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Basic nutritional investigation

A high-fat diet supplemented with fish oil improves metabolic features associated with type 2 diabetes

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ABSTRACT

Objective: The goal of this study was to investigate the effects of a high-fat diet supplemented with fish oil or olive oil, fed to C57BL/6J mice for an extended period, on metabolic features associated with type 2 diabetes.
Methods: Mice were fed one of four diets for 30 wk: a low-fat diet, a high-fat diet supplemented with lard, a high-fat diet supplemented with fish oil, or a high-fat diet supplemented with olive oil. Phenotypic and metabolic analysis were determined at 15 and 25 to 30 wk, thereby providing comparative analysis for weight gain, energy consumption, fat distribution, glucose and insulin tolerance, and hepatic/plasma lipid analysis.
Results: Mice fed a high-fat diet supplemented with fish oil had improved glucose tolerance after an extended period compared with mice fed a high-fat diet supplemented with lard. Moreover, mice fed a high-fat diet supplemented with fish oil had significantly decreased concentrations of liver cholesterol, cholesteryl ester, and triacylglycerol compared with mice fed a high-fat diet supplemented with either lard or olive oil.
Conclusion: Mice fed a high-fat diet supplemented with fish oil improved metabolic features associated with type 2 diabetes such as impaired glucose tolerance and hepatic steatosis.
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Introduction

The obesity pandemic serves as a major risk factor for chronic and life-threatening comorbidities, including hepatic steatosis, dyslipidemia, and type 2 diabetes (T2D) [1]. Recent genome-wide association studies have identified a number of obesity and T2D susceptibility genes, most of which are suspected to interact with environmental factors [2,3]. It is therefore necessary to investigate how the fatty acid composition of high-fat diets influences the etiology and pathophysiology of these complex, nutrition-related metabolic diseases.

In the past decade, appropriate mouse models fed a high-fat diet represent the best means for obtaining novel insight with regard to altered human metabolism and consequently obesity and T2D [4]. Studies have determined that wild-type C57BL/6J mice are genetically susceptible to obesity, impaired glucose tolerance, and T2D when fed a high-fat diet, but not a low-fat diet, and therefore represent an ideal animal model for investigating these metabolic diseases [5,6]. Moreover, studies indicate that C57BL/6J mice are susceptible to the fatty acid composition of high-fat diets, resulting in the manifestation of altered disease phenotypes [7]. For instance, a high-fat diet supplemented with fish oil has been reported to reduce adiposity and body weight, along with lessening adipose inflammation and inhibiting lipid synthesis [8,9].

The high-fat diets and time intervals for these studies varies widely, and despite using the C57BL/6J mouse model, the results vary as well. Therefore, the present study used C57BL/6J mice fed high-fat diets (45% kcal from fat) supplemented with 10% lard, 10% fish oil, or 10% olive oil, to investigate the health effects in relation to metabolic features associated with T2D.

Materials and methods

Mice

Wild-type male C57BL/6J weanling mice were obtained from The Jackson Laboratory (Bar Harbor, ME) and maintained at The University of New Mexico Health Sciences Center Animal Resources Facility according to Institutional

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Animal Care and Use Committee (IACUC) guidelines. The mice were housed (four mice per cage) in a room maintained at 23°C to 24°C, 31% to 32% humidity, with an alternating 12-h light/dark cycle, and fed diets with water ad libitum. The mice and food were weighed weekly up to 30 wk of age, after which mice were sacrificed using carbon dioxide asphyxiation.

Diets

The energy balanced diets were as follow:

1. a low-fat diet (LF; D07021301),
2. a high-fat diet supplemented with lard (HF; D07021302),
3. a high-fat diet supplemented with fish oil (FO; D07021303), and
4. a high-fat diet supplemented with olive oil (OO; D07021304)

The diets were formulated and produced by Research Diets (New Brunswick, NJ). The detailed composition of these diets is provided in Table 1. The LF diet served as the negative control diet, whereas the HF diet specifically designed to mimic the average Western-type diet served as the positive control diet. It must be noted that the FO and OO diets contain 75% lard as does the HF diet, therefore in the FO and OO diets, the fish oil or olive oil ingredient replaces 25% of the lard to sustain the same kcal% from fat in these high-fat diets. The fatty acid profile of these diets is provided (Supplementary Table 1).

Glucose and insulin tolerance tests

Glucose tolerance tests (GTT) and insulin tolerance tests (ITT) were performed at 15 and 25 wk of age, and 16 and 26 wk of age, respectively, to determine the presence of glucose intolerance and insulin sensitivity as previously described [10]. The Precision Xtra Advanced Diabetes Management System (Abbott Diabetes Care Inc., Alameda, CA) was used to measure blood glucose.

