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Effects of chronic intake of starch-, glucose- and fructose-containing diets on eating behaviour in adult minipigs

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ABSTRACT

Introduction: The aim of this study was to assess whether chronic intake of isocaloric high-fat diets differing partly in the source of carbohydrates (starch, glucose or fructose) and fed at the same level of intake impacts eating behaviour in the adult Yucatan minipig.
Methods: Adult minipigs were offered for 8 weeks either of three high-fat diets in which 20% of dry matter weight (36.3% of metabolizable energy) was provided as pure maize starch (SD), glucose (GD) or fructose (FD) ($n = 5$ per diet). Three eating behaviour tests, including a three-feed choice test, an eating microstructure test and operant conditioning with progressive ratio test were performed before and after dietary treatment in order to evaluate the impact of these carbohydrates on feed preferences and animal's motivation.
Results: After 8-week treatment, all groups had similar increases in body weight (from 36.2 ± 1.2 to 57.5 ± 0.1 kg, $P < 0.0001$). Animals showed initial preference and higher motivation for the GD over the SD, FD being intermediate. Importantly, only pigs chronically fed the FD developed a large preference for this diet: increase in FD intake (from 15 ± 3 to 35 ± 6 g/kg$^{0.75}$, $P < 0.05$). After 8 weeks of experimental diets, intake speed of FD (19 ± 6 g/min) was higher compared to GD and SD ($P = 0.001$).
Conclusion: Our data indicate that chronic intake of diets differing in a part of the carbohydrate source induced substantial weight gain, regardless of the carbohydrate source. Pigs' initial preference and higher motivation was for the GD, compared to SD and FD. Intake of the fructose-containing diet for 8 weeks induced a stronger preference for this diet. Our data may have important implications in terms of impact of prolonged fructose consumption on eating behaviour in humans.

1. Introduction

Excessive intake of high-sugar diets, in association with increasing rates of obesity in Western countries (Lustig, 2010) highlights the need to study the effects of sugars on eating behaviour among obese subjects. Eating behaviour is a complex process influenced by multiple factors such as food characteristics, as well as nutritional, physiological and neurological signals. A better understanding of the mechanisms underlying eating behaviour is crucial for detecting potential food components that may trigger eating disorders (Berthoud, 2006). Current fructose consumption has incrementally doubled in the last 30 years

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(Lustig, 2010; Tappy et al., 2010) in part because of a partial substitution of sucrose (composed of 50% glucose and 50% fructose) by high-fructose corn syrup (47–65% fructose, 53–35% glucose) (Ventura et al., 2011). However, since fructose and glucose intake may vary simultaneously in the diet, this has raised the question of whether these sugars may contribute differently to the development of eating disorders. Many behavioural studies have used sucrose as the source of sugar in their experimental diets and have found important effects on eating motivation and preferences induced by sucrose (Ackroff and Sclafani, 2011; Bonacchi et al., 2008; Colantuoni et al., 2002; Dickson et al., 2012). Other studies have found some addictive effects (e.g., escalation of intake) induced by intermittent or excessive sucrose intake (Avena et al., 2008; Lenoir et al., 2007). However, it is essential to elucidate whether these effects are attributable to the glucose or the fructose component of sucrose. Consistent data, especially in rodents, have shown suppression of feeding induced by glucose infusion, whereas fructose infusion lead to opposite effects (Havel, 2005; Shima et al., 1990; Steinert et al., 2011; Teff et al., 2004). These concepts have led to the hypothesis that fructose, compared to glucose may stimulate food-seeking behaviour. Fructose is considered sweeter than glucose by humans (relative sweetness: fructose 173%, glucose 74%, compared to sucrose set to 100% as the reference value) (Mahan and Escott-Stump, 2008). Fructose sweetness is perceived earlier than that of sucrose or glucose, and the taste sensation reaches a peak and decreases faster than that of sucrose (Hanover and White, 1993). As food palatability plays a major role in food preferences and motivation (Wilson, 2010), and because excessive sugar intake is partly motivated by the reward value of the sweet taste (Lenoir et al., 2007), we hypothesized that prolonged consumption of fructose may also influence eating behaviour by inducing a stronger specific preference than glucose. Fructose might also induce alterations in hedonic and motivational processes leading to blunted-reward/satiety responses and eating disorders (Lustig, 2010).

