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Maternal dietary fat intake during gestation and lactation alters tissue fatty acid composition in the adult offspring of C57Bl/6 mice

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ABSTRACT

We investigated the effects of maternal dietary fat intake during gestation and lactation on the tissue fatty acid composition of the adult offspring. Female C57Bl/6 mice were fed high fat diets enriched with lard or safflower oil or chow during mating, gestation and lactation. The offspring obtained from each group of mothers were continued on diets rich in lard, safflower oil or chow post-weaning until 11 weeks of age. Livers and hearts were collected for fatty acid analysis. A maternal diet rich in safflower oil was associated with enrichment of hepatic tissue with n-3 polyunsaturated fatty acids in the offspring fed chow post-weaning compared to the offspring fed chow throughout. However, a continuous exposure to a safflower oil- as well as lard-rich diet during the pre- and post-weaning time periods was associated with reduced content of docosahexaenoic acid in both liver and heart tissues compared to the offspring fed chow throughout. In conclusion, this study demonstrated lasting effects of maternal dietary fat intake, as well as an interaction between pre- and post-weaning diets, on the tissue fatty composition in adult offspring.

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1. Introduction

Dietary fat intake has long been associated with the development of cardiovascular disease (CVD). In addition to adult nutrition, recent evidence based on the concept of 'developmental programming' suggests that maternal dietary fat intake during pregnancy may lead to the development of dyslipidemia [1], insulin resistance [2], endothelial dysfunction and hypertension [3] in the offspring during adult life. However, the underlying mechanisms behind this phenomenon remain largely unknown.

Fatty acids play an important role in regulating the structure and function of various tissues. Tissue fatty acids occur in various lipids such as phospholipids, mono-, di-, tri-acylglycerols (TG) and free fatty acids (FFA). While TG and FFA can be utilized as a source of metabolic energy, fatty acids in the form of phospholipids serve as structural components of various membranes. Moreover, fatty acids can act as ligands for several nuclear receptors such as peroxisome proliferator-activated receptors and sterol-element regulatory binding proteins, which are known to participate in the sub-cellular control of a number of metabolic pathways [4]. Since fatty acids are involved in the regulation of a variety of cellular activities, changes in the fatty acid composition have been associated with a number of pathological conditions such as insulin resistance [5], obesity [6], non-alcoholic fatty liver disease [7], hypertension and CVD [8–10].

It is well known that the fatty acid composition of serum and adipose tissue TG can reflect the dietary fat intake over the previous weeks and years [11]. In addition, animal studies have indicated changes in both liver and heart fatty acid composition in a diet-specific manner [12,13]. All of these studies have focused on the influence of postnatal dietary fat intake on tissue fatty acid composition; however, till date there are only a handful of studies suggesting an effect of maternal dietary fat consumption on offspring tissue fatty acid composition. A recent study reported a reduction in hypothalamic docosahexaenoic acid (DHA) levels in 24-week-old rat offspring, which were exposed to a diet deficient in n-3 PUFA during the perinatal time period [14]. Another study reported reduced aortic content of arachidonic acid (AA) and DHA in 160-day-old Sprague-Dawley rats obtained from mothers fed a high fat diet rich in SFA during gestation and lactation [1]. We have also reported changes in the aortic fatty acid composition of the adult C57Bl/6 mice exhibiting aortic vascular dysfunction obtained from mothers fed a lard-rich diet during gestation and lactation [15].

The purpose of the current study was to investigate whether maternal dietary fat intake during gestation and lactation,

Abbreviations: SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; LA, linoleic acid; ALA, alpha-linolenic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosahexaenoic acid; CVD, cardiovascular disease; TG, triglycerides; FFA, free fatty acids; GLC, gas liquid chromatography

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differing with respect to its fatty acid composition, would affect the tissue fatty acid composition of the adult offspring. We compared the effects of pre- and post-weaning high fat diets containing lard or safflower oil with rodent chow, on the liver and heart fatty acid composition in the adult offspring of C57Bl/6 mice. Our study design further allowed us to investigate the interaction between pre- and post-weaning diets on the fatty acid composition of liver and heart in the adult offspring. The results of the current study indicate that while maternal dietary fat intake has the potential to induce long-lasting changes in the offspring heart fatty acid composition, it is the interaction between pre- and post-weaning diets that determines the fatty acid composition of liver and heart in the adult offspring.

2. Methods

2.1. Animals and diets

All the experimental procedures were in accordance with the principles and guidelines of the Canadian Council on Animal Care and were approved by the Memorial University's Animal Care Committee. 7-week-old female C57Bl/6 mice were purchased from Charles River Laboratories (MA, USA) and were housed in a single room with a 12 h light/12 h dark period cycle throughout the study period. The temperature and humidity were maintained at 21 °C and $35 \pm 5\%$, respectively. Animals were kept on a standard rodent chow diet (Agribrands Purina Inc., ON, Canada) for 1 week prior to feeding the experimental diets.

