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Effects of Soya Oil upon the Metabolic Syndrome of ω 3-Depleted Rats

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1. Introduction

The bolus intravenous injection of a novel medium-chain triglyceride:fish oil emulsion was recently proposed as a suitable tool to increase within 60 min the long-chain polyunsaturated ω 3 fatty acid content of cell phospholipids (Carpentier et al., 2010). The optimal procedure for the dietary correction of the metabolic and hormonal perturbations found in situations of ω 3-depletion, in terms of the total lipid content and source of ω 3 fatty acids in the diet, as well as the time course for the enrichment of tissue lipids in these ω 3 fatty acids, merits, however, further attention (Malaisse et al., 2011). In such a perspective, the present report deals mainly with the possible suitability of a diet containing 5% (w/w) soya oil, as assessed in rats first exposed for 3 months to an ω 3-deficient sunflower oil (also 5%) diet.

2. Materials and methods

Six groups of 4 fed female rats each were examined in the present study. Two groups consisted of control animals exposed from the age of 8 weeks after birth for 3 months to a diet containing 5% (w/w) soya oil and examined either at the end of this 3 months initial period or 8 weeks later whilst being maintained on the soya oil diet. The other 4 groups of rats were first exposed during the initial 3 months period to a diet containing 5% (w/w) sunflower oil (ω 3D rats) and examined either at the end of this 3 months initial period or after further exposure for one, two or eight weeks to the soya oil diet. Six further ω 3D rats were maintained after the end of the initial 3 months period and for the ensuing 8 weeks to the sunflower oil diet, but were only examined for their food intake and body weight. The rats were eventually sacrificed by CO₂ inhalation. The methods used for collection of intestinal mucosa at the jejunal and caecal level (Hacquebard et al., 2009), liver (Malaisse et al., 2009), red blood cell (Carpentier et al., 2011a), brain (Portois et al., 2009) and both visceral and parametrial adipose tissue (Portois et al., 2007) sampling, lipid extraction (Folch et al., 1957), separation by thin-layer chromatography (Dahlan et al., 1992) and determination of lipid fatty acid pattern by gas-liquid chromatography (Lepage & Roy, 1986), food intake measurements (Zhang et al., 2010) and plasma D-glucose (Lowry & Passonneau, 1972) and insulin (Leclercq-Meyer et al., 1985) determinations were previously described in the cited references.

All results are presented as mean values (\pm SEM) together with the number of individual observations (n) or degree of freedom (df). Except if otherwise mentioned, all tabulated values refer to four individual determinations. In the case of RBC, however, the measurements listed for ω 3D rats examined 1 or 2 weeks after the switch in diet refer to single measurements made in pooled material from 4 rats. In the Tables, the indication N.T. refers to non-tabulated data. The statistical significance of differences between mean values was assessed by use of Student's *t*-test.

3. Results

3.1 Fatty acid pattern of intestinal phospholipids

3.1.1 Long-chain polyunsaturated ω 3 fatty acids

At the end of the 3 months initial period, the relative weight content of all ω 3 fatty acids (C18:3 ω 3, C20:5 ω 3, C22:5 ω 3 and C22:6 ω 3) was significantly lower ($p < 0.005$ or less), whether in the jejunum or caecum, in the ω 3D rats than in the control animals (Table 1). When the former rats were then exposed for one week to the soya oil diet, a significant increase ($p < 0.02$ or less) in the C18:3 ω 3, C22:5 ω 3 and C22:6 ω 3 relative content of jejunal phospholipids and in the C22:5 ω 3 and C22:6 ω 3 content of caecal phospholipids was observed, whilst such was not the case for either the C20:5 ω 3 content of jejunal phospholipids or C18:3 ω 3 and C20:5 ω 3 content of caecal phospholipids. Nevertheless, the mean values reached in the ω 3D rats exposed for one week to the soya oil remained, as a rule, lower than those found in the control animals at the end of the 3 months initial period. Even, in the two out of eight instances in which such was not the case, i.e. for the C18:3 ω 3 content of jejunal phospholipids and C22:5 ω 3 content of caecal phospholipids, no significant difference ($p > 0.3$ or more) was found between the two groups of rats under consideration.

| Rats | C18:3 ω 3 | C20:5 ω 3 | C22:5 ω 3 | C22:6 ω 3 |
|--------------------|------------------|------------------|------------------|------------------|
| <u>Jejunum</u> | | | | |
| Control before | 7.10 \pm 1.46 | 0.00 \pm 0.00 | 4.18 \pm 0.39 | 39.51 \pm 2.00 |
| ω 3D before | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 14.86 \pm 1.62 |
| after (1 wk) | 8.30 \pm 1.35 | 0.42 \pm 0.42 | 2.89 \pm 0.32 | 25.88 \pm 2.18 |
| <u>Caecum</u> | | | | |
| Control before | 1.46 \pm 1.46 | 2.76 \pm 1.60 | 2.74 \pm 2.74 | 49.94 \pm 6.83 |
| ω 3D before | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 5.49 \pm 5.49 |
| after (1 wk) | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 5.60 \pm 0.65 | 23.80 \pm 1.57 |

Table 1. Relative weight content (%) of long-chain polyunsaturated ω 3 fatty acids in jejunum and caecum phospholipids

3.1.2 Long-chain polyunsaturated ω 6 fatty acids

As shown in Table 2, no significant difference between the three groups of rats was observed in terms of the relative weight content of C18:2 ω 6, C20:3 ω 6 and C20:4 ω 6 in the jejunal phospholipids. However, the content of C20:2 ω 6, C22:4 ω 6 and C22:5 ω 6, expressed relative to their respective overall mean values averaged 38.2 \pm 12.0% (n = 12) in the control animals examined at the end of the 3 months initial period, as distinct ($p < 0.001$) from 166.2

$\pm 17.6\%$ ($n = 12$) in the ω 3D rats examined before the switch in diet. After one week exposure to the soya oil diet, the latter percentage was decreased ($p < 0.005$) to $95.6 \pm 8.4\%$ ($n = 12$), the latter value remaining higher ($p < 0.001$) than that recorded in the control animals. The relative weight content of ω 6 fatty acids differed, on occasion, in the jejunal *versus* caecal phospholipids. For instance, the weight content of C18:2 ω 6 averaged $320.88 \pm 9.60\%$ ($n = 12$) at the jejunal level, as distinct ($p < 0.001$) from only $187.42 \pm 5.53\%$ ($n = 12$) at the caecal level. Moreover, as a rule, no significant difference between the mean values recorded in the three groups of rats was observed for the relative weight content of ω 6 fatty acids in the caecal phospholipids. Only in the case of C22:5 ω 6, a significant increase ($p < 0.001$) in the content of this fatty acid in caecal phospholipids was found when comparing control animals and ω 3D rats both examined at the end of the 3 months initial period, with an in-between value ($p < 0.01$ or less) in the ω 3D rats examined one week after the switch in diet.

| Rats | | C18:2 ω 6 | C20:2 ω 6 | C20:3 ω 6 | C20:4 ω 6 | C22:4 ω 6 | C22:5 ω 6 |
|-------------|--------------|--------------------|------------------|------------------|--------------------|------------------|------------------|
| | | Jejunum | | | | | |
| Control | before | 314.40 \pm 19.28 | 1.16 \pm 0.68 | 5.71 \pm 0.45 | 175.68 \pm 21.41 | 4.24 \pm 0.60 | 0.00 \pm 0.00 |
| ω 3D | before | 316.85 \pm 16.43 | 4.61 \pm 0.71 | 6.31 \pm 0.75 | 173.77 \pm 8.19 | 7.94 \pm 1.66 | 16.80 \pm 3.09 |
| | after (1 wk) | 331.38 \pm 17.79 | 2.87 \pm 0.41 | 4.94 \pm 0.58 | 167.09 \pm 11.11 | 4.94 \pm 0.39 | 8.48 \pm 1.84 |
| | | Caecum | | | | | |
| Control | before | 192.02 \pm 12.80 | 3.40 \pm 1.96 | 16.50 \pm 0.36 | 164.85 \pm 12.04 | 16.69 \pm 5.70 | 2.13 \pm 1.32 |
| ω 3D | before | 189.76 \pm 8.28 | 0.00 \pm 0.00 | 7.42 \pm 4.34 | 200.00 \pm 13.13 | 29.56 \pm 3.28 | 26.47 \pm 1.37 |
| | after (1 wk) | 180.50 \pm 8.92 | 3.66 \pm 2.12 | 16.59 \pm 0.62 | 214.29 \pm 10.21 | 24.39 \pm 1.05 | 16.12 \pm 2.25 |

Table 2. Relative weight content (%) of long-chain polyunsaturated ω 6 fatty acids in jejunum and caecum phospholipids

3.1.3 Saturated fatty acids

The relative weight content of saturated fatty acids often differed significantly in jejunal *versus* caecal phospholipids (Table 3). For instance, the C14:0 content was close to 15-fold higher ($p < 0.001$) in the caecal phospholipids ($9.44 \pm 1.13\%$; $n = 12$) than in the jejunal phospholipids ($0.64 \pm 0.23\%$; $n = 12$). Whether at the jejunal or caecal level, no significant difference was observed between the relative weight content of a given saturated fatty acid in the three groups of rats under consideration.

| Rats | | C14:0 | C16:0 | C18:0 | C20:0 | C22:0 | C24:0 |
|-------------|--------------|------------------|--------------------|--------------------|------------------|------------------|------------------|
| | | Jejunum | | | | | |
| Control | before | 0.00 \pm 0.00 | 167.22 \pm 3.42 | 198.25 \pm 9.42 | 7.00 \pm 0.79 | 7.58 \pm 0.53 | 6.25 \pm 0.51 |
| ω 3D | before | 0.78 \pm 0.45 | 164.31 \pm 10.29 | 204.77 \pm 5.02 | 9.32 \pm 3.02 | 10.83 \pm 2.73 | 9.24 \pm 2.38 |
| | after (1 wk) | 1.15 \pm 0.39 | 160.78 \pm 4.72 | 198.89 \pm 6.32 | 7.30 \pm 0.60 | 8.33 \pm 0.69 | 8.43 \pm 0.99 |
| | | Caecum | | | | | |
| Control | before | 7.79 \pm 3.03 | 247.74 \pm 15.67 | 123.27 \pm 10.61 | 15.05 \pm 3.28 | 18.09 \pm 5.06 | 18.20 \pm 7.70 |
| ω 3D | before | 9.01 \pm 0.69 | 242.60 \pm 10.81 | 129.05 \pm 4.07 | 11.83 \pm 2.12 | 12.85 \pm 2.12 | 9.61 \pm 1.39 |
| | after (1 wk) | 11.51 \pm 1.38 | 233.53 \pm 12.15 | 120.62 \pm 4.78 | 10.55 \pm 1.18 | 10.11 \pm 1.24 | 7.98 \pm 1.50 |

