 1. Composition and estimated nutrient content of the starter diet used in the experiments.

	g/kg DM
Ingredients	
Maize	350.0
Barley	187.1
Wheat	180.0
Extruded soybean	109.0
Soybean meal 44% crude protein	58.9
Fishmeal LT	50.0
Whey powder 50% fat	25.0
Commercial nucleus[a]	10.0
Monocalcium phosphate	8.8
Calcium carbonate	7.0
L-Lysine-HCl	5.2
L-Threonine	2.2
DL-Methionine	1.8
L-Tryptophan	0.5
Salt	4.5
Estimated nutrient content	
Dry matter	890.6
Net energy (MJ/kg)	10.4
Crude protein	179.8
Crude Fibre	31.5
Fat	59.3

[a] Supplied per kg of feed: 3060 μg of retinol, 52.5 μg of cholecalciferol, 39.9 mg of α-tocopherol, 3 mg of menadione, 2 mg of thiamin, 3 mg of riboflavin, 3 mg of pyridoxine, 0.025 mg of cyanocobalamin, 20 mg of calcium pantothenate, 60 mg of nicotinic acid, 0.1 mg of biotin, 0.5 mg of folic acid, 150 mg of Fe, 156 mg of Cu, 0.5 mg of Co, 120 mg of Zn, 49.8 mg of Mn, 2 mg of I, 0.3 mg of Se.

Table 2. Solution intake, feed intake and growth performance of piglets with access to an extra supply of water (control) or 16% sucrose solution for 12 consecutive days (Experiment 1).

	Control	16% sucrose	SEM	*P*-value
Days 1 to 7				
Initial body weight, kg	10.33	10.32	0.169	0.993
Fluid intake, mL/d	655.8[a]	1274.9[b]	157.3	0.019
Feed intake, g/d	448.0[a]	255.7[b]	31.2	0.001
Energy intake, MJ/d				
Sucrose	-	3.35 (SEM 0.38)	-	-
Feed	6.53[a]	3.72[b]	0.46	0.002
Weight gain, g/d	254.2[a]	111.6[b]	22.7	<0.001
Energy:gain ratio, kJ/g	26.04[a]	55.37[b]	3.860	<0.001
Final body weight, kg	12.11[a]	11.11[b]	0.247	0.007
Days 7 to 12				
Fluid intake, mL/d	889.6	1312.9	183.7	0.134
Feed intake, g/d	570.7[a]	367.2[b]	37.1	0.003
Energy intake, MJ/d				
Sucrose	-	3.43 (SEM 0.42)	-	-
Feed	8.28[a]	5.36[b]	0.54	0.003
Weight gain, g/d	424.5	327.6	37.9	0.080
Energy:gain ratio, kJ/g	20.86[a]	27.06[b]	1.990	0.052
Final body weight, kg	14.23[a]	12.74[b]	0.370	0.008

[a,b] Mean values within a row with unlike superscript letters were significantly different ($P < 0.05$).

Table 3. Solution intake, feed intake and growth performance of piglets with access to an extra supply of water (control) or 16% maltodextrin solution for 12 consecutive days (Experiment 2).

	Control	16% maltodextrin	SEM	*P*-value
Days 1 to 7				
Initial body weight, kg	10.41	10.43	0.219	0.945
Fluid intake, mL/d	594.2	520.8	102.5	0.624
Feed intake, g/d	493.5	455.2	16.7	0.135
Energy intake, MJ/d				
Maltodextrin	-	1.38 (SEM 0.21)	-	-
Feed	7.15	6.61	0.25	0.135
Weight gain, g/d	343.7	335.5	24.8	0.817
Energy:gain ratio, kJ/g	21.38	24.12	1.460	0.214
Final body weight, kg	12.82	12.78	0.321	0.937
Days 7 to 12				
Fluid intake, mL/d	759.0	947.0	126.1	0.317
Feed intake, g/d	617.9[a]	514.0[b]	22.5	0.009
Energy intake, MJ/d				
Maltodextrin	-	2.47 (SEM 0.29)	-	-
Feed	9.00[a]	7.49[b]	0.33	0.009
Weight gain, g/d	483.6[a]	395.0[b]	23.3	0.011
Energy:gain ratio, kJ/g	18.84[a]	25.41[b]	1.378	0.007
Final body weight, kg	15.23	14.75	0.368	0.364

[a,b] Mean values within a row with unlike superscript letters were significantly different ($P < 0.05$).

