Redistribution of abdominal fat after a period of food restriction in rats is related to the type of dietary fat

Federico Soriguer*, Felisa Moreno, Gemma Rojo-Martínez, Fernando Cardona, Francisco Tinahones, Juan M. Gómez-Zumaquero, Eduardo García-Fuentes and Sonsoles Morcillo

Endocrinology and Nutrition Service, Clinical and Experimental Investigation Unit, Civil Hospital, Carlos Haya Hospital Complex, Pza. del Hospital Civil s/n, 29009-Málaga, Spain

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The aim of the present experiment was to test the hypothesis that during refeeding a redistribution of intra-abdominal fat takes place and that both the recovery of weight and the redistribution of intra-abdominal fat are related to the type of dietary fat. The experimental study was carried out using male Sprague–Dawley rats. Three groups of animals were fed diets with three different fatty acid profiles. Each group contained two branches, one fed normally and the other fed initially with a 50% energy reduction followed by refeeding ad libitum with the same isoenergetic diet as the control branch, giving a total of six treatments. Measurements were made of the final and incremental weight of the rat, weight of the intra-abdominal adipose tissue (total intra-abdominal, epididymal, omental and retroperitoneal adipose tissue weight), and feed efficacy (weight increment/metabolizable energy intake). Carcass, epididymal, omental, and muscle lipid contents, carcass protein and energy density were also measured. The results revealed that diets rich in fish oil or olive oil increase catch-up growth more than diets rich in saturated fats. During refeeding the lipid content in the adipose tissue increases while that of muscle tissue decreases. A diet rich in saturated fats induces a relative increase in the amount of intra-abdominal adipose tissue. The lipid content in adipose and muscle tissues and the distribution of intra-abdominal fat can all be modified by the type of dietary fat.

Rat: Dietary fatty acids: Fat redistribution

The metabolic response to refeeding after a period of undernutrition has long been known (Keys et al. 1950), but the clinical consequences of refeeding in the context of such entities as anorexia nervosa, the ‘yo-yo’ effect of slimming diets, or artificial nutrition in potentially recoverable cachectic diseases are not so well known.

Undernourished children undergo a greater weight and height gain after initiating refeeding than non-malnourished children, a catch-up growth which is interpreted as a homeostatic phenomenon aimed at speedily recovering from the damage suffered during food restriction. Although this increase was initially thought to be at the expense of a positive protein balance (Waterlow, 1961), it was soon seen that in man and other mammals a disproportionate repletion of the fat compartment occurred during the refeeding phase (Lister & McCance, 1967; Ashworth, 1969; Harris & Widowson, 1979; MacLean & Graham, 1980).

This greater gain in fat during recovery from undernutrition is not only the result of a poorly balanced or excessively-high-energy diet, as initially thought, but rather it seems to be the result of a transitory increase in efficiency in the utilization of nutrients and a displacement in the distribution of the energy to the fat depots (Dulloo & Girardier, 1990, 1993). Studies with animals fed a fat-rich diet (400–500 g/kg) seem to show that the efficiency of refeeding in the accumulation of fat can be affected by the composition of the dietary fatty acids (Dulloo & Girardier, 1992), there being more and more evidence that the composition of dietary fatty acids can modulate the utilization of energy and affect body composition (Watkins et al. 1982; Leyton et al. 1987; Mercer & Trayhurn, 1987; Shimomura et al. 1990; Hill et al. 1993).

