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ORIGINAL ARTICLE

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Effect of exercise training on the fatty acid composition of lipid classes in rat liver, skeletal muscle, and adipose tissue

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Abstract The aim of the present study was to examine the effects of 8 weeks of exercise training on the fatty acid composition of phospholipids (PL) and triacylglycerols (TG) in rat liver, skeletal muscle (gastrocnemius medialis), and adipose tissue (epididymal and subcutaneous fat). For this purpose, the relevant tissues of 11 trained rats were compared to those of 14 untrained ones. Training caused several significant differences of large effect size in the concentrations and percentages of individual fatty acids in the aforementioned lipid classes. The fatty acid composition of liver PL, in terms of both concentrations and percentages, changed with training. The TG content of muscle and subcutaneous adipose tissue decreased significantly with training. In contrast to the liver, where no significant differences in the fatty acid profile of TG were found, muscle underwent more significant differences in TG than PL, and adipose tissue only in TG. Most differences were in the same direction in muscle and adipose tissue TG, suggesting a common underlying mechanism. Estimated fatty acid elongase activity was significantly higher, whereas Δ^9-desaturase activity was significantly lower in muscle and adipose tissue of the trained rats. In conclusion, exercise training modified the fatty acid composition of liver PL, muscle PL and TG, as well as adipose tissue TG. These findings may aid in delineating the effects of exercise on biological functions such as membrane properties, cell signaling, and gene expression.

Keywords Carnitine palmitoyltransferase · Exercise · Fatty acid profile · Gastrocnemius · 3-Hydroxyacyl CoA dehydrogenase

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Introduction

There is an increasing interest in the effect of exercise on the fatty acid composition of animal and human tissues, probably because of the gradual unravelling of the role that individual fatty acids play in tissue metabolism and signal transduction. For example, there is evidence linking insulin sensitivity to the fatty acid composition of skeletal muscle phospholipids (PL) (Borkman et al. 1993).

Exercise, both acute and chronic, has long been known to modulate the lipid makeup of many tissues in terms of not only concentration of lipid classes but also their fatty acid composition (reviewed by Nikolaidis and Mougios 2004). There are, however, limited and/or contradictory data on the changes elicited by exercise training in the fatty acid composition of different lipid classes in several tissues including the liver, skeletal muscle, and adipose tissue.

Concerning the liver, a number of studies have examined the effect of exercise training on the fatty acid profile of total lipids in either the whole tissue (Fiebig et al. 1998, 2002; Wirth et al. 1980) or subcellular fractions such as mitochondria (Mataix et al. 1998; Quiles et al. 1999) and microsomes (Venkatraman et al. 1998a, b). Only Šimko et al. (1970) have reported data on individual lipid classes, in particular triacylglycerols (TG) and cholesteryl esters of the whole tissue. We have been unable to find any data on the effect of exercise on the fatty acid profile of liver PL.

Many researchers have studied skeletal muscle in terms of the effect of exercise training on the fatty acid composition of total lipids (Szabó et al. 2002; Wirth

et al. 1980), PL (Andersson et al. 1998, 2000; Ayre et al. 1998; Helge et al. 1999, 2001; Helge and Dela 2003; Kriketos et al. 1995; Nikolaidis et al. 2004), and TG (Andersson et al. 1998, 2000; Helge et al. 2001; Helge and Dela 2003; Nikolaidis et al. 2004). Additionally, a number of researchers have analyzed total lipids in subcellular fractions of muscle tissue, i.e., mitochondria (Mataix et al. 1998; Quiles et al. 1999, 2001) and membranes (Thomas et al. 1977) before and after exercise training. However, there appears to be no consensus as to the effect of exercise.

Although there have been several studies addressing the effect of exercise training on the fatty acid profile of adipose tissue (Allard et al. 1973; Bailey et al. 1993; Danner et al. 1984; Rocquelin and Juaneda 1981; Šimko et al. 1970; Sutherland et al. 1981; Thorling and Overvad 1994; Wirth et al. 1980), again, a clear answer is missing. Except for Šimko et al. (1970), who separated TG, all studies have examined total lipids of adipose tissue. There seem to be no data on the effect of exercise training on the fatty acid profile of adipose tissue PL.

The aim of the present study was to examine the effect of 8 weeks of voluntary wheel running, a stress-free exercise model, on the fatty acid composition of PL and TG in rat liver, gastrocnemius medialis (a muscle involved in the particular exercise), and adipose tissue at two different sites (visceral and subcutaneous). The data in the present work complete our already published results on the differences between trained and untrained rats in the fatty acid composition of PL and TG in serum, skeletal muscle [soleus and extensor digitorum longus (EDL)], as well as the heart (Nikolaidis et al. 2004).

Methods

Animals

Thirty-five male Wistar rats were purchased at the age of 7 weeks from Charles River Laboratories (Sulzfeld, Germany) and were housed under controlled environmental conditions (21°C, 12:12-h light-dark cycle). The rats had free access to water and standard rodent chow, in which fat content was 3.5% and the predominant fatty acids were linoleate (18:2ω6), palmitate (16:0), and oleate (18:1ω9), accounting for 40, 28, and 21% of total fatty acids, respectively (Nikolaidis et al. 2004). The animals were maintained according to the European Union guidelines for the care and use of laboratory animals, as well as the ''Principles of laboratory animal care'' (NIH publication No. 86-23, revised 1985). The study design was approved by the Regional Administration of the city of Cologne (Bezirksregierung Köln).

Training

The animals were divided randomly into a trained ($n = 20$) and an untrained group ($n = 15$). The members of the trained group were housed individually in cages equipped with wheels, in which they exercised ad libitum for 8 weeks, while the members of the untrained group were housed individually in plain cages. The running activity of the trained group was recorded continuously through the DasyLab 5.0 data collection system from Datalog (Mönchengladbach, Germany).