Table 3. Relative weight content (%) of saturated fatty acids in jejunum and caecum phospholipids

3.1.4 Monodesaturated fatty acids

The C16:1 ω 7 and C18:1 ω 9 relative weight content of jejunal phospholipids averaged, respectively, $2.97 \pm 0.39\%$ and $60.66 \pm 2.82\%$ ($n = 12$ in both cases), as distinct ($p < 0.001$)

from $10.01 \pm 1.56\%$ and $117.51 \pm 2.01\%$ ($n = 12$ in both cases) in caecal phospholipids. Such contents failed to differ significantly from one another, whether in the jejunum or caecum, in the three groups of rats under consideration (Table 4). A sizeable amount of C20:1 ω 9 in intestinal phospholipids was only detected in one out of 4 rats in the ω 3D rats examined before or after the switch in diet. No C22:1 ω 9 could be detected in any of the 24 rats examined for such a purpose.

| Rats | | C16:1 ω 7 | C18:1 ω 9 | C20:1 ω 9 | C22:1 ω 9 |
|-------------|--------------|------------------|-------------------|------------------|------------------|
| Jejunum | | | | | |
| Control | before | 3.70 \pm 0.70 | 58.03 \pm 2.03 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| ω 3D | before | 2.50 \pm 0.92 | 64.77 \pm 2.11 | 0.43 \pm 0.43 | 0.00 \pm 0.00 |
| | after (1 wk) | 2.71 \pm 0.20 | 59.18 \pm 3.94 | 0.05 \pm 0.05 | 0.00 \pm 0.00 |
| Caecum | | | | | |
| Control | before | 5.54 \pm 3.34 | 120.28 \pm 1.42 | 0.00 \pm 0.00 | 0.00 \pm 0.00 |
| ω 3D | before | 12.18 \pm 2.09 | 118.44 \pm 4.76 | 1.01 \pm 1.01 | 0.00 \pm 0.00 |
| | after (1 wk) | 12.30 \pm 1.17 | 113.82 \pm 3.49 | 0.91 \pm 0.91 | 0.00 \pm 0.00 |

Table 4. Relative weight content (‰) of monodesaturated fatty acids in jejunum and caecum phospholipids

3.2 Relation between intestinal and hepatic phospholipids

In the case of long-chain polyunsaturated ω 3 fatty acids, highly significant positive correlations prevailed between the relative content of C18:3 ω 3 in jejunal and hepatic phospholipids ($r = + 0.8368$; $n = 12$; $p < 0.001$), that of C22:5 ω 3 also in jejunal and hepatic phospholipids ($r = + 0.9153$; $n = 12$; $p < 0.001$), and that of C22:6 ω 3 either in jejunal and hepatic phospholipids ($r = + 0.9716$; $n = 12$; $p < 0.001$) or in caecal and hepatic phospholipids ($r = + 0.8679$; $n = 12$; $p < 0.001$). The paired ratio between the C22:6 ω 3 relative weight content in hepatic/jejunal phospholipids did not differ significantly ($p > 0.14$ or more) in the three groups of rats under consideration, i.e. control and ω 3D rats examined at the end of the 3 months initial period and ω 3D rats exposed for one week to the soya oil diet, with an overall mean value of 4.13 ± 0.16 ($n = 12$).

In the case of long-chain polyunsaturated ω 6 fatty acids, a significant positive correlation ($r = + 0.5868$; $n = 12$; $p < 0.05$) was found between the C22:4 ω 6 relative weight content of jejunal and hepatic phospholipids in the same 12 rats. Such was not the case ($r = + 0.4924$; $n = 12$; $p > 0.1$) for the C20:2 ω 6 content of the same phospholipids. The tightest correlations concerned the C22:5 ω 6 or liver phospholipids and that of either jejunal phospholipids ($r = + 0.9776$; $n = 12$; $p < 0.001$) or caecal phospholipids ($r = + 0.9242$; $n = 12$; $p < 0.001$), with, in the latter two series of comparisons, either only one or no negative xy product among the 12 sets of data.

3.3 Fatty acid pattern of liver phospholipids

3.3.1 Long-chain polyunsaturated ω 3 fatty acids

In fair agreement with the jejunal data, the relative weight content of C18:3 ω 3 in liver phospholipids averaged at the end of the initial 3 months period $0.35 \pm 0.35\%$ ($n = 4$) in the

ω3D rats, as distinct ($p < 0.005$) from $2.30 \pm 0.19\%$ ($n = 4$) in the control animals, increasing ($p < 0.005$) in the former ω3D rats to, respectively, 1.91 ± 0.09 and $2.09 \pm 0.17\%$ ($n = 4$ in both cases) one and two weeks after the switch to the soya oil diet.

The relative weight content of the three other long-chain polyunsaturated ω3 fatty acids in liver phospholipids yielded comparable information (Table 5). First, the mean values recorded in the control animals before the switch in diet and 8 weeks thereafter never differed significantly ($p > 0.6$ or more) from one another, with overall mean values of $4.99 \pm 0.77\%$ ($n = 8$) for C20:5ω3, $9.29 \pm 0.58\%$ ($n = 8$) for C22:5ω3 and $170.43 \pm 2.92\%$ ($n = 8$) for C22:6ω3. Second, these mean values were all significantly higher ($p < 0.002$ or less) than those recorded in the ω3D rats at the end of the 3 months initial period. Third, in the ω3D rats, higher values ($p < 0.025$ or less) were found after the switch in diet then before such a switch, with mean values over the 8 weeks exposure to the soya oil diet averaging $2.47 \pm 0.55\%$ ($n = 12$) in the case of C20:5ω3, $7.15 \pm 0.67\%$ ($n = 12$) in the case of C22:5ω3 and $130.02 \pm 6.80\%$ ($n = 12$) in the case of C22:6ω3. Last, the latter three percentages all remained significantly lower ($p < 0.02$ or less) than the corresponding mean values recorded in the control animals over the same period of 8 weeks. In the ω3D rats, a progressive time-related increase in the relative weight content of a long-chain polyunsaturated ω3 fatty acid in the liver phospholipids between the first and last week of exposure to the soya oil diet was only observed in the case of C22:6ω3 ($r = + 0.6374$; $n = 12$; $p < 0.04$).

These findings indicate that, except as far as C18:3ω3 is concerned, a period of 8 weeks exposure of the ω3D rats to the soya oil diet was not quite sufficient to restore the liver phospholipid content of ω3 fatty acids to the same level as that otherwise found in control animals exposed to the same diet from the 8th week after birth.

| Rats | | C20:5ω3 | C22:5ω3 | C22:6ω3 |
|---------|--------------|-------------|-------------|----------------|
| Control | before | 5.05 ± 1.12 | 9.00 ± 0.41 | 169.11 ± 4.49 |
| | after (8 wk) | 4.93 ± 1.22 | 9.58 ± 1.17 | 171.81 ± 4.37 |
| ω3D | before | 0.00 ± 0.00 | 1.56 ± 0.80 | 54.52 ± 5.32 |
| | after (1 wk) | 2.80 ± 1.40 | 6.81 ± 1.23 | 112.62 ± 8.54 |
| | after (2 wk) | 1.90 ± 0.73 | 5.96 ± 0.33 | 128.16 ± 4.91 |
| | after (8 wk) | 2.71 ± 0.85 | 8.68 ± 1.40 | 149.37 ± 13.55 |

Table 5. Relative weight content (%) of long-chain polyunsaturated ω3 fatty acids in liver phospholipids

3.3.2 Long-chain polyunsaturated ω6 fatty acids

Except in the case of C22:4ω6 and C22:5ω6, the mean values recorded in the control animals were not significantly different at the end of the 3 months initial period and 8 weeks thereafter (Table 6). In the former two cases, however, the mean values found at the end of the experiments were higher ($p < 0.02$ or less) than those recorded at the end of the 3 months initial period.

No significant difference between the 6 groups of rats listed in Table 6 was observed for the C18:2ω6 relative weight content of liver phospholipids. Likewise, as far as C20:3ω6 is concerned, the mean value found in the control animals ($7.28 \pm 0.74\%$; $n = 8$) did not differ significantly ($p > 0.5$) from that recorded in the ω3D rats ($6.65 \pm 0.64\%$; $n = 16$)

In the case of the other 5 long-chain polyunsaturated ω6 fatty acids (C20:2ω6, C18:3ω3, C20:4ω6, C22:4ω6 and C22:5ω6), the mean value found in the ω3D rats examined before the switch in diet always exceeded both that recorded in the 8 control animals and those

measured in each of the three groups of ω 3D rats examined after the switch in diet. The relative magnitude of the difference between the values recorded in the ω 3D rats before the switch from the sunflower oil diet to the soya oil diet and the overall mean value found in the control animals at the end of the initial 3 months period and 8 weeks thereafter was quite variable, ranging from as little as $12.0 \pm 2.4\%$ ($df = 10$; $p < 0.001$) in the case of C20:4 ω 6 to as much as a tenfold increase ($p < 0.001$) in the case of C22:5 ω 6.

| Rats | C18:2 ω 6 | C20:2 ω 6 | C18:3 ω 6 | C20:3 ω 6 | C20:4 ω 6 | C22:4 ω 6 | C22:5 ω 6 |
|--------------------|------------------|------------------|------------------|------------------|-------------------|------------------|------------------|
| Control before | 82.51 \pm 5.16 | 1.59 \pm 0.18 | 1.72 \pm 0.25 | 6.05 \pm 0.63 | 303.65 \pm 5.77 | 2.87 \pm 0.16 | 5.27 \pm 0.48 |
| after (8 wk) | 78.23 \pm 4.70 | 1.57 \pm 0.12 | 1.64 \pm 0.06 | 8.52 \pm 1.06 | 308.73 \pm 8.17 | 3.99 \pm 0.13 | 9.27 \pm 1.07 |
| ω 3D before | 77.83 \pm 2.73 | 2.78 \pm 0.80 | 2.03 \pm 0.20 | 5.44 \pm 0.44 | 342.83 \pm 4.45 | 8.54 \pm 0.31 | 72.67 \pm 8.82 |
| after (1wk) | 74.16 \pm 5.52 | 1.64 \pm 0.17 | 1.85 \pm 0.29 | 6.73 \pm 1.51 | 330.74 \pm 6.44 | 5.38 \pm 0.04 | 37.21 \pm 5.54 |
| after (2 wk) | 77.23 \pm 2.55 | 1.94 \pm 0.15 | 1.61 \pm 0.13 | 6.19 \pm 0.97 | 330.51 \pm 2.11 | 4.63 \pm 0.23 | 23.63 \pm 2.55 |
| after (8 wk) | 76.92 \pm 6.60 | 1.44 \pm 0.05 | 1.74 \pm 0.19 | 8.22 \pm 1.84 | 324.40 \pm 3.48 | 4.45 \pm 0.25 | 14.71 \pm 4.07 |

Table 6. Relative weight content (‰) of long-chain polyunsaturated ω 6 fatty acids in liver phospholipids

However, when the values recorded in the ω 3D rats 1 week, 2 weeks and 8 weeks after the switch in diet, in excess of the reference value found in control animals, were expressed relative to the difference between the measurements made in the ω 3D rats before the switch in diet and the same reference value found in control animals, a time-related obliteration of the latter difference was often observed. As illustrated in Fig. 1, such a progressive decrease displayed an exponential pattern, with a half-life somewhat below one week.