However, the effect of different types of dietary fatty acids on the utilization of energy is controversial. In mice, diets rich in maize or sunflower-seed oil induce a lower increase in weight and accumulation of fat than a diet rich in beef tallow (Mercer & Trayhurn, 1987; Shimomura et al. 1990). Studies in rats have found that

Abbreviations: NNCG, normally nourished control group; UNRG, undernourished–refed group.
* Corresponding author: Dr Federico Soriguer, fax + 34 952 286 704, email soriguer@hch.sas.cica.es
diets rich in fish and olive oil induce a greater accumulation of fat and a lower increase in proteins than diets rich in sunflower-seed or coconut oil (Dulloo et al. 1995). Others, on the other hand, have studied energy output and body composition using doubly-labelled water and found that in rats a diet rich in fish oil induces a greater gain in lean body mass and a lower gain in fat than in animals fed with fats rich in olive oil or beef tallow (Su & Jones, 1993). Not all studies, though, have demonstrated a different effect of dietary fatty acids on the distribution of the body components (Award et al. 1990).

We studied the effect of three isoenergetic diets, differing only in their fatty acid composition, on weight recovery and on fat redistribution after a period of food restriction. We tested the hypothesis that during refeeding a redistribution of intra-abdominal fat takes place and that both the recovery of weight and the redistribution of intra-abdominal fat are related to the type of dietary fat.

Materials and methods

Study design

The study was undertaken with ninety male Sprague–Dawley rats (Criffa, S.A, Barcelona, Spain) divided into six groups of fifteen rats each, as follows:

(a) normally nourished control group (NNCG). Three groups of fifteen rats were separated from their mothers at 3 weeks of age (one rat/cage to control food intake and faeces). During the whole study period these rats had free access to water and food. From weeks 3 to 6 the animals received a standard laboratory diet. From weeks 7 to 13 they were fed one of three experimental isoenergetic diets, but differing only in their composition of fatty acids;

(b) undernourished–refed group (UNRG). Three groups of fifteen rats were separated from their mothers at 3 weeks of age (one rat/cage) and undernourished for 4 weeks (50% reduction in the daily intake of the standard laboratory diet compared with the NNCG), from weeks 3 to 6. From weeks 7 to 13 the animals were refed ad libitum with the same experimental diets as the NNCG (isoenergetic but with varying compositions of fatty acids).

Natural dark and light cycles were maintained over the whole study period, and the ambient temperature was kept at 22°C.

The weight of the rats at the start of the study (3 weeks) was 58.06 (SD 2.67) g. After week 6 the weight of the UNRG was 135.1 (SD 11.7) g and the NNCG 242.8 (SD 25.8) g (P = 0.0001). The animals were weighed each week and at the end of the study the weight gain achieved with the experimental diets was calculated as follows: (final weight – week 6 weight)/week 6 weight.

The protocol was approved by the Ethics and Clinical Investigation Committee of Carlos Haya Hospital.

Composition of the diets

The three experimental diets were isoenergetic, and the concentrations of fat, protein, and carbohydrates were similar. The only difference was in the quality of the fat. The lipid content in all the diets was 80 g/kg, with the source being olive oil in one, fish oil in another, and in the third a mixture of 82% palmitic acid enriched with 18% soybean oil (w/w), a proportion previously shown to be sufficient to prevent a deficit of essential fatty acids (Kaufman et al. 1994; Tinahones et al. 1998). The composition in fatty acids of the three diets, measured by GC (Soriguer et al. 2000), for the olive-oil, fish-oil and palmitic acid + soyabean-oil diets, respectively, was as follows (%): saturated fatty acids (12.0, 32.7, 84.3); monounsaturated fatty acids (78.8, 14.2, 4.5); n-6 fatty acids (5.3, 4.8, 9.6); n-3 fatty acids (0.12, 31.2, 1.24). The remaining components were identical in all the diets (g/kg): casein, 263; starch + sucrose, 588; minerals mix, 37; vitamins mix, 10; cellulose, 18; choline, 0.9; methionine, 3. The mineral mix supplied the following (g/kg diet): CaHPO₄, 18.4; NaCl, 2.7; potassium citrate, 8.1; K₂SO₄, 1.9; MgO, 0.9; MnCO₃, 0.13; ferric citrate, 0.22; ZnCO₃, 0.011; KI, 0.0004; Na₂SeO₃, 0.0004; CrKSO₄, 0.02. The vitamin mix supplied the following (mg/kg diet): thiamin HCl, 0.6; riboflavin, 0.6; pyridoxine, 0.7; nicotinic acid, 3; calcium pantothenate, 1.6; folic acid, 0.2; biotin, 0.02; vitamin B₁₂, 0.001; vitamin A + D₁; vitamin E, 10; menadione, 0.005. The materials for the preparation of the diets were obtained from Laboratorios Musal (Granada, Spain), Merck (Darmstadt, Germany) and Sigma Chemical Co. (St Louis, MO). The energy content of the diets was 1722 kJ/100 g, with the fats accounting for 17.5% of the total energy content.