Tissues

Upon completion of the training period, the 11 most active trained animals (having run at least over 2 km/day, average 5.2 km/day) and the 14 untrained animals (one died during the experimental period) were decapitated at approximately the same time of the day (1400–1600 hours). Wheels and food had been removed from the cages 12 h and 6 h earlier, respectively, to minimize the influence of the last exercise bout and the last feeding on the biochemical parameters of interest. The liver, gastrocnemius medialis muscle of the right hindlimb, epididymal fat, and subcutaneous fat from the buttock area were then removed as quickly as possible. The muscle was ridden of visible fat, nerves and fasciae, and all tissues were immediately immersed in liquid nitrogen. All specimens were stored at −80°C until analysis.

Fatty acid analysis

Tissues were pulverized with mortar and pestle in liquid nitrogen. Determination of the fatty acid composition of lipid classes was initiated by the addition of a mixture of diheptadecanoyl phosphatidylcholine and triheptadecanoyl glycerol (all from Sigma, St. Louis, MO, USA) as internal standards to 30 mg liver, 30 mg muscle or 10 mg adipose tissue. Lipids were extracted with 2-propanol–heptane–0.5 M H_2SO_4, 40:10:1 by volume (Dole 1956) and were separated on silica gel TLC plates (Sigma) developed with petroleum ether–diethyl ether–acetic acid, 130:20:1.5 by volume. Lipid spots were located under ultraviolet light after spraying with a solution of dichlorofluorescein in ethanol, were excised separately and transmethylated in methanolic sodium methoxide (Sigma) followed by methanolic boron trifluoride (Fluka, Buchs, Switzerland). The fatty acid methyl esters thus produced were extracted with hexane and separated in a Hewlett Packard 5890 Series II gas chromatograph (Waldbronn, Germany) equipped with a 30-m long AT-WAX capillary column from Alltech (Deerfield, IL, USA) and a flame ionization detector. The column temperature was programmed from 160°C to 250°C at 5°C/min. The carrier gas was helium at a flow rate of 1 ml/min (at 160°C). Methyl esters of individual fatty acids were identified in the chromatograms by comparing their retention times to those of pure methyl esters purchased from Sigma, and were quantified by comparing the area under their peaks to that of methyl heptadecanoate (derived from the internal standards)

with the aid of the HP 3365 ChemStation software from Hewlett Packard.

Enzyme assays

We assayed carnitine palmitoyltransferase (CPT) and 3-hydroxyacyl CoA dehydrogenase (HAD) spectrophotometrically according to Guglielmo et al. (2002) as indices of the capacity of tissues to oxidize fatty acids. CPT and HAD activities were expressed in U/g wet tissue at 25°C. The assays were performed on a single day to eliminate inter-assay variability. The intra-assay coefficient of variation was 7% for both assays.

Calculations and statistics

We calculated the following indices of the fatty acid profile: monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA), ω6 fatty acids, ω3 fatty acids, ω6/ω3, unsaturated to saturated ratio (U/S), and unsaturation index (UI; the average number of double bonds per fatty acid multiplied by 100). Additionally, we estimated fatty acid elongase and Δ^5-, Δ^6- as well as Δ^9-desaturase activities through appropriate product-to-precursor ratios. These were 18:0/16:0 for elongase, 20:4ω6/20:3ω6 for Δ^5-desaturase, 18:3ω6/18:2ω6 for Δ^6-desaturase, and 18:1ω9/18:0 for Δ^9-desaturase. The ratios were calculated from the sum of the concentrations of each fatty acid in PL and TG of each tissue.

Values are expressed as mean ± SD. The distribution of all dependent variables was examined by the Shapiro–Wilk test and was found not to differ significantly from normal. Differences between untrained and trained animals were examined by two-sided unpaired Student's *t*-tests. To determine the meaningfulness of the effects of exercise, we calculated effect sizes as the difference between means divided by the SD of the untrained group. The level of statistical significance was set at $\alpha = 0.05$. The SPSS version 10.0 (SPSS Inc., Chicago, IL, USA) was used for all analyses.

Results

Trained rats had significantly higher activities of muscle CPT ($P < 0.01$, effect size 1.14) and HAD ($P < 0.01$, effect size 1.13) compared to the untrained rats (Fig. 1). There were no differences between trained and untrained animals in liver CPT or HAD. Neither CPT nor HAD activity was detectable in the adipose tissue homogenates.

Gas chromatography revealed the presence of 15 fatty acids in PL and TG, namely, myristate (14:0), 16:0, palmitoleate (16:1ω7), stearate (18:0), 18:1ω9, cis-vaccenate (18:1ω7), 18:2ω6, γ-linolenate (18:3ω6), α-linolenate (18:3ω3), gondoate (20:1ω9), dihomo-γ-linolenate (20:3ω6), arachidonate (20:4ω6), eicosapentaenoate (20:5ω3), docosapentaenoate (22:5ω3), and docosahexaenoate (22:6ω3).

Liver lipids

The effect of training on the fatty acid composition of liver PL and TG is presented in Table 1. Significant differences between trained and untrained rats were limited to the concentrations of three fatty acids (all of which were higher in the trained rats), the percentages of three fatty acids, and the MUFA in PL.

Skeletal muscle lipids

The fatty acid profile of gastrocnemius muscle PL and TG is presented in Table 2. There were few significant differences between groups in the fatty acid profile of PL. On the contrary, all but two fatty acids in TG were significantly lower in the trained compared to untrained rats. As a result, there was a pronounced decrease in total TG concentration. There were also several significant differences in fatty acid percentages, ω3 fatty acids and U/S in TG. Finally, the estimated fatty acid elongase activity was significantly higher and Δ^9-desaturase activity was significantly lower in the trained animals.