Concentration of plasma components

The concentration of plasma insulin was determined using the Mouse High Range Insulin ELISA kit (ALPCO Immunoassays, Salem, NH). The concentration of plasma glucose, cholesterol, triacylglycerol, alanine aminotransferase (ALT), and aspartate aminotransferase (AST) were determined using the Infinity Glucose, Cholesterol, Triacylglycerol, ALT, and AST kits (Thermo Scientific, Middletown, VA). The concentration of inflammatory cytokines (interleukin [IL]-1β, IL-6, and tumor necrosis factor [TNF]-α) and anti-inflammatory cytokines (IL-4, IL-10, and IL-14) were determined using appropriate mouse Ready-SET-Go cytokine kits (eBioscience, San Diego, CA). The Homeostasis Model Assessment-Insulin Resistance index (HOMA-IR), Homeostasis Model Assessment-β cell function percentile (HOMA-β%), and quantitative insulin sensitivity check index (QUICKIE), were calculated as previously described [11,12].

Relative size of adipocytes

The relative size of adipocytes in adipose tissue was measured indirectly as the amount of DNA normalized to the weight of adipose tissue [10]. The concentration of DNA was determined using the DNA fluorescence quantification kit (Sigma, St. Louis, MO).

Concentration of liver lipids

The concentration liver lipids were determined after organic extraction, separation using thin layer chromatography, and measuring the amounts of each lipid (unesterified cholesterol, cholesteryl ester, free fatty acids, and triacylglycerol) using enzymatic kits as previously described [13]. The concentration of liver lipids was normalized to the amount of liver protein that precipitated during organic extraction.

Fatty acid profile of liver lipids

The total lipids were extracted from liver using hexane/isopropanol (3:2, v/v) as previously described [13]. The dried lipid extract was transferred to a clean reaction vial using chloroform and the solvent was evaporated under N_2 gas. Direct *trans*-esterification of the lipid extract was performed using 14% BF_3 in methanol to prepare fatty acid methyl esters (FAMEs) as previously described [14]. FAMEs were separated by gas liquid chromatography using a HP5890 series II gas chromatograph (Hewlett-Packard, Wilmington, DE) equipped with a HP5972 mass detector and 15 m × 0.1 mm fused silica capillary column (Omegawax-100, 0.1 μm film thickness, Sigma, St. Louis, MO). The temperature program started with an initial temperature of 110°C, which was increased at 30°C/min to 260°C, followed by a 10-min isothermal period. Injector and detector temperatures were 250°C and 280°C, respectively. Helium was used as a carrier gas at constant flow rate of 0.5 mL/min. Individual fatty acids were identified using MS spectra and confirmed with known FAMEs standards (Sigma, St. Louis, MO). Pentadecanoic acid was used as an internal standard. Peak integration was performed using the MS ChemStation software version G1034C. A FAME mixture (Supelco 37 Comp. FAME Mix, Sigma, St. Louis, MO) was used as an external

Table 1
Detailed composition of mouse diets

Diet	LF		HF		FO		OO	
Macronutrients	Mass (%)	Energy (%)	Mass (%)	Energy (%)	Mass (%)	Energy (%)	Mass (%)	Energy (%)
Protein	19	20	24	20	24	20	24	20
Carbohydrate	67	70	41	35	41	35	41	35
Fat	4	10	24	45	24	45	24	45
Fatty acid profile		% fat		% fat		% fat		% fat
Saturated		25.1		36.2		33.7		30.8
Monounsaturated		34.7		45.3		39.6		51.0
Polyunsaturated		40.2		18.5		26.7		18.2
Ingredient, *g/4057 kcal*	*g*	*kcal*	*g*	*kcal*	*g*	*kcal*	*g*	*kcal*
Casein, 80 Mesh	200	800	200	800	200	800	200	800
L-cystine	3	12	3	12	3	12	3	12
Corn Starch	427	1708	73	291	73	291	73	291
Maltodextrin 10	100	400	100	400	100	400	100	400
Sucrose	173	691	173	691	173	691	173	691
Cellulose, BW200	50		50		50		50	
Fish oil					45	407		
Olive oil							45	407
Soybean oil	25	225	25	225	25	225	25	225
Lard	20	180	177	1598	132	1191	132	1191
Mineral Mix S10026	10		10		10		10	
DiCalcium Phosphate	13		13		13		13	
Calcium Carbonate	5.5		5.5		5.5		5.5	
Potassium Citrate,	16.5		16.5		16.5		16.5	
Vitamin Mix V10001	10	40	10	40	10	40	10	40
Choline Bitartrate	2		2		2		2	
Total	1054	4057	858	4057	858	4057	858	4057
Energy density, *kcal/g*	3.85		4.73		4.73		4.73	

FO, high-fat diet supplemented with fish oil; HF, high-fat diet supplemented with lard; LF, low-fat diet; OO, high-fat diet supplemented with olive oil

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