Control of food intake and faeces

The study was started with the NNCG rats. This enabled us to calculate the amount of food that had to be withdrawn from the experimental group of UNRG rats in order to achieve a 50% reduction compared with the control group. The food was weighed and renewed daily. The spillage was weighed and subtracted in order to calculate the food intake. The animals were weighed and the faeces were collected and weighed weekly and then frozen at −80°C for later study.

Procedures

At the end of the study the animals were killed with CO₂ and carefully dissected immediately afterwards. The epidymal, omental and retroperitoneal adipose tissues were separated and a sample of muscle tissue was taken from the abdominal wall. The samples were weighed, and a part of each was frozen at −80°C for further analysis. The remainder of the animal’s body was also frozen at −80°C.

Analysis of carcass composition

After dissecting the various adipose tissue deposits, the skin and tail were carefully separated and the undigested food in the gut was extracted. After weighing the carcass, it was autoclaved at 112°C for 90 min, after which it was

Resolution: 1.5 × 1.5
homogenized in a waring blender with the addition of a volume of water equal to the weight of the body (Mickelsen & Anderson, 1959; Award et al. 1990). Different samples were frozen at −80°C for further study.

Calorimetry

The energy contained in duplicate samples of the lyophilized carcass was measured by calorimetry (Parr Instrument Company, 1989, IL) (Juhr & Franke, 1992).

Fat extraction and protein measurement

The lipid content in each tissue sample was made by gravimetry after extraction of the fat with chloroform–methanol (2:1, v/v) and butylated hydroxytoluene (BHT) at 0.025 % (Folch et al. 1957). The proteins from the body extract were measured by Kjehldal’s method (Ministerio de Sanidad y Consumo, 1986).

Markers of redistribution of the intra-abdominal fat

From the weight of the epididymal, omental and retroperitoneal tissues, the following quotients were calculated:

- weight of the intra-abdominal fat tissues (g) × 100/final weight of the rats (g);
- weight of the epididymal fat tissue (g) × 100/weight of the intra-abdominal fat (g);
- weight of the omental adipose tissue (g) × 100/weight of the intra-abdominal adipose tissue (g);
- weight of the retroperitoneal adipose tissue (g) × 100/weight of the intra-abdominal adipose tissue (g).

Metabolizable energy intake and feed efficacy

The digestible energy was calculated for each animal individually as the difference between the total amount of energy consumed and the total amount of energy lost through the faeces. The metabolizable energy consumed was calculated as 0.96 × the digestible energy consumed (Ministerio de Sanidad y Consumo, 1986; Su & Jones, 1993). The feed efficacy was calculated as the weight increment/metabolizable energy intake.

Statistical study

Data are presented as means and standard deviations. Hypothesis contrast was made by one-way ANOVA (diet) or by Student’s t test (groups). Statistical significance between subgroups was measured by Duncan’s multiple range test (Sokal & Rohlf, 1969). The tendency between variables was measured by the Pearson (r) linear correlation coefficient. The rejection level for a null hypothesis was 0.05 for two tails.