Epididymal fat lipids

Table 3 presents the fatty acid profile of epididymal fat PL and TG. There were no significant differences in the fatty acid profile of PL but the concentrations of several

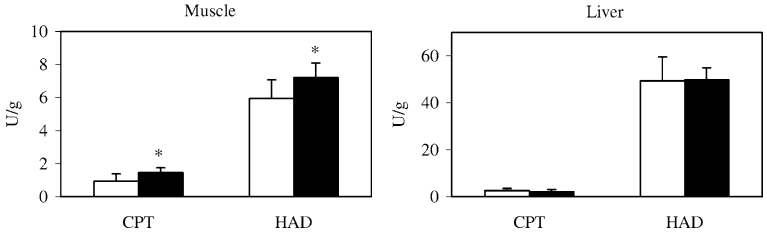

Fig. 1 Carnitine palmitoyltransferase (*CPT*) and 3-hydroxyacyl CoA dehydrogenase (*HAD*) activity in gastrocnemius medialis muscle and liver of untrained (*open bars*) and trained rats (*solid bars*). *Significantly different from untrained ($P < 0.01$)

Table 1 Concentrations and molar percentage distribution of individual fatty acids, as well as indices of the fatty acid profile in liver phospholipids (*PL*) and triacylglycerols (*TG*) of untrained and trained rats

Fatty acid	PL			TG		
	Untrained	Trained	ES	Untrained	Trained	ES
Wet weight (μmol/g)						
14:0	0.095 ± 0.029	0.107 ± 0.020	0.42	0.048 ± 0.036	0.051 ± 0.051	0.08
16:0	7.926 ± 1.696	9.064 ± 1.275	0.67	1.518 ± 1.039	1.376 ± 0.717	−0.14
16:1ω7	0.719 ± 0.387	0.551 ± 0.166	−0.43	0.257 ± 0.295	0.173 ± 0.159	−0.29
18:0	10.624 ± 2.590	12.245 ± 2.107	0.63	0.147 ± 0.071	0.146 ± 0.092	−0.02
18:1ω9	1.657 ± 0.458	1.782 ± 0.373	0.27	1.073 ± 0.928	0.886 ± 0.481	−0.20
18:1ω7	2.628 ± 0.689	2.463 ± 0.364	−0.24	0.233 ± 0.188	0.180 ± 0.094	−0.28
18:2ω6	10.766 ± 2.288	13.053 ± 2.453*	1.00	1.538 ± 0.762	1.479 ± 0.794	−0.08
18:3ω6	0.196 ± 0.032	0.238 ± 0.034*	1.30	0.034 ± 0.011	0.033 ± 0.008	−0.09
18:3ω3	0.082 ± 0.016	0.108 ± 0.032*	1.60	0.081 ± 0.053	0.072 ± 0.047	−0.16
20:1ω9	0.098 ± 0.024	0.103 ± 0.036	0.20	0.013 ± 0.007	0.012 ± 0.006	−0.17
20:3ω6	0.392 ± 0.185	0.413 ± 0.151	0.12	0.020 ± 0.010	0.019 ± 0.009	−0.10
20:4ω6	9.229 ± 2.531	10.366 ± 1.334	0.45	0.253 ± 0.281	0.166 ± 0.062	−0.31
20:5ω3	0.143 ± 0.058	0.178 ± 0.053	0.60	0.032 ± 0.015	0.028 ± 0.013	−0.30
22:5ω3	0.442 ± 0.171	0.534 ± 0.110	0.53	0.040 ± 0.019	0.039 ± 0.018	−0.07
22:6ω3	1.639 ± 0.498	1.718 ± 0.278	0.16	0.062 ± 0.023	0.062 ± 0.028	0.01
Sum	46.636 ± 10.906	52.922 ± 7.839	0.58	5.350 ± 3.393	4.723 ± 2.434	−0.18
Percent						
14:0	0.21 ± 0.06	0.20 ± 0.03	−0.05	0.86 ± 0.24	0.99 ± 0.41	0.53
16:0	17.10 ± 0.82	17.17 ± 0.94	0.09	27.92 ± 2.01	29.13 ± 2.65	0.60
16:1ω7	1.48 ± 0.57	1.04 ± 0.27*	−0.77	4.06 ± 1.79	3.46 ± 1.93	−0.34
18:0	22.82 ± 1.58	23.11 ± 1.66	0.18	3.09 ± 1.62	3.06 ± 0.61	−0.02
18:1ω9	3.54 ± 0.35	3.36 ± 0.41	−0.50	18.69 ± 3.42	18.69 ± 2.40	−0.00
18:1ω7	5.63 ± 0.63	4.67 ± 0.41*	−1.53	4.15 ± 0.92	3.85 ± 0.81	−0.32
18:2ω6	23.24 ± 1.45	24.55 ± 1.56*	0.91	30.19 ± 4.19	31.18 ± 4.81	−0.24
18:3ω6	0.43 ± 0.07	0.45 ± 0.04	0.26	0.74 ± 0.24	0.80 ± 0.24	0.26
18:3ω3	0.18 ± 0.05	0.20 ± 0.04	0.44	1.50 ± 0.28	1.46 ± 0.31	−0.15
20:1ω9	0.22 ± 0.05	0.19 ± 0.05	−0.47	0.27 ± 0.07	0.26 ± 0.06	−0.06
20:3ω6	0.82 ± 0.24	0.77 ± 0.17	−0.21	0.40 ± 0.12	0.43 ± 0.12	0.23
20:4ω6	19.54 ± 2.19	19.65 ± 0.87	0.05	5.38 ± 6.11	3.80 ± 1.07	−0.26
20:5ω3	0.30 ± 0.09	0.34 ± 0.10	0.42	0.65 ± 0.25	0.61 ± 0.17	−0.16
22:5ω3	0.93 ± 0.23	1.02 ± 0.22	0.40	0.80 ± 0.26	0.87 ± 0.28	0.28
22:6ω3	3.56 ± 0.88	3.27 ± 0.46	−0.33	1.29 ± 0.36	1.41 ± 0.45	0.33
Sum	100.00	100.00		100.00	100.00	
Indices						
MUFA (%)	10.86 ± 1.39	9.27 ± 0.91*	−1.15	27.17 ± 5.94	26.26 ± 4.67	−0.15
PUFA (%)	49.01 ± 1.46	50.25 ± 1.92	0.85	40.96 ± 7.01	40.56 ± 6.38	−0.06
ω6 (%)	44.03 ± 1.93	45.42 ± 1.79	0.72	36.72 ± 6.91	36.21 ± 5.60	−0.07
ω3 (%)	4.97 ± 1.00	4.83 ± 0.64	−0.14	4.23 ± 0.95	4.35 ± 1.04	0.12
ω6/ω3	9.19 ± 1.87	9.57 ± 1.45	0.20	9.17 ± 3.43	8.54 ± 1.35	−0.18
U/S	1.50 ± 0.11	1.47 ± 0.10	−0.20	2.16 ± 0.27	2.04 ± 0.27	−0.45
UI	167.3 ± 7.0	167.7 ± 6.0	0.05	132.0 ± 19.4	127.7 ± 13.5	−0.22
Elongase[a]	1.15 ± 0.10	1.19 ± 0.13	−0.41			
Δ^5-desaturase[a]	25.28 ± 8.21	26.10 ± 5.98	−0.10			
Δ^6-desaturase[a]	0.019 ± 0.003	0.019 ± 0.003	0.03			
Δ^9-desaturase[a]	0.25 ± 0.07	0.22 ± 0.04	0.46			

