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Differential effects of chow and purified diet on the consumption of sucrose solution and lard and the development of obesity ☆

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ABSTRACT

Obesity has been associated with increased consumption of sweetened beverages and a high-fat diet. We determined whether the composition of the dry pellet offered with liquid sucrose (LS) and lard influenced the development of obesity. We hypothesized that animals offered LS or LS and lard (choice), in addition to chow or purified low fat diet pellet (LFD; 10% fat), would gain more body fat than controls. We compared the effects of LFD vs. chow on voluntary consumption of LS and lard, serum triglyceride (TG), glucose, and body fat over 21 days. Male Sprague Dawley rats (n = 10/group) were offered chow, chow + LS, chow choice, LFD, LFD + LS, LFD choice or solid high-sucrose diet (70% sucrose). Energy intakes of rats fed chow, LFD, and high-sucrose diets were similar. Energy intake was increased by 16% in chow + LS, 15% in LFD + LS, 11% in LFD choice, and 23% in chow choice rats. Chow choice rats consumed 142% more lard than LFD choice rats. Fasting glucose increased in all choice rats compared with the chow and high-sucrose diet rats. Fasting TG increased in LFD choice rats and were ~75% higher than those of chow, LFD, or high-sucrose rats. Chow choice had higher carcass fat than chow, chow + LS, and LFD groups however LFD choice was not different from their controls. Another experiment confirmed rats consumed 158% more lard when given chow choice compared to LFD choice. The diet offered to rats with free access to LS and lard influenced the development of obesity, sucrose and lard selection, and TG.

1. Introduction

The common rat models used for obesity research include those with a genetic mutation or those that have been fed a high fat diet. Genetic mutations may influence a variety of physiologic and metabolic parameters [1,2]. For example, Zucker rats with a mutation of the leptin receptor have changes in energy expenditure, immune response, reproduction, glucose homeostasis, thyroid axis, and inflammatory response [3,4]. The most common model of diet-induced obesity involves rats fed a composite high fat (solid) diet with dietary fat ranging from 30% to 60% MJ. These animals generally take 8–12 weeks to become obese and their phenotype is variable [5]. Americans also consume a high fat diet (>30% MJ), [6,7], but are consuming 20–25% of their energy in fluid form [8,9] which equates to approximately 2.2 MJ (535 kcal) day [8]. This is alarming because in a previous meta-analysis in humans there was no compensation for energy added to the diet in liquid form. Consumption of energy in liquid form increased total energy intake by 9% and may have increased weight gain. By contrast, 64% of the energy consumed in solid form was compensated for in the diet [10]. The laboratory rat studies described here used a choice diet that involved free access to dry pellet, 30% sucrose solution, and lard which may be more representative of the diet consumed by humans.

The choice diet is unique in that the 30% sucrose solution and lard are not incorporated into the pellet, but are each offered individually (i.e., as a choice). When combined with chow, the physical form of sucrose and fat affects preference because rats consume more energy from sucrose when consumed in liquid form compared to solid, but consume more energy from fat in solid form compared to oil [11,12]. Liquid sucrose has previously been shown to promote overeating in chow fed rats by Castonguay et al. [13] and Ackroff and Sclafani [14] and lard by Ackroff and Sclafani [14]. The latter study found that a chow, 32% liquid sucrose solution, and fat (vegetable shortening) group did not increase energy intake compared to a chow and liquid sucrose group. The liquid sucrose and chow and the chow, liquid sucrose, and fat groups consumed more energy than the chow and fat and the chow only groups. This coincided with the chow and liquid sucrose group having a similar body weight as the chow, liquid sucrose, and fat group but a higher body weight than the chow and fat and the chow only groups [14]. A similar model of diet induced weight gain has been associated with changes in hypothalamic neuropeptide expression and the development of glucose intolerance and insulin insensitivity [15,16]. The purpose of

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the experiments described here was to determine if the composition of the dry pellet (chow vs. purified diet) offered with the sucrose and lard influenced the development of obesity or insulin tolerance which was used as a measure of glucose clearance. We also compared the effects of feeding a purified dry high sucrose diet with those of dry pellet plus liquid sucrose. We hypothesized that the animals offered liquid sucrose or liquid sucrose and lard would gain more body fat than the control animals because of increased energy intake regardless of diet.

2. Methods

2.1. Animals

All animal procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Georgia Health Sciences University and followed the recommendations of the NIH Intramural Animal Care and Use program. All rats were housed in a climate controlled room at ~21 °C with lights on for 12 h/day starting at 6 am. In both experiments, male Sprague Dawley rats (Harlan, Indianapolis, IN, USA) were individually housed in hanging wire mesh cages.