Results

Final weight and weight increase

The final weight of the rats was greater in the NNCG, but the weight increase after the period of undernutrition was significantly greater in the UNRG rats (Table 1). The final weight and the weight increase were influenced by both nutritional status (group) and the type of dietary fatty acid (diet). The greatest increase occurred in the UNRG rats fed with fish oil, but there were no significant differences with the group fed with olive oil.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group</th>
<th>Olive-oil diet</th>
<th>Mean</th>
<th>SD</th>
<th>Fish-oil diet</th>
<th>Mean</th>
<th>SD</th>
<th>Soyabean oil + palmitic acid diet</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Final weight (g)</td>
<td>UNRG</td>
<td>324.3±</td>
<td>18.0</td>
<td></td>
<td>334.3±</td>
<td>26.2</td>
<td></td>
<td>328.7±</td>
<td>33.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>410.3±</td>
<td>18.7</td>
<td></td>
<td>425.6±</td>
<td>33.4</td>
<td></td>
<td>355.3±</td>
<td>28.9</td>
<td></td>
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<td>Weight increase (%)</td>
<td>UNRG</td>
<td>155.5±</td>
<td>3.7</td>
<td></td>
<td>158.3±</td>
<td>29.2</td>
<td></td>
<td>123.6±</td>
<td>25.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>57.4±</td>
<td>6.7</td>
<td></td>
<td>72.7±</td>
<td>7.7</td>
<td></td>
<td>62.4±</td>
<td>8.0</td>
<td></td>
</tr>
<tr>
<td>Intra-abdominal fat tissue weight (g)</td>
<td>UNRG</td>
<td>9.8±</td>
<td>2.8</td>
<td></td>
<td>11.0±</td>
<td>1.7</td>
<td></td>
<td>9.9±</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>20.0±</td>
<td>4.8</td>
<td></td>
<td>18.6±</td>
<td>5.3</td>
<td></td>
<td>8.6±</td>
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<td></td>
</tr>
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<td>Epididymal fat tissue weight (g)</td>
<td>UNRG</td>
<td>3.7±</td>
<td>0.8</td>
<td></td>
<td>4.0±</td>
<td>0.7</td>
<td></td>
<td>3.8±</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>6.7±</td>
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<td></td>
<td>5.7±</td>
<td>1.7</td>
<td></td>
<td>2.9±</td>
<td>0.6</td>
<td></td>
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<tr>
<td>Omental fat tissue weight (g)</td>
<td>UNRG</td>
<td>2.5±</td>
<td>0.9</td>
<td></td>
<td>2.9±</td>
<td>0.5</td>
<td></td>
<td>2.5±</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>4.7±</td>
<td>1.2</td>
<td></td>
<td>5.2±</td>
<td>1.6</td>
<td></td>
<td>2.2±</td>
<td>0.4</td>
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<tr>
<td>Retroperitoneal fat tissue weight (g)</td>
<td>UNRG</td>
<td>3.5±</td>
<td>1.2</td>
<td></td>
<td>4.1±</td>
<td>0.8</td>
<td></td>
<td>3.5±</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>8.5±</td>
<td>2.2</td>
<td></td>
<td>7.6±</td>
<td>2.1</td>
<td></td>
<td>3.5±</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Metabolizable energy intake (kJ × 10⁻³)</td>
<td>UNRG</td>
<td>11.4±</td>
<td>4.8</td>
<td></td>
<td>10.4±</td>
<td>1.1</td>
<td></td>
<td>9.5±</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>15.0±</td>
<td>2.3</td>
<td></td>
<td>11.7±</td>
<td>1.2</td>
<td></td>
<td>10.0±</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>Feed efficacy (g/kJ × 10³)</td>
<td>UNRG</td>
<td>16.5±</td>
<td>1.9</td>
<td></td>
<td>19.1±</td>
<td>2.2</td>
<td></td>
<td>16.6±</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>10.1±</td>
<td>2.1</td>
<td></td>
<td>14.0±</td>
<td>2.7</td>
<td></td>
<td>11.7±</td>
<td>1.0</td>
<td></td>
</tr>
</tbody>
</table>

UNRG, undernourished–refed group; NNCG, normally nourished control group.