The experimental high fat diets were prepared using a base semi-synthetic diet obtained in powdered form with fat source omitted, designed specifically to permit the control of fat level at 20% w/w (MP Biomedicals, OH, USA). Experimental high-fat diets were enriched with lard or safflower oil, obtained from a local supermarket. Gas–liquid chromatography (GLC) was utilized to determine the fatty acid composition of the experimental diets (Table 1). In order to assess the impact of diets enriched with different fatty acids during pre- and post-weaning time period, three separate studies were designed.

Study I: After the acclimatization period, mice were divided into two groups: one group continued on rodent chow, while the other group was fed the lard-rich diet. Female breeders were fed these diets for 2 weeks *ad libitum* before mating, while the males were fed chow. The females continued on the same diets during mating, pregnancy and lactation. At weaning, the offspring obtained from each mother were divided into 2 balanced groups: one group continued on the lard-rich diet (SFA) and the other group was fed rodent chow. Thus, 4 groups of offspring were obtained that were identified by *pre-/post-weaning diet* combinations: SFA/SFA (S/S), SFA/chow (S/C), chow/chow (C/C) and chow/SFA (C/S). The offspring were fed their assigned diets *ad libitum* for another 8 weeks.

Study II: After the acclimatization period, mice were divided into two groups: one group continued on rodent chow, while the other group was fed a diet rich in safflower oil (PUFA). Female breeders were fed these diets for 2 weeks *ad libitum* before mating, while the males were fed chow. The females continued on the same diets during mating, pregnancy and lactation. At weaning, the offspring obtained from each mother were divided into two balanced groups: one group continued on safflower-oil rich diet and the other group was fed rodent chow. Thus, 4 groups of offspring were obtained that were identified by *pre-/post-weaning diet* combinations: PUFA/PUFA (P/P), PUFA/chow (P/C), chow/chow (C/C) and chow/PUFA (C/P). The offspring were fed their assigned diets *ad libitum* for another 8 weeks.

Study III: After the acclimatization period, mice were divided into two groups: one group continued on a lard-rich diet (SFA), while the other group was fed the safflower oil-rich diet (PUFA). Female breeders were fed experimental diets for 2 weeks *ad libitum* before mating, while the males were fed chow. The females continued on the same diets during mating, pregnancy and lactation. At weaning, the offspring obtained from each mother were divided into two balanced groups; one group continued on the lard-rich diet and the other group was fed the safflower oil-rich diet. Thus, 4 groups of offspring were obtained that were identified by *pre-/post-weaning diet* combinations: SFA/SFA (S/S), SFA/PUFA (S/P), PUFA/PUFA (P/P) and PUFA/SFA (P/S). The offspring were fed their assigned diets *ad libitum* for another 8 weeks.

At the end of the feeding period, mice were fasted for 12 h overnight and then sacrificed by anaesthetizing with halothane vapor in a closed chamber. Liver and heart tissues were snap frozen and stored at −70 °C until further use.

Table 1
Fatty acid composition of the experimental high-fat diets.

Fatty acids	Lard-rich diet	Safflower oil-rich diet
C14:0	3	ND
C16:0	18	8
C18:0	14	3
∑SFA	35	11
C16:1	3	ND
C18:1	42	15
C20:1	1	ND
∑MUFA	46	15
C18:2 n-6	15	70
C18:3 n-3	4	4
∑PUFA	19	74

Data represent weight percentage of total extracted fatty acids. ND = Not detected, ΣSFA = sum of saturated fatty acids, ΣMUFA = sum of monounsaturated fatty acids, ΣPUFA = sum of polyunsaturated fatty acids.

2.2. Gas liquid chromatography analysis

Lipids were extracted from diet and also from various tissues using the Folch method (chloroform/methanol) [16]. Fatty acid methyl esters were then prepared by heating the sample with 2 ml of trans-methylation reagent (6% concentrated sulfuric acid and 94% methanol; hydroquinone was added as an anti-oxidant) for 2 h at 65 °C. Organic extractions were performed using hexane and water and the organic layer was dried under nitrogen. Samples were dissolved in 20 μl of carbon disulfide and used for GLC analysis [17]. Samples were run for 60 min on an Omegawax X 320 (30 m × 0.32 mm) column from Supelco (Sigma-Aldrich, Canada) using a flame ionization detector. The GLC parameters were set as follows: oven, 200 °C; injector, 240 °C; detector, 260 °C. Fatty acid standards (PUFA-1, -2 and -3, Sigma-Aldrich Canada) were used for identification of fatty acids by retention time.

2.3. Statistical analysis

The fatty acid data are reported as percent of total extracted fatty acids. Data were arcsine transformed prior to statistical analysis. The transformed data sets from dietary groups of each experimental set were then compared using one-way ANOVA followed by Newman–Keuls *post-hoc* test (GraphPad Prism software version 3.2), where $P < 0.05$ was considered significant. All

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