3.3.3 Saturated fatty acids

Except in the case of C16:0 and C24:0 ($p < 0.05$ or less), no significant change was observed in the control animals between the liver phospholipid relative weight content of the six saturated fatty acids listed in Table 7, as measured at the end of the 3 months initial period and 8 weeks thereafter.

| Rats | C14:0 | C16:0 | C18:0 | C20:0 | C22:0 | C24:0 |
|--------------------|-----------------|-------------------|-------------------|-----------------|-----------------|-----------------|
| Control before | 1.56 \pm 0.15 | 133.92 \pm 2.71 | 237.04 \pm 4.67 | 0.70 \pm 0.01 | 2.23 \pm 0.69 | 6.84 \pm 0.34 |
| after (8 wk) | 1.52 \pm 0.11 | 120.29 \pm 4.39 | 241.12 \pm 5.76 | 0.75 \pm 0.04 | 3.62 \pm 0.13 | 8.79 \pm 0.05 |
| ω 3D before | 1.86 \pm 0.22 | 144.02 \pm 5.75 | 273.82 \pm 1.42 | 0.20 \pm 0.20 | 4.42 \pm 0.20 | 9.63 \pm 0.24 |
| after (1 wk) | 1.74 \pm 0.14 | 133.30 \pm 3.77 | 261.74 \pm 7.20 | 0.35 \pm 0.20 | 2.78 \pm 0.93 | 8.01 \pm 0.16 |
| after (2 wk) | 1.81 \pm 0.10 | 130.91 \pm 1.67 | 252.75 \pm 1.55 | 0.20 \pm 0.20 | 3.42 \pm 0.40 | 7.86 \pm 0.05 |
| after (8 wk) | 1.51 \pm 0.15 | 116.45 \pm 4.95 | 251.72 \pm 9.17 | 0.00 \pm 0.00 | 3.34 \pm 0.19 | 8.42 \pm 0.56 |

Table 7. Relative weight content (‰) of saturated fatty acids in liver phospholipids

The C20:0 relative weight content of liver phospholipids was lower ($p < 0.001$) in the ω 3D rats ($0.19 \pm 0.08\%$; $n = 16$) than in the control animals ($0.72 \pm 0.02\%$; $n = 8$). The opposite situation prevailed for the other five saturated fatty acids (C14:0, C16:0, C18:0, C22:0 and C24:0). As documented in Fig. 2, using the same analytical procedure as that applied to the data relative to content of long-chain polyunsaturated ω 6 fatty acids (Fig. 1), the switch from the sunflower oil diet to the soya oil diet provoked a time-related normalization of the liver

phospholipid content of the just mentioned five saturated fatty acids, with a half-life close to one week. Such a progressive decrease represented a mirror image of the progressive increase in the C22:6 ω 3 relative weight content of liver phospholipids in the ω 3D rats examined after the switch in diet, with again a half-life close to one week.

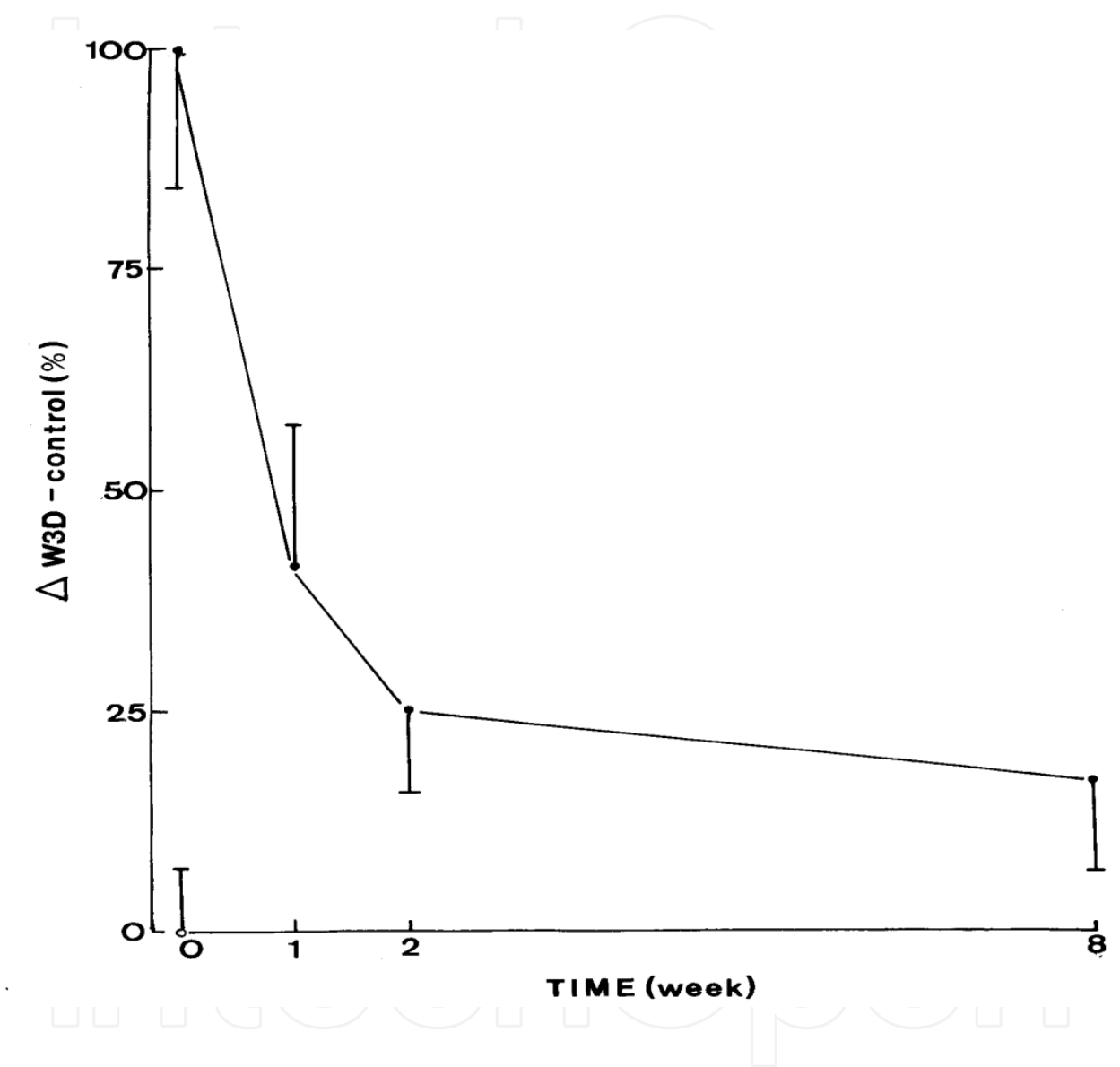


Fig. 1. Time course for the changes in the relative weight content of C20:2 ω 6, C18:3 ω 6, C20:4 ω 6, C22:4 ω 6 and C22:5 ω 6 in the liver phospholipids of ω 3D rats after the switch from the sunflower oil to soya oil diet. For each of these five fatty acids, all individual results are expressed relative to the difference between the mean value recorded in the ω 3D rats before the switch in diet and the overall mean value found in the control animals examined at the end of the 3 months initial period and 8 weeks thereafter. Mean values (\pm SEM) refer to 20 individual measurements in the ω 3D rats (closed circles) and 40 individual measurements in the control animals (open circle)