Data are mean ± SD

ES Effect size (difference between means divided by the SD of the untrained group); *MUFA* monounsaturated fatty acids; *PUFA* polyunsaturated fatty acids; *U*/*S* unsaturated/saturated; *UI* unsaturation index

*Significantly different from untrained ($P < 0.05$)

[a]Indices of enzyme activity were calculated from the sum of the concentration of each fatty acid in PL and TG

fatty acids and the percentages of most fatty acids in TG differed significantly between groups. Trained rats had significantly decreased percentage of MUFA, increased percentages of PUFA and ω6, as well as increased ω6/ω3 in TG. Finally, elongase activity increased, whereas Δ^5- and Δ^9-desaturase activities decreased significantly in the trained rats. The differences in elongase and Δ^9-desaturase activities were in the same directions as in muscle.

Subcutaneous fat lipids

The effect of training on the fatty acid composition of subcutaneous fat PL and TG is presented in Table 4. Similarly to epididymal fat, there were no significant differences between groups in PL, whereas there were several significant differences in TG in terms of both fatty acid concentrations and percentages. Total TG concentration was significantly lower, while ω6/ω3 was significantly

Table 2 Concentrations and molar percentage distribution of individual fatty acids, as well as indices of the fatty acid profile in gastrocnemius medialis PL and TG of untrained and trained rats

Fatty acid	PL			TG		
	Untrained	Trained	ES	Untrained	Trained	ES
Wet weight (μmol/g)						
14:0	0.398 ± 1.013	0.135 ± 0.041	−0.26	0.072 ± 0.052	0.016 ± 0.008*	−1.08
16:0	5.620 ± 1.383	5.362 ± 0.524	−0.19	1.526 ± 1.225	0.344 ± 0.152*	−0.96
16:1ω7	0.238 ± 0.067	0.206 ± 0.054	−0.48	0.238 ± 0.220	0.031 ± 0.021*	−0.94
18:0	9.312 ± 0.797	9.808 ± 0.770	0.62	0.223 ± 0.115	0.118 ± 0.030*	−0.91
18:1ω9	0.909 ± 0.274	0.949 ± 0.118	0.15	0.960 ± 0.824	0.231 ± 0.129*	−0.88
18:1ω7	1.028 ± 0.164	1.030 ± 0.163	0.01	0.160 ± 0.139	0.037 ± 0.021*	−0.88
18:2ω6	9.174 ± 1.669	10.857 ± 2.110*	1.01	0.748 ± 0.605	0.173 ± 0.115*	−0.95
18:3ω6	0.109 ± 0.015	0.122 ± 0.018	0.85	0.015 ± 0.002	0.014 ± 0.002	−0.64
18:3ω3	0.059 ± 0.014	0.071 ± 0.016	0.86	0.017 ± 0.013	0.005 ± 0.001*	−0.90
20:1ω9	0.035 ± 0.010	0.049 ± 0.013*	1.41	0.011 ± 0.009	0.005 ± 0.002*	−0.62
20:3ω6	0.155 ± 0.037	0.157 ± 0.037	0.06	ND	ND	
20:4ω6	2.873 ± 0.624	3.013 ± 0.528	0.22	0.020 ± 0.014	0.005 ± 0.003*	−1.05
20:5ω3	0.099 ± 0.093	0.084 ± 0.054	−0.16	0.012 ± 0.005	0.008 ± 0.005	−0.74
22:5ω3	0.978 ± 0.206	0.957 ± 0.228	−0.10	ND	ND	
22:6ω3	3.167 ± 0.780	3.585 ± 0.670	0.54	ND	ND	
Sum	34.154 ± 4.500	36.387 ± 4.461	0.50	4.002 ± 2.843	0.988 ± 0.474*	−1.06
Percent						
14:0	1.06 ± 2.55	0.38 ± 0.13	−0.27	1.85 ± 0.60	1.74 ± 0.40	−0.18
16:0	16.48 ± 3.19	14.80 ± 1.16	−0.52	37.39 ± 13.50	35.51 ± 1.91	−0.14
16:1ω7	0.69 ± 0.17	0.56 ± 0.11*	−0.78	5.52 ± 2.43	2.90 ± 0.95*	−1.08
18:0	27.45 ± 1.93	27.13 ± 2.13	−0.17	6.59 ± 2.34	13.37 ± 3.44*	2.90
18:1ω9	2.63 ± 0.73	2.61 ± 0.18	−0.03	23.36 ± 5.80	22.45 ± 2.38	−0.16
18:1ω7	3.01 ± 0.29	2.83 ± 0.25	−0.62	3.90 ± 0.90	3.53 ± 0.60	−0.41
18:2ω6	26.83 ± 2.58	29.65 ± 2.32*	1.10	19.07 ± 6.08	16.14 ± 3.73	−0.48
18:3ω6	0.32 ± 0.05	0.34 ± 0.04	0.31	0.56 ± 0.39	1.75 ± 0.89*	3.02
18:3ω3	0.17 ± 0.03	0.19 ± 0.03	0.66	0.54 ± 0.59	0.61 ± 0.32	0.12
20:1ω9	0.10 ± 0.03	0.13 ± 0.03*	1.24	0.29 ± 0.14	0.55 ± 0.18*	1.88
20:3ω6	0.46 ± 0.09	0.43 ± 0.07	−0.28			
20:4ω6	8.39 ± 1.19	8.25 ± 0.72	−0.12	0.54 ± 0.20	0.50 ± 0.19	−0.19
20:5ω3	0.29 ± 0.26	0.24 ± 0.17	−0.21	0.38 ± 0.16	0.94 ± 0.41*	3.39
22:5ω3	2.85 ± 0.34	2.64 ± 0.52	−0.62			
22:6ω3	9.25 ± 1.65	9.81 ± 1.01	0.34			
Sum	100.00	100.00		100.00	100.00	
Indices						
MUFA (%)	6.44 ± 1.03	6.14 ± 0.43	−0.30	33.07 ± 8.54	29.43 ± 3.43	−0.43
PUFA (%)	48.56 ± 5.18	51.55 ± 2.84	0.58	21.10 ± 6.79	19.94 ± 2.75	−0.17
ω6 (%)	36.00 ± 3.53	38.67 ± 2.49*	0.76	20.17 ± 6.36	18.39 ± 3.09	−0.28
ω3 (%)	12.56 ± 1.88	12.88 ± 1.27	0.17	0.92 ± 0.61	1.55 ± 0.59*	1.03
ω6/ω3	2.89 ± 0.25	3.03 ± 0.35	0.54	24.81 ± 8.85	15.73 ± 13.26	−1.03
U/S	1.25 ± 0.25	1.37 ± 0.17	0.49	1.27 ± 0.38	1.00 ± 0.21*	−0.73
UI	167.7 ± 19.8	174.6 ± 9.9	0.35	78.6 ± 18.5	75.5 ± 6.6	−0.17
Elongase[a]	1.39 ± 0.29	1.75 ± 0.18*	1.23			
Δ^5-desaturase[a]	19.10 ± 3.39	19.68 ± 3.42	0.17			
Δ^6-desaturase[a]	0.013 ± 0.002	0.013 ± 0.002	−0.12			
Δ^9-desaturase[a]	0.20 ± 0.10	0.12 ± 0.02*	−0.81			