Most of the studies on the effects of sugars on eating behaviour or appetite regulation have been performed in rodents. Pigs display anatomical and physiological similarities to humans (Clouard et al., 2012b; Sauleau et al., 2009; Val-Laillet et al., 2011). Pigs are able to distinguish between different diets for their palatability and they have a high innate preference for sweet taste (Seabolt et al., 2010) and a strong appetite for sugar solutions (Baldwin, 1996).

The aim of this study was to examine whether chronic intake of isocaloric diets at the net energy level and containing pure glucose or fructose provokes modifications of eating behaviour compared to a control starch-containing isocaloric diet in the adult Yucatan minipig model (*Sus scrofa*). Maize starch represents a good ingredient in the control diet given its low palatability (Kim et al., 1998), and its frequent use as a carbohydrate major energy-yielding ingredient in diets for pigs (Bach Knudsen et al., 2006; Wiseman, 2006). We hypothesized that chronic intake of isocaloric diets with fructose, and to a lesser degree glucose, but not starch, could induce a stronger preference and higher motivation for these sugar-containing diets.

2. Materials and methods

2.1. Animals and diets

The present study was conducted in 2011–2012 in accordance with the current ethical standards of the European (Directive 2010/63/EU) and French legislations (agreement number A35-622 and authorization numbers 01894 and 3588). Trained staff members provided animal care and management under the supervision of a veterinarian. Fifteen male adult Yucatan minipigs (36.2 ± 1.2 kg at the beginning of the experiment) of 12–14 months of age from the herd of INRA St-Gilles, France were used. Only male animals were used because evidence has shown an implication of oestrogens in obesity and eating behaviour (Meyer et al., 2011). Animals were housed in individual cages (dimensions: 126 cm × 75 cm × 86 cm) under controlled conditions of temperature (22–24 °C) and humidity (between 50 and 70%). Animals were maintained on a 12-h light–dark cycle and each subject had free access to water. Before the beginning of the experiments, animals had access to 1 kg of pelleted standard diet for minipigs from 8:00 to 16:00 h each day (Table 1). Animals were weighed weekly for 8 weeks of experimental diets, as well as before and after the beginning of the eating behaviour tests.

Animals were randomly assigned to one of three groups of dietary treatments: starch-containing control diet, glucose-containing diet, and fructose-containing diet ($n = 5$ per diet). The three diets had the same net energy content (10.89 MJ/kg), and ingredient and nutritional composition, except for a substantial part of carbohydrates

Table 1
Composition of standard and experimental diets for minipigs.

Composition (%)	Experimental diets			
	Standard	Starch	Glucose	Fructose
Wheat	10.00	6.00	6.00	6.00
Barley	33.00	12.00	12.00	12.00
Wheat bran	25.00	14.00	14.00	14.00
Soybean meal	6.00	9.00	9.00	9.00
Sunflower meal	10.00	8.00	8.00	8.00
Soybean hulls	12.00	11.00	11.00	11.00
Sucrose	1.00			
Corn starch		25.00	5.10	6.50
Glucose source[a]			19.90	
Fructose source[a]				18.50
Lard	0.00	12.00	12.00	12.00
Dicalcium phosphate	0.60	0.60	0.60	0.60
Calcium carbonate	1.30	1.30	1.30	1.30
Salt	0.60	0.60	0.60	0.60
Oligoelements and vitamins	0.50	0.50	0.50	0.50
Nutritional value (calculated: % or MJ/kg)				
Metabolizable energy	10.31	14.06	14.06	14.06
Net energy	7.27	10.89	10.89	10.89
Dry matter		89.64	89.64	89.64
Crude protein	15.22	12.18	12.18	12.18
Crude fat	2.17	13.45	13.45	13.45
Cellulose	11.05	8.00	8.00	8.00
Minerals	6.81	5.56	5.56	5.56

[a] Pure glucose and fructose sources with water content of 9.5 and 0.5%, respectively, thus they both provided exactly 20.05% of the diets' dry matter.