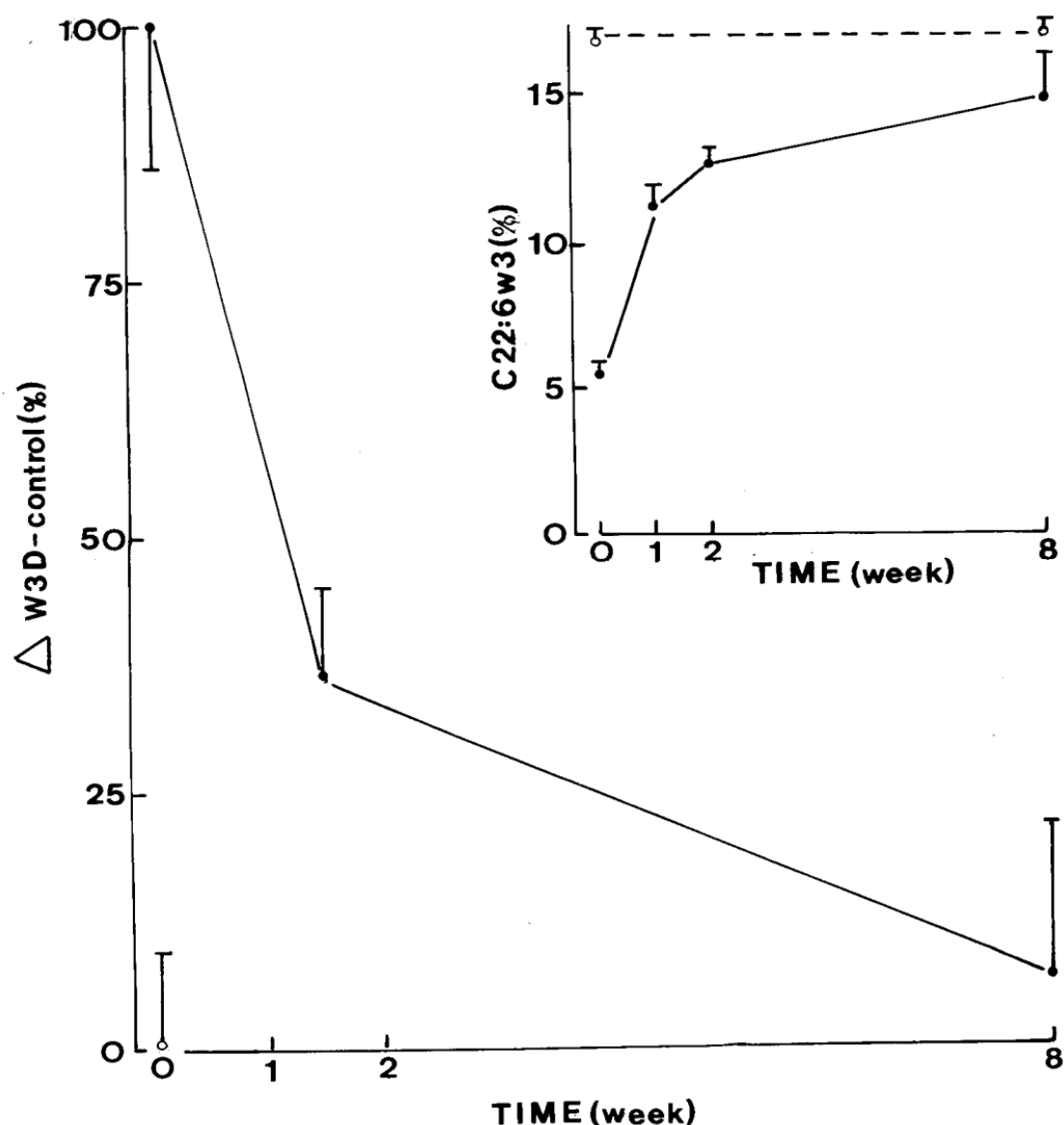


Fig. 2. Time course for the changes in the relative weight content of C14:0, C16:0, C18:0, C22:0 and C24:0 in the liver phospholipids of ω 3D rats after the switch from the sunflower oil to soya oil diet. Same presentation as in Fig. 1. The inset illustrates the time course for the changes in the relative weight content (%) of C22:6 ω 3 in the liver phospholipids of control animals (open circles and dashed line) and ω 3D rats (closed circles and solid line); mean values (\pm SEM) refer to 4 individual determinations in each case.

3.3.4 Monodesaturated fatty acids

No significant difference in the relative weight content of monodesaturated fatty acids (C16:1 ω 7, C18:1 ω 9, C20:1 ω 9 and C22:1 ω 9) in liver phospholipids was detected when comparing control animals and ω 3D rats, whether examined at the end of the 3 months initial period or thereafter (Table 8). For instance, the C22:1 ω 9 content averaged $2.08 \pm 0.20\%$ ($n = 8$) in the control animals, and respectively $2.92 \pm 0.63\%$ ($n = 4$) and $2.74 \pm 0.40\%$ ($n = 12$) in the ω 3D rats examined before and after the switch in diet. None of the latter three percentages differed significantly from one another ($p > 0.2$ or more).

| Rats | | C16:1ω7 | C18:1ω9 | C20:1ω9 | C22:1ω9 |
|---------|--------------|-------------|--------------|-------------|-------------|
| Control | before | 5.16 ± 1.06 | 23.91 ± 2.57 | 0.33 ± 0.19 | 2.04 ± 0.24 |
| | after (1 wk) | 6.14 ± 0.44 | 23.04 ± 0.80 | 0.00 ± 0.00 | 2.11 ± 0.37 |
| | before | 5.83 ± 0.96 | 27.04 ± 2.78 | 0.00 ± 0.00 | 2.92 ± 0.63 |
| | after (1 wk) | 5.20 ± 1.02 | 23.79 ± 2.17 | 0.16 ± 0.16 | 2.05 ± 0.49 |
| | after (2 wk) | 5.57 ± 0.74 | 24.90 ± 1.35 | 0.00 ± 0.00 | 2.12 ± 0.54 |
| ω3D | after (8 wk) | 5.75 ± 0.78 | 24.58 ± 1.46 | 0.00 ± 0.00 | 4.06 ± 0.57 |

Table 8. Relative weight content (‰) of monodesaturated fatty acids in liver phospholipids

3.4 Fatty acid pattern of RBC phospholipids

3.4.1 Long-chain polyunsaturated ω3 fatty acids

The mean values for the relative weight content of long-chain polyunsaturated ω3 fatty acids in RBC phospholipids are listed in Table 9.

In the ω3D rats, the C18:3ω3 relative weight content of RBC phospholipids increased ($p < 0.005$) from a mean value of $0.62 \pm 0.36\text{‰}$ ($n = 4$) before the switch in diet to an overall mean value of $1.79 \pm 0.07\text{‰}$ ($n = 6$) thereafter. The latter mean value remained somewhat lower ($p < 0.06$) than that recorded in the control animals at the end of the 3 months initial period ($2.11 \pm 0.14\text{‰}$; $n = 4$). A minor amount of C18:4ω3 ($1.60 \pm 0.21\text{‰}$; $n = 4$) was only detected in the ω3D rats examined before the switch in diet.

| Rats | | C18:3ω3 | C20:5ω3 | C22:5ω3 | C22:6ω3 |
|---------|--------------|-------------|-------------|--------------|--------------|
| Control | before | 2.11 ± 0.14 | 4.33 ± 0.57 | 19.11 ± 0.64 | 68.11 ± 1.39 |
| | after (8 wk) | N.T. | 3.01 ± 0.37 | 21.37 ± 2.25 | 64.84 ± 2.84 |
| ω3D | before | 0.62 ± 0.36 | 0.00 ± 0.00 | 1.82 ± 0.14 | 19.76 ± 1.12 |
| | after (1 wk) | 1.88 (1) | 1.06 (1) | 4.53 (1) | 27.75 (1) |
| | after (2 wk) | 1.69 (1) | 1.36 (1) | 5.80 (1) | 36.31 (1) |
| | after (8 wk) | 1.79 ± 0.10 | 2.86 ± 0.35 | 14.02 ± 1.10 | 49.64 ± 3.84 |

Table 9. Relative weight content (‰) of long-chain polyunsaturated ω3 fatty acids in RBC phospholipids

In the ω3D rats, the C20:5ω3 content of RBC phospholipids also progressively increased from $0.00 \pm 0.00\text{‰}$ ($n = 4$) before the switch in diet to $1.21 \pm 0.15\text{‰}$ ($n = 2$) one to two weeks thereafter and $2.86 \pm 0.35\text{‰}$ ($n = 4$) 8 weeks thereafter. Once again, the latter mean value remained lower ($p < 0.05$) than that recorded in the control animals over the same period of 8 weeks ($4.12 \pm 0.33\text{‰}$; $n = 8$). The time-related increase in the C20:5ω3 content of RBC phospholipids was less rapid than that found, in the same ω3D rats, for the C20:5ω3 content of liver phospholipids. Indeed the paired RBC/liver ratio for such contents increased in the ω3D rats from $0.0 \pm 0.0\%$ ($n = 4$) before the switch in diet to respectively 37.9% ($n = 1$), 71.6% ($n = 1$) and $120.9 \pm 17.2\%$ ($n = 4$) one, two and 8 weeks thereafter. The latter mean value was no more significantly different ($p > 0.25$) from the RBC/liver ratio found in the control animals examined either before ($98.6 \pm 19.6\%$; $n = 4$) or after ($90.6 \pm 16.7\%$; $n = 4$) the last 8 weeks of the present experiments.

A delayed alignment of the C22:5ω3 content of RBC phospholipids on that of liver phospholipids in the ω3D rats eventually exposed to the soya oil diet was also observed, as illustrated in Fig. 3. Thus, the liver/RBC ratio for this variable transiently increased in the

ω 3D rats switched to the soya oil diet before resuming a mean value ($60.9 \pm 5.4\%$; $n = 4$) still somewhat higher ($p < 0.02$) than that recorded in the control animals over the same period of 8 weeks ($46.2 \pm 2.5\%$; $n = 8$).

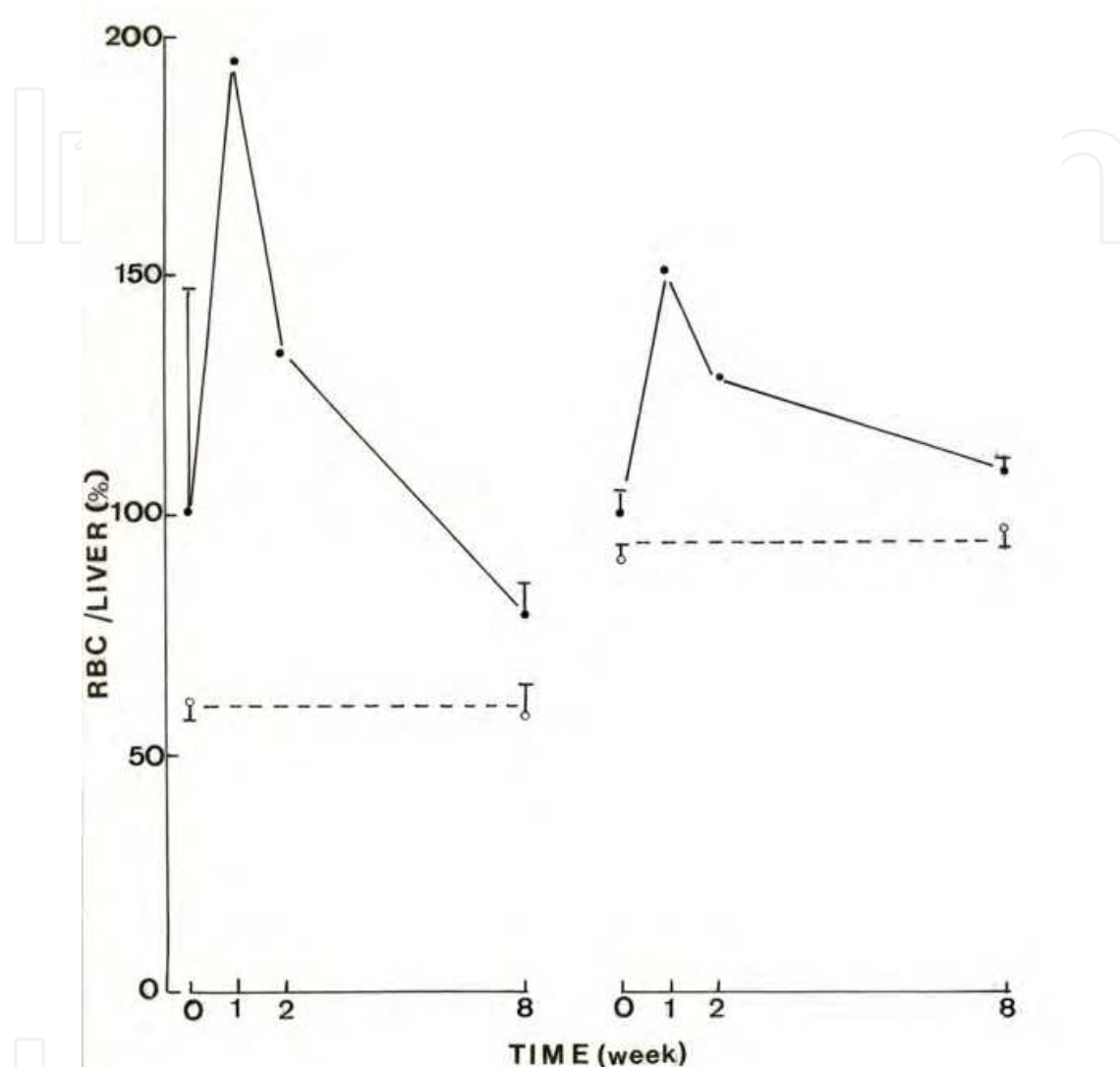


Fig. 3. Time course for the changes in the RBC/liver ratio for the C22:5 ω 3 (left) and C22:6 ω 3 (right) relative weight content of phospholipids in control animals (open circles and dashed line) and ω 3D rats (closed circles and solid line). Single measurements made in pooled samples from 4 rats (week 1 and 2) or mean values (\pm SEM; $n = 4$) are expressed relative to the mean value found in the ω 3D rats before the switch in diet.