Data are mean ± SD

ES Effect size (difference between means divided by the SD of the untrained group); *MUFA* monounsaturated fatty acids; *ND* not detected; *PUFA* polyunsaturated fatty acids; *U*/*S* unsaturated/saturated; *UI* unsaturation index

*Significantly different from untrained ($P < 0.05$)

[a]Indices of enzyme activity were calculated from the sum of the concentration of each fatty acid in PL and TG

higher in TG of the trained rats. Again, elongase activity was higher and Δ^9-desaturase activity was lower in the trained rats, as in muscle and epididymal fat.

Discussion

Interest in the effects of exercise on the fatty acid composition of tissues has been rising at an exponential rate in recent years (Nikolaidis and Mougios 2004), as it is becoming increasingly apparent that individual fatty acids play distinct roles in many biological functions including ion homeostasis, gene expression, signal transduction, and synthesis of lipid or lipid-derived messengers (Kogteva and Bezuglov 1998). We have attempted to contribute to the elucidation of how exercise affects the fatty acid profile of tissues by employing a model of spontaneous physical activity, wheel running.

Table 3 Concentrations and molar percentage distribution of individual fatty acids, as well as indices of the fatty acid profile in epididymal adipose tissue PL and TG of untrained and trained rats

Fatty acid	PL			TG		
	Untrained	Trained	ES	Untrained	Trained	ES
Wet weight (μmol/g)						
14:0	0.298 ± 0.218	0.332 ± 0.152	0.16	30.2 ± 5.0	27.9 ± 4.2	−0.46
16:0	2.943 ± 1.235	3.586 ± 1.441	0.52	627.3 ± 81.0	589.3 ± 58.7	−0.47
16:1ω7	0.364 ± 0.129	0.411 ± 0.131	0.36	132.3 ± 37.1	93.3 ± 25.1*	−1.05
18:0	1.594 ± 0.694	2.091 ± 0.948	0.72	69.8 ± 10.3	79.7 ± 6.4*	0.97
18:1ω9	1.972 ± 0.734	2.529 ± 0.928	0.76	477.1 ± 62.5	446.1 ± 42.1	−0.50
18:1ω7	0.332 ± 0.114	0.411 ± 0.138	0.69	97.0 ± 13.8	79.4 ± 10.9*	−1.27
18:2ω6	1.925 ± 0.683	2.439 ± 0.815	0.75	806.3 ± 159.3	871.4 ± 115.0	0.41
18:3ω6	0.062 ± 0.035	0.098 ± 0.066	1.03	4.9 ± 0.8	5.5 ± 0.9	0.63
18:3ω3	0.130 ± 0.068	0.169 ± 0.075	0.58	63.8 ± 12.0	60.4 ± 9.7	−0.28
20:1ω9	0.093 ± 0.043	0.116 ± 0.045	0.53	7.3 ± 1.5	8.6 ± 2.0	0.84
20:3ω6	0.029 ± 0.018	0.038 ± 0.020	0.48	3.5 ± 0.7	4.5 ± 0.7*	1.45
20:4ω6	0.091 ± 0.031	0.116 ± 0.050	0.80	20.4 ± 4.6	22.0 ± 5.2	0.35
20:5ω3	ND	ND		3.3 ± 1.0	3.2 ± 1.0	−0.18
22:5ω3	ND	ND		6.0 ± 1.8	6.0 ± 2.0	−0.01
22:6ω3	ND	ND		ND	ND	
Sum	9.834 ± 3.714	12.336 ± 4.665	0.67	2349.2 ± 309.1	2303.7 ± 207.2	−0.15
Percent						
14:0	2.88 ± 1.25	2.68 ± 0.49	−0.16	1.28 ± 0.12	1.21 ± 0.15	−0.61
16:0	29.65 ± 2.69	28.96 ± 1.77	−0.26	26.68 ± 1.24	25.59 ± 1.37*	−0.87
16:1ω7	3.77 ± 0.41	3.49 ± 0.60	−0.69	5.67 ± 1.58	4.05 ± 1.00*	−1.03
18:0	16.00 ± 2.49	16.35 ± 2.03	0.14	2.96 ± 0.17	3.47 ± 0.23*	3.04
18:1ω9	20.17 ± 1.05	20.57 ± 0.83	0.39	20.31 ± 1.44	19.39 ± 1.07	−0.64
18:1ω7	3.45 ± 0.46	3.41 ± 0.43	−0.09	4.14 ± 0.46	3.44 ± 0.36*	−1.51