2.2. Experiment 1: effects of chow, LFD, high sucrose diet, LS, and choice on body composition

The purpose of this experiment was to establish the changes in body composition and serum metabolic profile of rats offered access to a 30% sucrose solution (w/v; Kroger Sugar, Hood Packing Corporation, Hamlet, NC, USA) or sucrose solution and lard (Armour, ConAgra Foods, Omaha, NE, USA) in addition to a chow or low fat diet pellet (Table 1; LFD: 10% MJ fat, 20% MJ protein, and 70% MJ carbohydrate; D124450B Research Diets, Inc., New Brunswick, NJ, USA). In order to determine if the form of sucrose influenced the development of obesity in rats, another group was offered solid high sucrose diet (Table 1; 10% MJ fat, 20% MJ protein, and 70% MJ sucrose; D09082001 Research Diets, Inc.). The LFD had similar fat, protein, and micronutrient content as the solid high sucrose diet. During the baseline period, all rats had free access to chow (Harlan Teklad Rodent Diet 8604; 24% minimum protein, 4% minimum fat, 0.14 MJ/g) and water. Following the baseline period, animals were weight matched into 7 groups ($n = 10$): chow, LFD, chow + 30% sucrose solution (LS), LFD + LS, chow choice (chow, LS, and lard), LFD choice (diet, LS, and lard), and solid high sucrose diet. The LS was placed next to the water bottle and the lard was given in a dish inside the cage with the pellet. Body weight was measured every other day. Five hour fasting tail blood samples were collected on day 5 and day 12 for measurement of whole blood glucose (EasyGluco Blood Glucose Monitoring System, US Diagnostics, Inc., New York, NY, USA) and serum total triglycerides (TG; Wako Chemicals, Richmond, VA, USA). Energy intakes, corrected for spillage, were measured on days 14–18 (5 days). An insulin tolerance test (ITT) was performed on day 19. This was also started at 1 pm following a 5 h fast. At time 0, each rat was injected i.p. with 0.75 units/kg of Humulin® (Eli Lilly, Indianapolis, IN, USA) and tail blood glucose samples were measured at 0, 5, 10, 20, 30, and 45 min.

On day 21, food was removed at 7 am and the rats were decapitated starting at 9:30 am. The right side inguinal, epididymal, retroperitoneal, and entire mesenteric fat pads and liver were dissected, weighed, and returned to the carcass. One lobe of the liver was flash frozen for measurement of lipid content [17] and trunk blood was collected. Serum insulin (Rat Insulin RIA kit, Millipore, St. Charles, MO, USA) and leptin (Multi-species Leptin RIA, Millipore, Billerica, MA, USA) were measured. Carcass composition, less the gastrointestinal tract, was analyzed as described previously [18].

Table 1
Composition of the diets (g/1055 g).

	LFD (D12450B)	High sucrose diet (D09082001)
Casein	200	200
L-cysteine	3	3
Corn starch	315	0
Maltdextrin 10	35	0
Sucrose	350	700
Cellulose	50	50
Soybean oil	25	13.5
Lard	20	31.5
Mineral mix S 100026	10	10
Dicalcium phosphate	13	13
Calcium carbonate	5.5	5.5
Potassium citrate	16.5	16.5
Vitamin mix V10001	10	10
Choline bitartrate	2	2
Energy density (MJ/g)	0.016	0.016

LFD, low fat diet. These diets are from Research Diet, Inc. (New Brunswick, NJ).

2.3. Experiment 2: effect of pellet composition on lard and sucrose selection

Since experiment 1 showed that rats offered LFD choice consumed significantly less lard than those offered chow choice, experiment 2 was designed to determine if this was an effect of pellet composition on food selection. Twenty male Sprague Dawley rats were housed as described above and baseline measures were made for 1 week during which all rats were offered chow. Body weight and energy intake were measured daily. The rats were weight matched to a control chow group ($n = 6$) or a chow choice group ($n = 14$). A partial crossover design was utilized. The control chow rats remained on ad libitum chow during the entire experiment. After 31 days, the chow choice group was divided into two weight-matched groups, one remained on chow choice and the other group was offered LFD choice. An ITT was performed on day 27 when all rats were on chow choice and again on day 58 when rats were on different choice diets. The experiment ended on day 62 when the same end point measures were made as described in experiment 1 with the addition of liver glycogen [17], glycerol (Free Glycerol Determination Kit, Sigma St. Louis, MO, USA), and non-esterfied fatty acids (NEFA; NEFA C kit, Wako Chemicals) measurements.

2.4. Statistical analysis

Values are mean ± SEM. For the ITT, the rate of change was calculated as the slope between time 0 and 45 min. Comparisons among groups were performed using a one-way ANOVA and post-hoc analyses with Tukey HSD (Statistica, version 9, StatSoft, Inc., Tulsa, OK, USA). Statistical significance was defined as $P \leq 0.05$.

3. Results

3.1. Experiment 1

End body weight was not different among groups, but LFD + LS and LFD choice groups gained more weight than did the chow group (Fig. 1A). Chow, LFD, and high sucrose diet groups had similar energy intakes (Fig. 1B). These were lower than those of the LS and choice groups. Chow choice rats consumed more energy than did the LFD choice group, but intake did not differ from that of the chow + LS and LFD + LS groups. The latter group consumed more pellet, but less sucrose solution than did the chow + LS group (Fig. 1B; chow + LS, 1.2 ± 0.1 MJ/5 days; LFD + LS, 0.9 ± 0.1). The chow choice group had an increased lard intake (chow choice, 1.0 ± 0.1 MJ/5 days; LFD choice, 0.4 ± 0.1), but decreased pellet intake compared with that of the LFD choice group, however the sucrose intakes were similar for the two choice groups (Fig. 1B; chow choice 0.5 ± 0.1 MJ/5 days; LFD