Likewise, the liver/RBC ratio for the C22:6 ω 3 content of phospholipids transiently increased in the ω 3D rats exposed to the soya oil diet before resuming a mean value of $300.0 \pm 6.2\%$ ($n = 4$), still somewhat higher ($p < 0.003$) than that recorded in the control animals over the same period of 8 weeks ($257.9 \pm 7.9\%$; $n = 8$). Incidentally, Fig. 3 also documents that, in the control animals, the liver/RBC ratio for either the C22:5 ω 3 or C22:6 ω 3 content of phospholipids was not significantly different ($p > 0.27$ or more) at the onset and end of the last 8 weeks period in the present experiments, as also observed ($p > 0.7$) for the RBC/liver ratio for the C20:5 ω 3 content of phospholipids in the control animals (see above).

3.4.2 Long-chain polyunsaturated ω 6 fatty acids

A mirror image of that recorded for C22:5 ω 3 or C22:6 ω 3 was observed concerning the liver/RBC ratio for the relative weight content of C22:4 ω 6. Thus, such a ratio, which was significantly higher ($p < 0.001$) in the ω 3D rats ($33.9 \pm 1.1\%$; $n = 4$) than in the control rats ($21.7 \pm 1.3\%$; $n = 4$) both examined at the end of the 3 months initial period, first decreased ($p < 0.025$) in the ω 3D rats to $22.0 \pm 0.1\%$ ($n = 2$) one to two weeks after the switch in diet and then increased again ($p < 0.02$) to $27.0 \pm 1.4\%$ ($n = 4$) 8 weeks after the switch in diet, reaching a value virtually identical ($p > 0.49$) to that recorded at the same time in the control animals ($28.5 \pm 1.5\%$; $n = 4$). In the case of C22:5 ω 6, the liver/RBC ratio was again significantly higher ($p < 0.001$) in the ω 3D rats ($230.2 \pm 9.9\%$; $n = 4$) than in the control animals ($95.5 \pm 4.4\%$; $n = 4$) both examined at the end of the 3 months initial period. It decreased ($p < 0.005$) in the ω 3D rats to $124.5 \pm 9.3\%$ ($n = 2$) one to two weeks after the switch in diet, such a value being comparable to that reached 8 weeks after the switch in diet ($125.6 \pm 14.3\%$; $n = 4$) in the ω 3D rats. The latter two mean values were no more significantly different ($p > 0.25$) than that recorded in the control animals at the end of the present experiments ($149.2 \pm 13.3\%$; $n = 4$) and virtually identical to that prevailing in the same animals over the last 8 weeks of such experiments ($122.4 \pm 12.0\%$; $n = 8$).

| Rats | | C18:2 ω 6 | C18:3 ω 6 | C20:2 ω 6 | C20:3 ω 6 | C20:4 ω 6 | C22:4 ω 6 | C22:5 ω 6 |
|-------------|--------------|------------------|------------------|------------------|------------------|--------------------|------------------|------------------|
| Control | before | 80.09 \pm 4.08 | 0.17 \pm 0.17 | 0.00 \pm 0.00 | 4.44 \pm 0.20 | 330.00 \pm 6.00 | 13.35 \pm 0.79 | 5.48 \pm 0.31 |
| | after (8 wk) | 72.40 \pm 4.76 | 0.79 \pm 0.28 | 0.38 \pm 0.38 | 5.78 \pm 0.55 | 329.36 \pm 3.91 | 14.06 \pm 0.44 | 6.23 \pm 0.44 |
| ω 3D | before | 78.13 \pm 0.51 | 0.22 \pm 0.22 | 0.00 \pm 0.00 | 3.69 \pm 0.22 | 341.09 \pm 10.40 | 25.21 \pm 0.43 | 31.37 \pm 3.06 |
| | after (1 wk) | 69.30 (1) | 0.00 (1) | 0.00 (1) | 4.45 (1) | 347.89 (1) | 24.37 (1) | 27.82 (1) |
| | after (2 wk) | 78.11 (1) | 0.00 (1) | 1.86 (1) | 4.23 (1) | 350.33 (1) | 21.10 (1) | 20.50 (1) |
| | after (8 wk) | 75.82 \pm 4.75 | 0.00 \pm 0.00 | 0.96 \pm 0.55 | 5.42 \pm 0.48 | 335.95 \pm 2.91 | 16.57 \pm 0.14 | 11.21 \pm 1.73 |

Table 10. Relative weight content (%) of long-chain polyunsaturated ω 6 fatty acids in RBC phospholipids

3.4.3 Saturated fatty acids

Significant differences were also on occasion observed when comparing the relative weight content of selected saturated fatty acids in the RBC phospholipids of control and ω 3D rats (Table 11). For instance, the content of C18:0 averaged $178.46 \pm 2.09\%$ ($n = 8$) in control animals, as distinct ($p < 0.003$) from $188.11 \pm 1.64\%$ ($n = 10$) in ω 3D rats. Inversely, the C24:0 content of RBC phospholipids was higher ($p < 0.025$) in the control animals ($17.05 \pm 0.87\%$; $n = 8$) than in the ω 3D rats examined before the switch in diet ($13.46 \pm 0.52\%$; $n = 4$), reascending ($p < 0.001$) to $18.50 \pm 0.68\%$ ($n = 6$) when the latter ω 3D rats were switched to the soya oil diet.

| Rats | | C14:0 | C16:0 | C18:0 | C20:0 | C22:0 | C24:0 |
|-------------|--------------|-----------------|-------------------|-------------------|-----------------|-----------------|------------------|
| Control | before | 1.36 \pm 0.04 | 212.94 \pm 3.33 | 179.33 \pm 2.25 | 1.15 \pm 0.04 | 6.38 \pm 0.26 | 15.03 \pm 0.77 |
| | after (8 wk) | 1.51 \pm 0.07 | 217.35 \pm 2.26 | 177.60 \pm 3.84 | 1.00 \pm 0.34 | 7.50 \pm 0.32 | 19.08 \pm 0.46 |
| ω 3D | before | 1.50 \pm 0.06 | 219.93 \pm 8.24 | 189.75 \pm 3.12 | 1.23 \pm 0.08 | 6.52 \pm 0.33 | 13.46 \pm 0.52 |
| | after (1 wk) | 1.44 (1) | 218.9 (1) | 187.6 (1) | 1.42 (1) | 7.52 (1) | 16.10 (1) |
| | after (2 wk) | 1.44 (1) | 205.6 (1) | 184.9 (1) | 1.33 (1) | 7.77 (1) | 17.84 (1) |
| | after (8 wk) | 1.46 \pm 0.08 | 210.37 \pm 3.67 | 187.4 \pm 2.93 | 1.31 \pm 0.10 | 8.16 \pm 0.54 | 19.27 \pm 0.66 |

Table 11. Relative weight content (%) of saturated fatty acids in RBC phospholipids

3.4.4 Monodesaturated fatty acids

The C16:1ω7 relative weight content of RBC phospholipids averaged $2.90 \pm 0.15\%$ (n = 8) in the control animals, and $2.58 \pm 0.41\%$ (n = 4) and $2.96 \pm 0.21\%$ (n = 6) in the ω3D rats examined, respectively, before and after the switch in diet. The corresponding values for the C18:1ω9 content of RBC phospholipids averaged $53.08 \pm 1.46\%$ (n = 8), $52.91 \pm 2.47\%$ (n = 4) and $54.47 \pm 1.56\%$ (n = 6). No C20:1ω9 was detected in any of the 18 samples concerned by this study. Sizeable amounts of C22:1ω9 ($8.14 \pm 0.20\%$; n = 4) were only detected in the samples prepared from the ω3D rats examined before the switch in diet.