18:2ω6	19.96 ± 2.25	20.20 ± 1.57	0.11	34.05 ± 4.11	37.79 ± 3.13*	0.91
18:3ω6	0.61 ± 0.22	0.76 ± 0.44	0.67	0.21 ± 0.03	0.24 ± 0.03*	0.98
18:3ω3	1.28 ± 0.31	1.33 ± 0.18	0.19	2.69 ± 0.28	2.62 ± 0.31	−0.27
20:1ω9	0.94 ± 0.34	0.96 ± 0.21	0.07	0.31 ± 0.05	0.37 ± 0.08*	1.28
20:3ω6	0.31 ± 0.18	0.31 ± 0.15	0.03	0.15 ± 0.03	0.20 ± 0.03*	1.70
20:4ω6	1.00 ± 0.34	0.97 ± 0.29	−0.07	0.86 ± 0.13	0.95 ± 0.19	0.71
20:5ω3				0.14 ± 0.04	0.14 ± 0.04	−0.11
22:5ω3				0.26 ± 0.07	0.26 ± 0.08	0.01
Sum	100.00	100.00		100.00	100.00	
Indices						
MUFA (%)	28.33 ± 1.54	28.43 ± 1.23	0.07	30.44 ± 3.39	27.25 ± 2.28*	−0.94
PUFA (%)	23.16 ± 2.68	23.58 ± 1.72	0.16	38.64 ± 4.46	42.47 ± 3.61*	0.86
ω6 (%)	21.88 ± 2.54	22.25 ± 1.74	0.14	35.27 ± 4.14	39.17 ± 3.23*	0.94
ω3 (%)	1.28 ± 0.31	1.33 ± 0.18	0.19	3.37 ± 0.35	3.30 ± 0.44	−0.20
ω6/ω3	17.84 ± 3.63	17.01 ± 2.99	−0.23	10.46 ± 0.55	11.97 ± 1.04*	2.75
U/S	1.07 ± 0.16	1.09 ± 0.12	0.10	2.24 ± 0.14	2.31 ± 0.16	0.51
UI	78.8 ± 7.3	79.9 ± 5.0	0.15	114.8 ± 6.2	119.5 ± 5.9	0.76
Elongase[a]	0.11 ± 0.01	0.14 ± 0.01*	2.99			
Δ^5-desaturase[a]	5.99 ± 1.64	4.87 ± 0.76*	−0.68			
Δ^6-desaturase[a]	0.006 ± 0.001	0.006 ± 0.001	0.04			
Δ^9-desaturase[a]	6.77 ± 0.78	5.49 ± 0.41*	−1.64			

Data are mean ± SD

ES Effect size (difference between means divided by the SD of the untrained group); *MUFA* monounsaturated fatty acids; *PUFA* polyunsaturated fatty acids; *ND* not detected; *U*/*S* unsaturated/saturated; *UI* unsaturation index

*Significantly different from untrained ($P < 0.05$)

[a]Indices of enzyme activity were calculated from the sum of the concentration of each fatty acid in PL and TG

The training stimulus was sufficient to elicit adaptive responses, judging from the increases in muscle CPT and HAD activities. These increases can be considered large in terms of percentage (55% and 22%, respectively) and effect size (over 1.1) according to the classification of Cohen (1988), who set the threshold for large effect sizes at 0.8.

Most of the studies that have investigated the effects of exercise on fatty acid composition have reported data on individual fatty acids as percentages of total rather than concentrations. Percentage distribution is easier to determine (as there is no need for a reference standard) and permits comparisons among biological samples while normalizing differences in total fatty acid content. However, by comparing percentages only, one may miss significant changes in concentrations if most or all are in the same direction. Alternatively, a large change in the concentration of one fatty acid may alter the percentages of fatty acids whose concentrations have not changed, thus confounding data interpretation. Thus we decided

Table 4 Concentrations and molar percentage distribution of individual fatty acids as well as indices of the fatty acid profile in subcutaneous adipose tissue PL and TG of untrained and trained rats