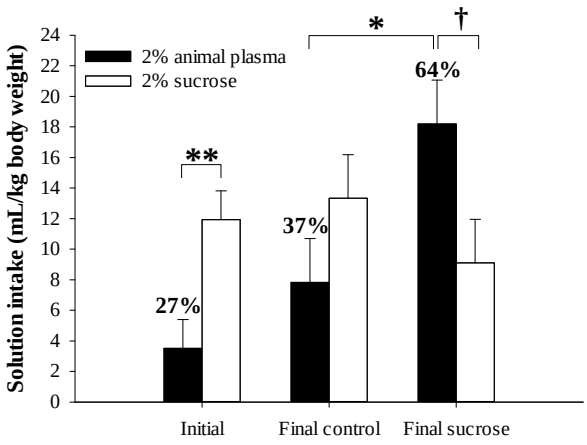
Figure captions

Figure 1. Intake and preference of piglets for 2% animal plasma or 2% sucrose solutions during the initial or final choice tests, conducted 12 days after the exposure to an extra supply of water (final control), or 16% sucrose (final sucrose, (a)) or 16% maltodextrin (final MTD, (b)) solutions. Error bars represent the SEM. Clasps indicate different intakes between both solutions ($^{\dagger}P<0.1$, $*P<0.05$, $**P<0.01$). Numbers on top of the bars represent percent intake of 2% animal plasma.

Figure 2. Intake of piglets of 2% animal plasma and 2% sucrose solutions during the one-pan test conducted 12 days after the exposure to an extra supply of water (control), 16% sucrose (S 16%) or 16% maltodextrin (MTD 16%) solutions. Error bars represent the SEM. Clasps indicate different intakes between both solutions ($^{\dagger}P<0.1$, $*P<0.05$).

Figure 3. Intake and preference of piglets for 16% sucrose (S 16%) vs. 2% sucrose (S 2%, (a)) and 16% maltodextrin (MTD 16%) vs. 2% sucrose (S 2%, (b)) in two-pan tests. Error bars represent the SEM. Clasps indicate different intakes between both solutions ($^{\dagger}P<0.1$, $*P<0.05$). Numbers on top of the bars represent percent intake of the corresponding solution and its difference from the neutral value of 50% ($^{\dagger}P<0.1$, $*P<0.05$).

(a)


Solution intake (mL/kg body weight)
2% animal plasma
2% sucrose
*
†
**
64%
37%
27%
Initial
Final control
Final sucrose

(b)

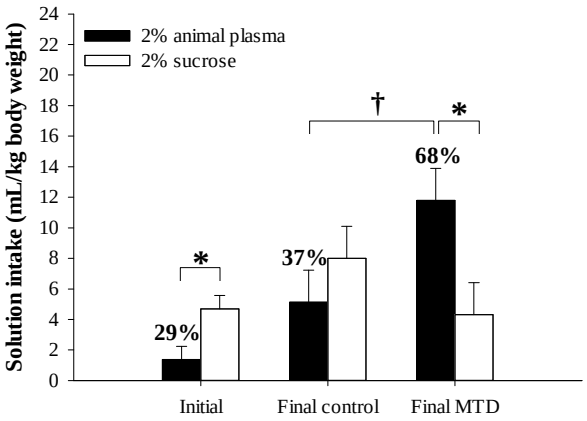

Solution intake (mL/kg body weight)
2% animal plasma
2% sucrose
†
*
68%
37%
*
29%
Initial
Final control
Final MTD