*a,b,cMean values within a row with unlike superscript letters were significantly different (Duncan’s test) (P<0.01).

*Mean value was significant different from that of the NNCG (Student’s t test) (P<0.01).

†For details of diets and procedures, see p. 116.
Intra-abdominal fat

In the UNRG rats refed with olive oil or fish oil, the intra-abdominal fat weighed less than in the NNCG rats (Table 1), while in the rats fed with soyabean oil + palmitic acid the weight of the intra-abdominal fat was similar between both groups. The type of dietary fatty acid had no influence on the overall amount of intra-abdominal fat in the UNRG rats, whereas in the normally nourished rats those animals fed with soyabean oil + palmitic acid had significantly less intra-abdominal fat than those fed with olive or fish oil (Table 1).

The weight of the epididymal adipose tissue was less in the UNRG rats than in the NNCG rats, though only in those fed with olive or fish oil. In the rats fed with palmitic acid + soyabean oil, however, the weight was greater in the UNRG (Table 1). In the UNRG rats the weight of the epididymal fat was similar in the three types of diet, but in the NNCG rats it was greater in the olive- and fish-oil groups than the palmitic acid + soyabean-oil group (Table 1).

The weight of the omental tissue was also less in the UNRG rats consuming olive oil or fish oil than in the NNCG rats. The weight of the omental tissue in the UNRG rats fed with palmitic acid + soyabean oil, however, was greater in the UNRG (Table 1). In the group of NNCG rats the weight of the omental tissue was significantly greater in those fed with fish oil and olive oil.

The weight of the retroperitoneal adipose tissue was significantly less in the UNRG animals, except for those rats fed with palmitic acid + soyabean oil. The greatest weight in the NNCG rats corresponded to those fed with olive oil and fish oil (Table 1).

Metabolizable energy intake and feed efficacy

The metabolizable energy intake was less in the UNRG than in the NNCG rats, the difference being greatest in the rats fed with olive oil (Table 1). The feed efficacy (weight increment/metabolizable energy intake) was significantly greater in the UNRG rats, for all the diets (Table 1). In both the UNRG and the NNCG animals the greatest feed efficacy was seen in the animals fed with fish oil.

Lipid content and tissue proteins

The lipid content in the carcass extract was no different between both main groups, but within each group the rats fed with palmitic acid + soyabean oil had a lower lipid content than those fed with olive oil or fish oil (Table 2), though this difference was only significant in the NNCG rats. In both the epididymal and the omental tissues (Table 2) the lipid content was greater in the UNRG rats than in the NNCG rats. Within each group and in both tissues (epididymal and omental), the UNRG animals fed with fish oil had a greater lipid content, while in the normally nourished rats the type of dietary fatty acid had no influence on the lipid content in either the epididymal or the omental tissues.

In the muscles the opposite occurred to what was seen in the intra-abdominal tissue. The lipid content was greater in the NNCG than in the UNRG rats, for all three diets. The UNRG rats that were refed with fish oil had the greatest lipid content in the muscle (Table 2).

The energy density of the carcass was not significantly different between the two groups (Table 2). Within each