Fatty acid	PL			TG		
	Untrained	Trained	ES	Untrained	Trained	ES
Wet weight (μmol/g)						
14:0	0.828 ± 0.291	0.909 ± 0.323	0.28	33.0 ± 8.9	23.8 ± 7.5*	−1.04
16:0	7.604 ± 1.851	8.381 ± 2.502	0.42	579.6 ± 47.9	445.6 ± 84.7*	−2.80
16:1ω7	0.488 ± 0.110	0.502 ± 0.212	0.13	111.8 ± 45.9	67.2 ± 29.3*	−0.97
18:0	7.342 ± 1.856	7.985 ± 2.531	0.35	65.7 ± 9.6	64.1 ± 16.3	−0.16
18:1ω9	4.189 ± 1.355	4.659 ± 1.664	0.35	450.2 ± 45.6	363.0 ± 72.1*	−1.91
18:1ω7	0.566 ± 0.208	0.724 ± 0.392	0.76	86.9 ± 9.3	63.7 ± 10.8*	−2.49
18:2ω6	3.430 ± 1.139	4.018 ± 1.569	0.52	782.1 ± 106.6	704.2 ± 173.4	−0.73
18:3ω6	0.305 ± 0.349	0.241 ± 0.162	−0.18	4.4 ± 0.9	4.4 ± 1.0	−0.02
18:3ω3	0.321 ± 0.082	0.399 ± 0.239	0.95	55.2 ± 9.7	43.0 ± 10.8*	−1.27
20:1ω9	0.196 ± 0.065	0.204 ± 0.138	0.13	7.5 ± 0.8	6.8 ± 1.7	−0.92
20:3ω6	0.191 ± 0.079	0.198 ± 0.075	0.09	2.8 ± 0.6	2.8 ± 0.8	0.09
20:4ω6	0.490 ± 0.149	0.747 ± 0.370*	1.73	17.5 ± 5.2	16.0 ± 5.0	−0.29
20:5ω3	ND	ND		1.8 ± 1.9	1.4 ± 0.4	−0.21
22:5ω3	ND	ND		4.3 ± 1.7	3.7 ± 1.2	−0.34
22:6ω3	ND	ND		4.7 ± 2.3	3.8 ± 1.1	−0.40
Sum	25.951 ± 6.235	28.968 ± 8.579	0.48	2207.7 ± 80.1	1813.3 ± 367.1*	−4.93
Percent						
14:0	3.18 ± 0.65	3.17 ± 0.81	−0.02	1.50 ± 0.40	1.28 ± 0.33	−0.55
16:0	29.31 ± 1.40	28.90 ± 1.28	−0.30	26.26 ± 1.99	24.65 ± 1.08*	−0.81
16:1ω7	1.92 ± 0.34	1.73 ± 0.47	−0.56	5.04 ± 2.00	3.78 ± 1.75	−0.63
18:0	28.40 ± 3.75	27.82 ± 4.27	−0.15	2.98 ± 0.47	3.54 ± 0.58*	1.17
18:1ω9	15.95 ± 2.11	15.90 ± 1.84	−0.02	20.38 ± 1.77	20.12 ± 1.56	−0.15
18:1ω7	2.18 ± 0.59	2.44 ± 0.63	0.45	3.93 ± 0.37	3.56 ± 0.42*	−1.01
18:2ω6	13.18 ± 2.81	13.74 ± 2.86	0.20	35.45 ± 4.80	38.56 ± 3.45	0.65
18:3ω6	1.19 ± 1.45	0.80 ± 0.28	−0.27	0.20 ± 0.04	0.24 ± 0.04*	1.08
18:3ω3	1.25 ± 0.21	1.34 ± 0.41	0.41	2.50 ± 0.41	2.36 ± 0.23	−0.35
20:1ω9	0.77 ± 0.30	0.69 ± 0.30	−0.30	0.34 ± 0.05	0.38 ± 0.06	0.72
20:3ω6	0.73 ± 0.24	0.69 ± 0.23	−0.17	0.12 ± 0.03	0.16 ± 0.04*	1.23
20:4ω6	1.94 ± 0.54	2.79 ± 1.83	1.57	0.79 ± 0.23	0.88 ± 0.18	0.38
20:5ω3				0.08 ± 0.08	0.08 ± 0.03	0.00
22:5ω3				0.19 ± 0.08	0.21 ± 0.07	0.22
22:6ω3				0.21 ± 0.10	0.21 ± 0.04	−0.05
Sum	100.00	100.00		100.00	100.00	
Indices						
MUFA (%)	20.82 ± 2.63	20.75 ± 2.51	−0.02	29.70 ± 3.81	27.84 ± 3.49	−0.49
PUFA (%)	18.29 ± 2.72	19.36 ± 2.50	0.39	39.56 ± 5.45	42.70 ± 3.66	0.58
ω6 (%)	17.05 ± 2.63	18.03 ± 2.30	0.37	36.57 ± 4.99	39.84 ± 3.52	0.65
ω3 (%)	1.25 ± 0.21	1.34 ± 0.41	0.41	2.99 ± 0.57	2.86 ± 0.30	−0.23
ω6/ω3	13.91 ± 2.52	14.41 ± 3.69	0.20	12.41 ± 1.41	14.03 ± 1.46*	1.15
U/S	0.65 ± 0.13	0.68 ± 0.12	0.21	2.27 ± 0.25	2.40 ± 0.16	0.52
UI	64.5 ± 7.3	67.9 ± 7.4	0.47	114.9 ± 8.6	119.4 ± 4.8	0.53
Elongase[a]	0.13 ± 0.02	0.16 ± 0.02*	1.45			
Δ^5-desaturase[a]	6.19 ± 1.68	5.68 ± 1.64	−0.30			
Δ^6-desaturase[a]	0.006 ± 0.001	0.007 ± 0.001	0.61			
Δ^9-desaturase[a]	6.35 ± 1.16	5.22 ± 1.04*	−0.97			

Data are mean ± SD

ES Effect size (difference between means divided by the SD of the untrained group); *MUFA* monounsaturated fatty acids; *PUFA* polyunsaturated fatty acids; *ND* not detected; *U/S* unsaturated/saturated; *UI* unsaturation index

*Significantly different from untrained ($P < 0.05$)

[a]Indices of enzyme activity were calculated from the sum of the concentration of each fatty acid in PL and TG

to determine and present concentrations along with percentages.

We found no significant differences in the total concentrations of liver PL or TG between trained and untrained rats, in agreement with other studies (reviewed by Górski et al. 1990). Regarding the fatty acid profile of these lipids, we found a limited number of differences in PL and no differences in TG. Our findings disagree with those of Šimko et al. (1970), who reported increased TG MUFA and PUFA in rats after 105 days of swimming training. The difference in the type of exercise may be responsible for this discrepancy. No other comparison with the literature can be made, since other studies examining the effect of exercise training on fatty acid composition in the liver have not separated lipid classes. Obviously, data from this type of analysis are of limited value, since it is impossible to assign any changes in the fatty acid pattern to specific lipid classes.