Figure 1

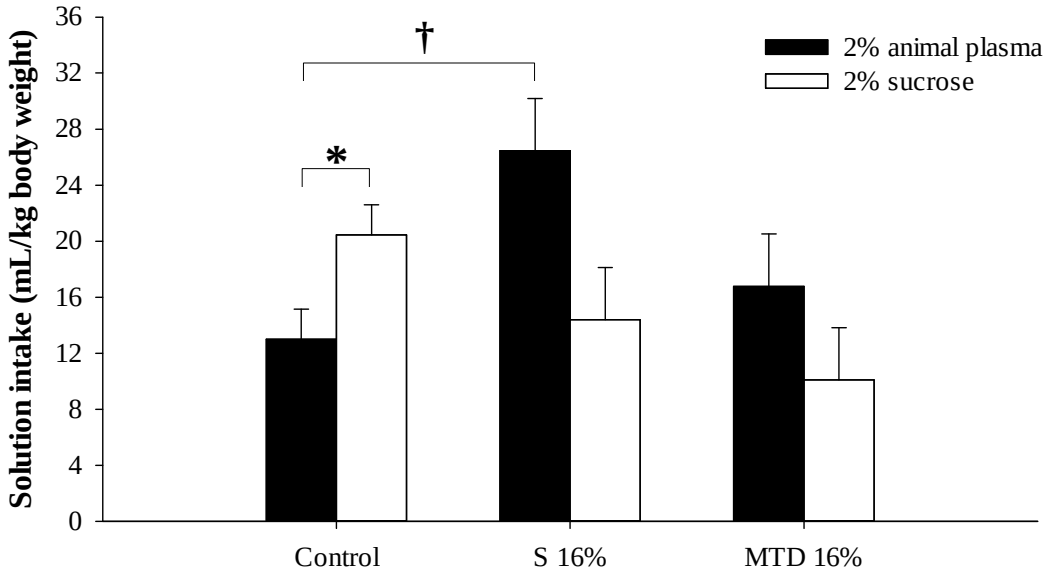

Solution intake (mL/kg body weight)
36
32
28
24
20
16
12
8
4
0
†
*
2% animal plasma
2% sucrose
Control
S 16%
MTD 16%

Figure 2

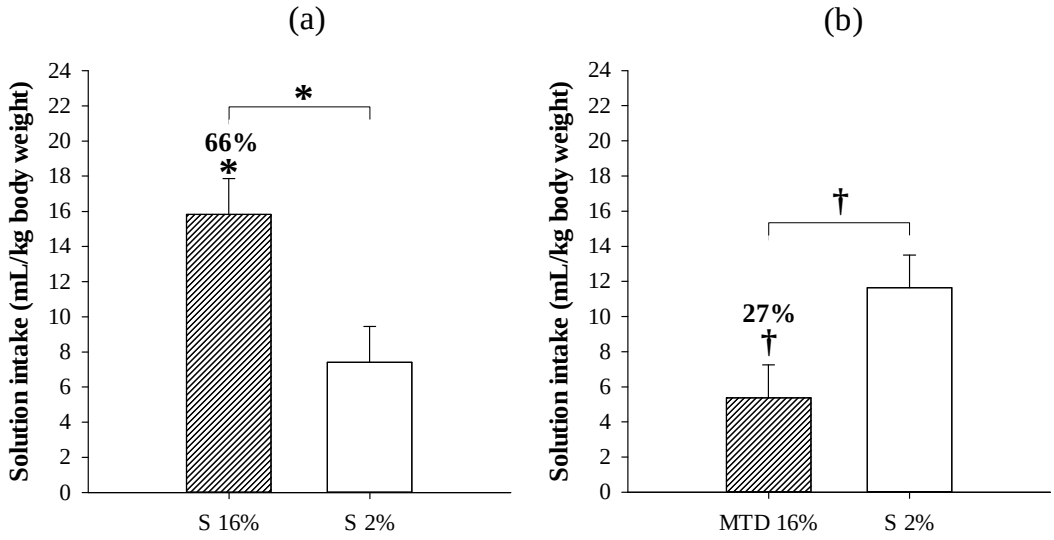

(a)
(b)
Solution intake (mL/kg body weight)
24
22
20
18
16
14
12
10
8
6
4
2
0
*
66%
*
S 16%
S 2%
†
27%
†
MTD 16%
S 2%

Figure 3