3.5 Fatty acid pattern of brain phospholipids

3.5.1 Long-chain polyunsaturated ω3D fatty acids

No C18:3ω3, C18:4ω3 or C20:5ω3 was detected in any of the 20 samples examined for the fatty acid pattern of brain phospholipids. The C22:5ω3 and C22:6ω3 relative weight content of brain phospholipids were significantly lower in ω3D rats than in control animals both examined at the end of the 3 months initial period and, in the former ω3D rats, slowly returned towards control values after the switch in diet (Table 12).

| Rats | | C22:5ω3 | C22:6ω3 |
|---------|--------------|-----------------|-------------------|
| Control | before | 2.29 ± 0.04 | 235.93 ± 6.60 |
| | after (8 wk) | 2.30 ± 0.20 | 213.34 ± 7.43 |
| ω3D | before | 0.00 ± 0.00 | 186.65 ± 5.01 |
| | after (1 wk) | 0.27 ± 0.27 | 193.19 ± 3.72 |
| | after (8 wk) | 1.95 ± 0.14 | 209.04 ± 4.89 |

Table 12. Relative weight content (‰) of long-chain polyunsaturated ω3 fatty acids in brain phospholipids

3.5.2 Long-chain polyunsaturated ω6 fatty acids

The C18:2ω6 relative weight content of brain phospholipids was higher ($p < 0.02$) in the control animals ($7.30 \pm 0.24\%$; n = 8) than in the ω3D rats examined before and one week after the switch in diet ($6.27 \pm 0.29\%$; n = 8), resuming in the ω3D rats exposed for 8 weeks to the soya oil diet a mean value ($7.55 \pm 0.14\%$; n = 4) no more significantly different ($p > 0.5$) from that recorded in the control animals (Table 13). A comparable situation prevailed

| Rats | | C18:2ω6 | C20:2ω6 | C20:3ω6 | C20:4ω6 | C22:4ω6 | C22:5ω6 |
|---------|--------------|-----------------|-----------------|-----------------|-------------------|------------------|------------------|
| Control | before | 7.16 ± 0.39 | 1.31 ± 0.06 | 2.48 ± 0.09 | 131.66 ± 6.04 | 26.85 ± 1.70 | 3.12 ± 0.23 |
| | after (8 wk) | 7.45 ± 0.31 | 1.56 ± 0.13 | 2.99 ± 0.17 | 116.71 ± 8.21 | 27.23 ± 0.93 | 3.08 ± 0.37 |
| ω3D | before | 6.27 ± 0.58 | 1.34 ± 0.14 | 2.07 ± 0.21 | 137.94 ± 7.23 | 30.21 ± 1.63 | 22.94 ± 1.46 |
| | after (1 wk) | 6.27 ± 0.20 | 1.48 ± 0.07 | 2.30 ± 0.19 | 125.04 ± 3.90 | 28.88 ± 1.40 | 19.00 ± 1.41 |
| | after (8 wk) | 7.55 ± 0.14 | $1.48/1.58$ | 2.55 ± 0.15 | 122.74 ± 3.38 | 26.49 ± 2.79 | 8.30 ± 0.54 |

Table 13. Relative weight content (‰) of long-chain polyunsaturated ω6 fatty acids in brain phospholipids

in the case of C20:3ω6, with a lower value ($p < 0.025$) in ω3D rats ($2.31 \pm 0.11\%$; n = 12) than in control animals ($2.74 \pm 0.13\%$; n = 18). Except in one control animal with a C18:3ω6 relative content of 0.79% in brain phospholipids, no sizeable amount of this fatty acid could be detected in any of the other 19 samples. In the case of both C22:4ω6 and C22:5ω6, the mean value recorded at the end of the initial 3 months period was higher in ω3D rats than in

control animals, a progressive decrease being recorded in the former ω3D rats after the switch in diet. Such changes were most obvious in the case of C22:5ω6.

3.5.3 Saturated fatty acids

As a rule, the relative weight content of saturated fatty acids in the brain phospholipids of ω3D rats were comparable to the overall mean values found in control animals (Table 14). In the case of C14:0 and C16:0, however, the individual values collected in ω3D rats differed significantly ($p < 0.004$) from those recorded in control animals, averaging $114.0 \pm 3.1\%$ ($n = 24$) of the mean corresponding measurements made in the latter control animals ($100.0 \pm 2.5\%$; $n = 16$).

| Rats | | C14:0 | C16:0 | C18:0 | C20:0 | C22:0 | C24:0 |
|---------|--------------|-----------------|--------------------|-------------------|-----------------|-----------------|------------------|
| Control | before | 1.03 ± 0.06 | 228.96 ± 6.45 | 184.97 ± 2.01 | 3.06 ± 0.14 | 2.90 ± 0.18 | 6.90 ± 0.58 |
| | after (8 wk) | 0.92 ± 0.04 | 194.74 ± 5.20 | 193.39 ± 2.13 | 5.31 ± 0.91 | 5.50 ± 0.79 | 12.95 ± 1.42 |
| ω3D | before | 1.11 ± 0.07 | 232.34 ± 6.19 | 188.85 ± 2.19 | 3.44 ± 0.38 | 3.54 ± 0.80 | 8.65 ± 1.62 |
| | after (1 wk) | 1.15 ± 0.03 | 231.48 ± 8.04 | 182.90 ± 2.40 | 4.32 ± 0.44 | 4.41 ± 0.46 | 10.13 ± 0.98 |
| | after (8 wk) | 1.21 ± 0.13 | 231.30 ± 22.37 | 186.66 ± 6.29 | 3.89 ± 0.40 | 4.09 ± 0.76 | 9.08 ± 1.84 |

Table 14. Relative weight content (‰) of saturated fatty acids in brain phospholipids

3.5.4 Monodesaturated fatty acids

In the same manner as noticed in the case of most saturated fatty acids, the relative weight content of monodesaturated fatty acids in brain phospholipids displayed in the ω3D rats values not vastly different from the overall mean values recorded in control animals (Table 15). Thus, relative to the latter overall mean values for each monodesaturated fatty acids found in control animals ($100.0 \pm 12.9\%$; $n = 32$), those recorded in the ω3D rats averaged $100.0 \pm 7.1\%$; $n = 48$).

| Rats | | C16:1ω7 | C18:1ω9 | C20:1ω9 | C22:1ω9 |
|---------|--------------|-----------------|--------------------|------------------|-----------------|
| Control | before | 3.20 ± 0.16 | 149.78 ± 3.34 | 8.39 ± 1.01 | 0.00 ± 0.00 |
| | after (9 wk) | 3.36 ± 0.13 | 187.77 ± 13.66 | 16.71 ± 2.21 | 2.73 ± 1.04 |
| ω3D | before | 3.05 ± 0.24 | 161.33 ± 13.22 | 9.70 ± 2.38 | 0.58 ± 0.58 |
| | after (1 wk) | 3.12 ± 0.08 | 171.48 ± 6.09 | 12.37 ± 2.34 | 2.19 ± 0.32 |
| | after (8 wk) | 3.34 ± 0.15 | 168.53 ± 7.92 | 10.40 ± 1.32 | 2.06 ± 0.71 |

Table 15. Relative weight content (‰) of monodesaturated fatty acids in brain phospholipids

3.5.5 Comparison of brain, RBC and liver data

As already observed, in the case of RBC phospholipids, the changes in the relative weight content of selected fatty acids in brain phospholipids, as recorded in the ω3D rats after the switch from the sunflower oil diet to the soya oil diet, occurred less rapidly than those found in liver phospholipids. In such a respect, there was no significant difference ($p > 0.6$ or more) when comparing the data collected in either the RBC or brain phospholipids. For instance, in the case of C22:5ω3 and C22:6ω3, the increment found in the ω3D rats examined one week after the switch in diet, above the mean value recorded before such a switch, only represented, in brain and RBC respectively, $21.6 \pm 10.5\%$ ($n = 8$) and $26.0 \pm 3.8\%$ ($n = 2$) of the corresponding mean increment found 8 weeks after the switch in diet. The latter

percentages yielded an overall mean value of $22.5 \pm 8.3\%$ ($n = 10$), significantly lower ($p < 0.004$) than that recorded under the same experimental conditions in liver, i.e. $67.5 \pm 9.3\%$ ($n = 8$). Likewise, in the case of C22:4 ω 6 and C22:5 ω 6, the decrement recorded in the ω 3D rats one week after the switch in diet, below the mean corresponding reference values found before such a switch, yielded in the brain and RBC, when expressed relative to the corresponding mean decrement observed 8 weeks after the switch in diet, an overall mean value of $27.8 \pm 14.4\%$ ($n = 10$), significantly lower ($p < 0.03$) than that recorded under the same experimental conditions in liver, i.e. $69.2 \pm 5.4\%$ ($n = 8$). The latter two mean values relative to two long-chain polyunsaturated ω 6 fatty acids were virtually identical ($p > 0.75$ or more) to the corresponding mean values found in the case of the two long-chain polyunsaturated ω 3 fatty acids under consideration (see above), yielding overall mean percentages of $25.1 \pm 8.1\%$ ($n = 20$) in brain and RBC, as compared ($p < 0.001$) to $68.4 \pm 5.2\%$ ($n = 16$) in liver.

3.6 Fatty acid pattern in liver triglycerides

The total fatty acid content of liver triglycerides did not differ significantly ($p > 0.64$) in the control animals and ω 3D rats, with an overall mean values of 18.3 ± 2.5 mg/g wet wt. ($n = 24$).

3.6.1 Long-chain polyunsaturated ω 3 fatty acids

The relative weight content of C18:3 ω 3, C20:5 ω 3, C22:5 ω 3 and C22:6 ω 3 in liver triglycerides was significantly lower ($p < 0.02$ or less) in the ω 3D rats than in the control animals, both examined at the end of the 3 months initial period (Table 16). In the control animals, no significant difference was observed between the former results and those recorded 8 weeks later. In the ω 3D rats examined after the switch in diet, C20:5 ω 3 remained below the limit of detection in all, except one, rats. The C18:3 ω 3, C22:5 ω 3 and C22:6 ω 3 contents increased, however, in the ω 3D rats within one week after the switch in diet, remaining then at a plateau level somewhat lower than the mean value otherwise found in control rats. Thus, relative to such a reference value ($100.0 \pm 7.9\%$; $n = 24$), the measurements made in the ω 3D rats examined after the switch in diet averaged $66.1 \pm 5.3\%$ ($n = 36$; $p < 0.001$).

| Rats | C18:3 ω 3 | C20:5 ω 3 | C22:5 ω 3 | C22:6 ω 3 |
|--------------------|------------------|------------------|------------------|------------------|
| Control before | 12.82 \pm 2.96 | 2.01 \pm 0.27 | 3.41 \pm 0.56 | 7.04 \pm 1.08 |
| after (8 wk) | 11.94 \pm 3.03 | 1.61 \pm 0.51 | 3.06 \pm 0.90 | 6.45 \pm 1.20 |
| ω 3D before | 1.81 \pm 0.69 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.48 \pm 0.48 |
| after (1 wk) | 8.86 \pm 2.26 | 0.00 \pm 0.00 | 1.81 \pm 0.83 | 3.66 \pm 1.48 |
| after (2 wk) | 10.23 \pm 0.56 | 0.00 \pm 0.00 | 2.07 \pm 0.19 | 4.55 \pm 0.47 |
| after (8 wk) | 8.84 \pm 1.99 | 0.12 \pm 0.12 | 1.81 \pm 0.55 | 4.80 \pm 1.70 |

Table 16. Relative weight content (‰) in long-chain polyunsaturated ω 3 fatty acids in liver triglycerides