Concerning muscle, its total TG content was greatly reduced with training. Most of the relevant studies have found decreases (Froberg et al. 1972; Kaciuba-Uscilko et al. 1981; Oscai et al. 1982), although no differences between trained and untrained rats have also been reported (Lee et al. 2002). The reduction found in the present study (by 75%) was larger than the ones found in the soleus (32%) and EDL (34%) of the same animals (Nikolaidis et al. 2004), suggesting a greater responsiveness of gastrocnemius muscle TG to training.

We found several differences in the fatty acid profile of muscle PL and TG between groups. Comparison with relevant studies (Andersson et al. 1998, 2000; Ayre et al. 1998; Helge and Dela 2003; Helge et al. 1999, 2001; Kriketos et al. 1995; Szabó et al. 2002) is very difficult, since there is no agreement as to the effect of exercise training on the fatty acid profile of muscle PL and TG. This is probably due to the near uniqueness of each of these studies in terms of type of exercise, species, diet, and lipids examined. Nevertheless, a comparison can be made with the effect of training on the fatty acid profile of PL and TG in soleus and EDL of the same animals (Nikolaidis et al. 2004). In general, this effect was similar in the three skeletal muscles.

The absence of differences in the fatty acid composition of PL in either visceral or subcutaneous fat between trained and untrained rats suggests that adipose tissue PL are rather insensitive to exercise training. In contrast to PL, there were many exercise training-induced differences in the fatty acid profile of adipose tissue TG and a remarkable decrease in the TG content of subcutaneous fat (by 18%). Differences in the fatty acid profile with training were in the same direction in the two fat depots examined. These differences can be summarized in decreased MUFA and increased PUFA, especially the ω6 fatty acids. The similarity between fat depots is in agreement with the only other study which compared the effect of training on the fatty acid profile of more than one fat depot (Bailey et al. 1993).

All the studies on the effect of exercise training on the fatty acid composition of adipose tissue, except for that of Šimko et al. (1970), have analyzed total lipids rather than separate lipid classes. In order to compare our adipose tissue data with those of the other studies, we assumed that the reported differences in the fatty acid profile emanated from TG, since TG represent 90–99% of adipose tissue lipids (Jeanrenaud 1965). In this sense, our findings generally agree with the relevant literature (Allard et al. 1973; Danner et al. 1984; Rocquelin and Juaneda 1981; Šimko et al. 1970; Sutherland et al. 1981; Thorling and Overvad 1994; Wirth et al. 1980).

Comparison of the fatty acid profile among the tissues examined yields some interesting results. To begin with, the lipid pools with the most similar fatty acid composition to that of the diet (one of the main determinants of the fatty acid composition of tissue lipids) appear to be liver and adipose tissue TG, possibly reflecting their major roles in handling and storing dietary fat. Muscle TG had a quite different fatty acid composition suggesting considerable fatty acid selectivity in TG biosynthesis and/or degradation. Regarding PL, their fatty acid profile was very similar in liver and muscle, and differed from the profiles of the two fat depots. The two fat depots had unexpectedly different profiles in PL as evidenced, for example, by the different order of the four most abundant fatty acids (16:0, 18:1ω9, 18:2ω6, and 18:0 in epididymal fat vs. 16:0, 18:0, 18:1ω9, and 18:2ω6 in subcutaneous fat). Of course, the aforementioned similarities and differences among the tissues are also reflected in the indices of their fatty acid profiles (MUFA, PUFA, etc.).

Despite the aforementioned differences in fatty acid profile among tissues, most of the differences in the fatty acid percentages with training were in the same direction in muscle and adipose tissue TG (but not liver TG), as reflected in the signs of the corresponding effect sizes. This striking similarity extends to the organs analyzed in our previous work, i.e., soleus muscle, EDL muscle, and heart (Nikolaidis et al. 2004). Significant differences in the fatty acid concentrations and percentages of PL in the peripheral tissues examined in this study (i.e., skeletal muscle and adipose tissue) were fewer than those of TG. In contrast, no differences in TG were found in the liver. These findings suggest that exercise training affects storage lipids more than it affects structural lipids in peripheral tissues.

Almost all of the effect sizes that accompanied significant differences in fatty acid composition (49 out of 50) were large. To further explore the meaningfulness of these differences, we calculated them as percentages relative to the respective values of the untrained group. These were, on average, 18% in liver, 70% in muscle (because of the large decrease in the concentrations of TG fatty acids), and 22% in adipose tissue. Thus, whether expressed as SD units (i.e., effect size) or percentage change, the effects of exercise training on the fatty acid composition of tissues were large in this study.

At present we have no hint as to what the mechanism of the observed differences in fatty acid profile between trained and untrained animals might be. Possibilities include altered rates and/or selectivities in (1) fatty acid transport across cellular membranes, (2) fatty acid production through TG and PL hydrolysis, (3) fatty acid oxidation, and (4) lipid biosynthesis. These alterations may be due to changes in the activity and/or expression of the proteins involved.

In conclusion, the present study showed that exercise training with wheel running for 8 weeks modified the fatty acid composition of rat liver PL, skeletal muscle PL and TG, as well as adipose tissue TG. In contrast, exercise training had no effect on liver TG and adipose tissue PL. Data on liver and adipose tissue PL are appearing for the first time. Differences in the fatty acid profile of TG and differences in the indices of activity of two enzymes involved in fatty acid biosynthesis (elongase and Δ^9-desaturase) were in the same direction in peripheral tissues, implying that a common mechanism may underlie the effect of exercise training on the fatty

acid composition of these tissues. The physiological significance of the observed differences is unknown. However, given the involvement of fatty acids in membrane properties, cell signaling, and gene expression, one may assume that such alterations affect tissue physiology and biochemistry. In this sense, the exercise-induced differences in the fatty acid profile may be promising in delineating the effects of exercise on the aforementioned biological functions.

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