3.6.2 Long-chain polyunsaturated ω 6 fatty acids

The C18:2 ω 6 relative weight content of liver triglycerides was virtually identical in control animals and ω 3D rats, whether at the onset or end of the last 8 weeks period of the present experiments (Table 17). Likewise, no significant difference was found between the mean values found in the six groups of rats when considering the relative weight content of C18:3 ω 6, C20:2 ω 6 and C20:3 ω 6 in the liver triglycerides. In the case of C20:4 ω 6, C22:4 ω 6 and C22:5 ω 6,

no significant difference ($p > 0.3$ or more) was observed between the control animals examined either at the end of the initial period or 8 weeks thereafter. In the ω3D rats, the C20:4ω6 content progressively decreased as a function of the length of exposure to the soya oil diet ($r = -0.5059$; $n = 16$; $p < 0.05$), eventually reaching a mean value comparable ($p > 0.9$) to that recorded at the same time in the control animals. A comparable situation prevailed in the case of C22:4ω6 and C22:5ω6. Thus, for the last three fatty acids (C20:4ω6, C22:4ω6 and C22:5ω6), the increment in the relative weight content found in ω3D rats above the mean corresponding value ($n = 8$ in each case) recorded in the control animals, when expressed relative to the initial increment found before the switch in diet, decreased ($p < 0.02$) from $100.0 \pm 17.5\%$ ($n = 12$) to $49.6 \pm 11.3\%$ ($n = 24$) one to two weeks after the switch in diet and further decreased ($p < 0.025$) to $3.6 \pm 15.6\%$ ($n = 12$) eight weeks after the switch in diet.

| Rats | | C18:2ω6 | C18:3ω6 | C20:2ω6 | C20:3ω6 | C20:4ω6 | C22:4ω6 | C22:5ω6 |
|---------|--------------|----------------|-------------|-------------|-------------|--------------|-------------|-------------|
| Control | before | 235.21 ± 34.54 | 5.35 ± 0.38 | 1.78 ± 0.09 | 1.65 ± 0.22 | 20.14 ± 2.57 | 2.61 ± 0.63 | 0.73 ± 0.45 |
| | after (8 wk) | 174.06 ± 38.86 | 4.44 ± 0.88 | 1.80 ± 0.17 | 1.78 ± 0.49 | 15.22 ± 4.02 | 2.92 ± 0.59 | 0.72 ± 0.27 |
| ω3D | before | 237.23 ± 42.90 | 6.17 ± 0.88 | 1.75 ± 0.65 | 1.92 ± 0.83 | 33.92 ± 6.30 | 6.15 ± 1.30 | 4.62 ± 0.78 |
| | after (1 wk) | 194.60 ± 39.29 | 5.01 ± 0.45 | 1.94 ± 0.34 | 1.65 ± 0.22 | 23.07 ± 6.69 | 4.49 ± 1.47 | 3.17 ± 1.08 |
| | after (2 wk) | 218.50 ± 30.62 | 4.73 ± 0.30 | 1.73 ± 0.60 | 2.24 ± 0.50 | 24.75 ± 3.55 | 4.93 ± 0.86 | 2.42 ± 0.55 |
| | after (8 wk) | 173.01 ± 45.75 | 4.25 ± 0.66 | 1.76 ± 0.27 | 1.79 ± 0.63 | 16.08 ± 5.93 | 3.29 ± 1.08 | 0.93 ± 0.55 |

Tale 17. Relative weight content (%) of long-chain polyunsaturated ω6 fatty acids in liver triglycerides

3.6.3 Saturated fatty acids

The C12:0 relative weight content of liver triglycerides averaged $0.72 \pm 0.16\%$ ($n = 8$) and $0.35 \pm 0.12\%$ ($n = 16$) in the control animals and ω3D rats, respectively, these two mean values failing to differ significantly ($p < 0.09$) from one another. Likewise, the C14:0, C16:0 and C18:0 contents of liver triglycerides were essentially comparable in the six groups of rats considered in Table 18. A significant amount of C20:0 ($0.37 \pm 0.14\%$; $n = 8$; $p < 0.05$) was detected in the control animals, whilst such was not the case ($0.02 \pm 0.02\%$; $n = 16$; $p > 0.3$) in the ω3D rats. Inversely, a significant amount of C22:0 ($0.52 \pm 0.17\%$; $n = 12$; $p < 0.02$) was detected in the ω3D rats examined before the switch in diet and one to two weeks thereafter, whilst such was no more the case 8 weeks after the switch in diet, null values being also recorded in the 8 control animals. No C24:0 was detected in any of the 24 samples examined in this study.

| Rats | | C12:0 | C14:0 | C16:0 | C18:0 | C20:0 | C22:0 | C24:0 |
|---------|--------------|-------------|--------------|----------------|--------------|-------------|-------------|-------------|
| Control | before | 0.77 ± 0.26 | 11.54 ± 1.47 | 291.91 ± 14.36 | 21.83 ± 2.40 | 0.41 ± 0.23 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| | after (8 wk) | 0.70 ± 0.24 | 14.22 ± 2.13 | 345.81 ± 27.78 | 25.09 ± 3.20 | 0.33 ± 0.21 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| ω3D | before | 0.21 ± 0.21 | 11.92 ± 1.75 | 307.56 ± 20.99 | 29.56 ± 3.48 | 0.00 ± 0.00 | 0.66 ± 0.38 | 0.00 ± 0.00 |
| | after (1 wk) | 0.73 ± 0.24 | 13.54 ± 1.17 | 349.41 ± 34.67 | 27.83 ± 2.86 | 0.00 ± 0.00 | 0.34 ± 0.07 | 0.00 ± 0.00 |
| | after (2 wk) | 0.00 ± 0.00 | 13.54 ± 1.59 | 304.80 ± 16.14 | 24.35 ± 1.64 | 0.00 ± 0.00 | 0.56 ± 0.41 | 0.00 ± 0.00 |
| | after (8 wk) | 0.45 ± 0.27 | 15.13 ± 1.74 | 344.48 ± 35.98 | 28.62 ± 2.99 | 0.08 ± 0.08 | 0.00 ± 0.00 | 0.00 ± 0.00 |

Table 18. Relative weight content (%) of saturated fatty acids in liver triglycerides

3.6.4 Monodesaturated fatty acids

No significant difference in the relative weight content of either C16:1ω7 or C18:1ω9 in liver triglycerides was observed between the six groups of rats listed in Table 19. Except in one

instance, such was also the case for the C20:1ω9 content of liver triglycerides. No C22:1ω9 was detected in any of the 24 samples under consideration. The sole statistically significant finding consisted in the positive correlation ($r = + 0.9958$; $n = 4$; $p < 0.01$) prevailing between the mean values for the C16:1ω7 and C18:1ω9 relative content recorded in the ω3D rats (all expressed relative to the mean corresponding value found in the eight control animals) and the length of exposure to the soya oil diet (semi-logarithmic analysis). Indeed, relative to such a reference value ($100.0 \pm 4.9\%$; $n = 16$), the measurements made in the ω3D rats averaged $85.7 \pm 6.9\%$ ($n = 8$) before the switch in diet and $91.9 \pm 5.7\%$ ($n = 8$), $93.9 \pm 6.6\%$ ($n = 8$) and $101.5 \pm 6.7\%$ ($n = 8$), respectively, one, two and eight weeks thereafter.

| Rats | C16:1ω7 | C18:1ω9 | C20:1ω9 | C22:1ω9 |
|----------------|--------------|----------------|-------------|-------------|
| Control before | 54.15 ± 9.90 | 325.12 ± 16.65 | 1.30 ± 0.13 | 0.00 ± 0.00 |
| after (8 wk) | 65.55 ± 5.93 | 322.72 ± 13.35 | 1.28 ± 0.15 | 0.00 ± 0.00 |
| ω3D before | 45.40 ± 6.55 | 309.22 ± 20.00 | 1.27 ± 0.49 | 0.00 ± 0.00 |
| after (1 wk) | 53.92 ± 6.96 | 303.93 ± 11.47 | 1.37 ± 0.49 | 0.00 ± 0.00 |
| after (2 wk) | 51.78 ± 7.12 | 327.78 ± 16.36 | 1.42 ± 0.49 | 0.00 ± 0.00 |
| after (8 wk) | 59.68 ± 8.20 | 334.84 ± 14.10 | 0.41 ± 0.25 | 0.00 ± 0.00 |

Table 19. Relative weight content (%) of monodesaturated fatty acids in liver triglycerides

3.7 Fatty acid profile of visceral adipose tissue lipids

As indicated in Table 20, no significant difference was observed between control animals and ω3D rats in terms of body weight and visceral or parametrial adipose tissue weight, whether at the end of the 3 months initial period or 8 weeks thereafter.

| Rats | Body wt (g) | Visceral adipose tissue (g) | Parametrial adipose tissue (g) |
|----------------|--------------|-----------------------------|--------------------------------|
| Control before | 360.5 ± 17.6 | 9.5 ± 1.4 | 16.0 ± 3.4 |
| after (8 wk) | 463.0 ± 18.8 | 16.5 ± 2.1 | 23.0 ± 3.2 |
| ω3D before | 380.5 ± 21.8 | 13.5 ± 1.6 | 14.1 ± 4.0 |
| after (8 wk) | 445.8 ± 49.1 | 12.3 ± 1.8 | 19.1 ± 1.1 |

Table 20. Body weight and visceral or parametrial adipose tissue weight

The total fatty acid content of visceral adipose tissue lipids was not significantly different ($p > 0.5$) in control animals (1.19 ± 0.03 mg/mg wet wt.; $n = 8$) and ω3D rats (1.21 ± 0.03 mg/mg wet wt.; $n = 8$).

3.7.1 Long-chain polyunsaturated ω3 fatty acids

No C18:4ω3 or C20:5ω3 was detected in any of the 16 samples of adipose tissue. The C18:3ω3 relative weight content averaged 20.36 ± 0.83 and $18.39 \pm 0.62\%$ ($n = 4$ in both cases) in the control animals examined at the end of the 3 months initial period and 8 weeks thereafter. In the ω3D rats, it increased ($p < 0.001$) from 0.00 ± 0.00 to $11.67 \pm 0.92\%$ ($n = 4$ in both cases) before and 8 weeks after the switch in diet. It thus remained lower ($p < 0.001$) in the ω3D rats than in the control animals even at the end of the experiments. The C22:5ω3 content of adipose tissue was comparable at the end of the 3 months initial period and 8 weeks thereafter, with overall mean values of $1.21 \pm 0.11\%$ ($n = 8$) in control

animals and $0.00 \pm 0.00\%$ ($n = 8$) in ω3D rats. Likewise, no C22:6ω3 was detected in any of the eight ω3D rats, as distinct ($p < 0.05$) from an overall mean value of $1.14 \pm 0.44\%$ in the eight control animals (Table 21).

| Rats | C18:3ω3 | C20:5ω3 | C22:5ω3 | C22:6ω3 |
|----------------|------------------|-----------------|-----------------|-----------------|
| Control before | 20.36 ± 0.83 | 0.00 ± 0.00 | 1.11 ± 0.19 | 0.00 ± 0.00 |
| after (8 wk) | 18.39 ± 0.62 | 0.00 ± 0.00 | 1.32 ± 0.12 | 2.29 ± 0.21 |
| ω3D before | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| after (8 wk) | 11.67 ± 0.92 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |

Table 21. Relative weight content (‰) of long-chain polyunsaturated ω3 fatty acids in visceral adipose tissue lipids

3.7.2 Long-chain polyunsaturated ω6 fatty acids

The C18:2ω6 relative weight content of adipose tissue lipids was comparable ($p > 0.45$ or more) in control animals and ω3D rats, whether at the onset or end of the last 8 weeks period (Table 22).

| Rats | C18:2ω6 | C20:2ω6 | C20:3ω6 | C20:4ω6 | C22:4ω6 | C22:5ω6 |
|----------------|--------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Control before | 303.06 ± 13.00 | 2.52 ± 0.06 | 0.00 ± 0.00 | 6.72 ± 1.13 | 1.28 ± 0.29 | 0.00 ± 0.00 |
| after (8 wk) | 276.14 ± 3.41 | 2.57 ± 0.05 | 0.36 ± 0.36 | 6.52 ± 0.48 | 1.50 ± 0.17 | 0.14 ± 0.14 |
| ω3D before | 324.61 ± 23.71 | 2.67 ± 0.10 | 0.00 ± 0.00 | 8.21 ± 0.93 | 2.09 ± 0.25 | 1.45 ± 0.21 |
| after (8 wk) | 288.77 ± 19.45 | 2.46 ± 0.04 | 0.36 ± 0.36 | 6.94 ± 0.35 | 1.56 ± 0.11 | 0.63 ± 0.25 |

Table 22. Relative weight content (‰) of long-chain polyunsaturated ω6 fatty acids in visceral adipose tissue lipids

No C18:3ω6 was detected in any of the 16 samples under consideration. The C20:2ω6 content was comparable in the 4 groups of rats. A sizeable amount of C20:3ω6 (1.46 ± 0.00 ; $n = 2$) was only detected in two out of 16 samples. The C20:4ω6 content was not significantly higher ($p > 0.1$) in the ω3D rats examined before the switch in diet ($8.21 \pm 0.93\%$; $n = 4$) than in the other rats ($6.73 \pm 0.39\%$; $n = 12$). The C22:4ω6 content was significantly higher ($p < 0.02$), however, in the ω3D rats examined before the switch in diet ($2.09 \pm 0.25\%$; $n = 4$) than in the other animals ($1.45 \pm 0.11\%$; $n = 12$). Likewise, the C22:5ω6 content found in the ω3D rats examined before the switch in diet ($1.45 \pm 0.21\%$; $n = 4$) exceeded ($p < 0.05$ or less) that found in either the control animals ($0.07 \pm 0.07\%$; $n = 8$) or the ω3D rats examined 8 weeks after the switch in diet ($0.63 \pm 0.25\%$; $n = 4$).

3.7.3 Saturated fatty acids

The relative weight content of C12:0, C14:0, C16:0 and C18:0 were comparable to one another in the four groups of rats (Table 23). The sole significant difference ($p < 0.02$)

| Rats | C12:0 | C14:0 | C16:0 | C18:0 |
|----------------|-----------------|------------------|--------------------|------------------|
| Control before | 0.72 ± 0.09 | 9.57 ± 0.93 | 253.51 ± 5.71 | 30.07 ± 1.20 |
| after (8 wk) | 0.68 ± 0.04 | 9.52 ± 0.59 | 264.89 ± 2.80 | 30.26 ± 0.76 |
| ω3D before | 0.77 ± 0.07 | 10.57 ± 1.13 | 253.17 ± 11.65 | 34.09 ± 1.78 |
| after (8 wk) | 0.74 ± 0.05 | 10.48 ± 0.59 | 261.90 ± 7.80 | 29.79 ± 1.61 |

Table 23. Relative weight content (‰) of saturated fatty acids in visceral adipose tissue lipids

concerned the comparison between the C18:0 content of the ω3D rats examined before the switch in diet ($34.1 \pm 1.8\%$; $n = 4$) and the other animals ($30.0 \pm 0.7\%$; $n = 12$). No C20:0 or C24:0 was detected in any of the 16 samples of adipose tissue. A sizeable amount of C22:0 ($0.55 \pm 0.04\%$; $n = 2$) was only found in two out of four ω3D rats examined before the switch in diet.

3.7.4 Monodesaturated fatty acids

The mean values for the relative weight content of C16:1ω7, C18:1ω9 or C20:1ω9 did not differ significantly from one another in the four groups of rats under consideration (Table 24). No C22:1ω9 could be detected in any of the 16 samples of visceral adipose tissue.

| Rats | | C16:1ω7 | C18:1ω9 | C20:1ω9 |
|---------|--------------|------------------|--------------------|-----------------|
| Control | before | 39.95 ± 3.73 | 328.06 ± 7.87 | 1.83 ± 0.10 |
| | after (8 wk) | 40.90 ± 3.13 | 341.94 ± 3.67 | 1.77 ± 0.05 |
| ω3D | before | 38.02 ± 7.35 | 321.17 ± 9.80 | 1.75 ± 0.16 |
| | after (8 wk) | 40.07 ± 3.25 | 342.42 ± 13.01 | 1.68 ± 0.03 |

Table 24. Relative weight content (%) of monodesaturated fatty acids in visceral adipose tissue lipids

3.8 Food intake and body weight

As indicated in Table 25, over the last 7-8 weeks of the present experiments, both the food intake and relative gain in body weight were higher ($p < 0.05$ or less) in the ω3D rats maintained on the sunflower oil diet than in either the control rats maintained on the soya oil diet or the ω3D rats switched to the latter diet. It could be objected that the relative magnitude of the changes in body weight exceeded that of the changes in food intake. However, taking into account the differences in both body weight gain and food intake, the estimated caloric efficiency was close to the expected theoretical value, as documented by the following considerations. In one group of 4 ω3D rats maintained for a further period of 7 weeks on the sunflower diet, the daily food intake (19.61 ± 0.27 g/day per rat; $n = 30$) exceeded by 1.93 ± 0.51 g/day per rat ($p < 0.001$) that recorded in one group of 4 control animals maintained on the soya oil diet (17.68 ± 0.43 g/day per rat; $n = 30$). In these two groups of rats, the gain in body weight over the same period of 7 weeks averaged 1.93 ± 0.14 g/day per rat in the ω3D rats as distinct ($p < 0.02$) from 1.09 ± 0.11 g/day per rat in the control animals. The caloric requirement to account for the difference in body weight gain ($\leq 7.6 \pm 1.6$ cal) was thus commensurate with the increase in the caloric supply of the diet (6.2 ± 1.6 cal), which provided about 3.2 cal/g.

| Rats | | Food intake ^a | Relative gain in body weight ^b |
|---------|--------------------|--------------------------|---|
| Control | soya oil diet | 100.0 ± 1.6 (31) | 13.35 ± 1.38 (4) |
| ω3D | sunflower oil diet | 112.1 ± 2.5 (56) | 24.67 ± 1.82 (2) |
| ω3D | soya oil diet | 104.4 ± 1.6 (45) | 12.97 ± 2.70 (4) |

^aThe food intake over the last 8 weeks of the present experiments is expressed relative to the mean value found at the same time after the initial 3 months period in control animals maintained on the soya oil diet
^bThe relative gain in body weight (%) was assessed by comparison of individual measurements made at the end of the initial 3 months period and seven weeks thereafter

Table 25. Food intake and relative gain in body weight

3.9 HOMA index for insulin resistance

At the end of the 3 months initial period, the logarithmic values of the HOMA index for insulin resistance were higher ($df = 4$; $p < 0.02$) in the ω 3D rats than in the control animals. In the former ω 3D rats, such values progressively decreased after the switch in diet as a function of the length of exposure to the soya oil diet ($r = -0.5956$; $n = 12$; $p < 0.05$). Eight weeks after the switch in diet, the HOMA index eventually reached in the ω 3D rats a mean value (1.16 ± 0.09 U/l.mM; $n = 3$) comparable ($p > 0.7$) to that found at the same time in the control animals also exposed to the soya oil diet (1.20 ± 0.05 U/l.mM; $n = 3$).

4. Discussion

The present experimental design prevents any undesirable aggravation of liver steatosis and visceral obesity, as well as food intake, otherwise resulting from an increase in the lipid content of the diet from 5 to 10% (Malaisse et al., 2009; Sener et al., 2009). It also caused correction of insulin resistance in the ω 3D rats.

The exposure of ω 3D to the soya oil diet also allowed the repletion of long-chain polyunsaturated ω 3 fatty acids in the intestinal tract, liver, red blood cell and brain phospholipids.

The changes in the fatty acid pattern of tissue lipids were not always merely and directly attributable to the respective content of each diet in a given fatty acid, as documented by the accumulation of selected long-chain polyunsaturated ω 6 fatty acids in the phospholipids of ω 3D rats and the correction of this situation after the switch from the sunflower oil to soya oil diet. Incidentally, before such a switch the total amount of four ω 3 fatty acids (C18:3 ω 3, C20:5 ω 3, C22:5 ω 3 and C22:6 ω 3) and three ω 6 fatty acids (C20:4 ω 6, C22:4 ω 6 and C22:5 ω 6) was comparable in the control animals and ω 3D rats (Carpentier et al., 2011b).

The present findings also support the view that a transfer of information takes place between the liver and either RBC or brain, as documented for instance by the delayed alignment of the phospholipid fatty acid pattern in the latter two sites on that prevailing at the hepatic level. It was recently proposed that such a process may even be operative in the absence of any dietary deprivation of long-chain polyunsaturated ω 3 fatty acids (Malaisse et al., 2010).

Last, the present findings provide further evidence to the fact that changes in the dietary supply of ω 3 fatty acids may also affect the relative content of tissue lipids in selected saturated and monodesaturated fatty acids.

In conclusion, the procedure used in the present experiments appears indeed suitable to ensure the repletion of long-chain polyunsaturated ω 3 fatty acids in previously ω 3-depleted rats.

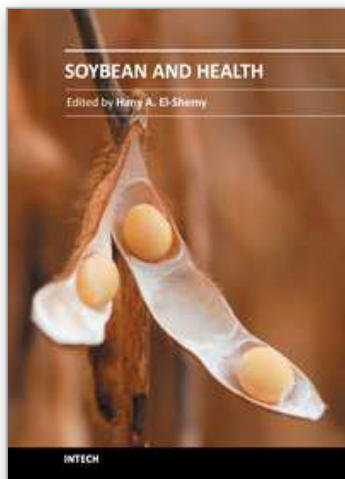
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