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group</th>
<th>Olive-oil diet</th>
<th>Fish-oil diet</th>
<th>Soyabean oil + palmitic acid diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcass lipid content (g/100 g)</td>
<td>UNRG</td>
<td>9.2a 2.6</td>
<td>8.4a 2.9</td>
<td>6.7a 2.1</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>9.6a 0.8</td>
<td>8.4a 2.7</td>
<td>6.1b 1.6</td>
</tr>
<tr>
<td>Epididymal fat lipid content (g/100 g)</td>
<td>UNRG</td>
<td>86.5a 3.6</td>
<td>91.1a 4.5</td>
<td>87.1b 5.4</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>82.2a 6.5</td>
<td>81.9a 6.5</td>
<td>83.9a 5.0</td>
</tr>
<tr>
<td>Omental fat lipid content (g/100 g)</td>
<td>UNRG</td>
<td>83.9b 5.6</td>
<td>89.1a 5.9</td>
<td>83.7b 4.3</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>77.4a 6.1</td>
<td>77.0a 7.7</td>
<td>78.1a 4.0</td>
</tr>
<tr>
<td>Muscle lipid content (g/100 g)</td>
<td>UNRG</td>
<td>1.7a 0.6</td>
<td>2.99a 0.9</td>
<td>2.0a 0.1</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>4.7a 1.6</td>
<td>4.5a 1.0</td>
<td>4.1a 1.1</td>
</tr>
<tr>
<td>Carcass energy density (kJ/g)</td>
<td>UNRG</td>
<td>25.8b 1.3</td>
<td>27.0a 1.8</td>
<td>24.4b 2.5</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>26.4b 1.5</td>
<td>26.8a 1.7</td>
<td>25.0b 1.2</td>
</tr>
<tr>
<td>Carcass protein concentration (g/100 g)</td>
<td>UNRG</td>
<td>18.8a 0.8</td>
<td>17.9a 1.1</td>
<td>17.5a 1.1</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>17.6a 1.9</td>
<td>17.0a 0.8</td>
<td>19.6a 1.1</td>
</tr>
<tr>
<td>Carcass total protein (g)</td>
<td>UNRG</td>
<td>43.81a 1.88</td>
<td>42.14a 4.97</td>
<td>42.98b 4.5</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>50.64a 6.26</td>
<td>52.39a 4.32</td>
<td>49.25a 3.81</td>
</tr>
</tbody>
</table>

UNRG, undernourished—refed group; NNCG, normally nourished control group.

*Mean values within a row with unlike superscript letters were significantly different (Duncan’s test) (P<0.01).

*Mean value was significantly different from that of the NNCG (Student’s t test) (P<0.01).

†For details of diets and procedures, see p. 116.
group those animals fed with fish oil had a greater energy density, with significant differences compared with the rats fed palmitic acid + soyabean oil in the NNCG and significantly different to both the other diets, olive oil and palmitic acid + soyabean oil, in the UNRG (Table 2).

The UNRG rats refed with olive oil had a greater concentration of proteins/g total body tissue than the animals fed with fish oil and palmitic acid + soyabean oil. However, in the NNCG group those rats fed with palmitic acid + soyabean oil had a greater amount of protein/unit of whole body extract (Table 2).

As expected, the total amount of proteins was significantly lower in the UNRG rats, though the type of dietary fat had no significant influence on the overall amount of proteins in either main group (Table 2).

Indices of fat redistribution

The proportion of intra-abdominal fat with respect to total weight was less in the UNRG compared with the NNCG in the rats fed with olive oil or fish oil, but not in those fed with palmitic acid + soyabean oil. Within the NNCG rats those fed with olive oil or fish oil had a greater proportion of intra-abdominal fat in relation to total weight than those fed with palmitic acid + soyabean oil (Table 3).

The proportion of epididymal adipose tissue compared with total intra-abdominal fat was significantly greater in the UNRG, whichever the dietary fat. In both main groups the lowest proportion of epididymal weight compared with total abdominal weight was found in those animals fed with fish oil (although this was only statistically significant in the NNCG group (Table 3)).

The proportion of omental tissue within the total intra-abdominal fat tissues was not significantly different between the two main groups of rats. Unlike what was seen in the epididymal tissue, the subgroups fed with fish oil had the greatest proportion of omental fat compared with total abdominal fat (Table 3), although this difference was only significant in the NNCG rats.

The proportion of retroperitoneal fat compared with total intra-abdominal fat was less in the rats of the UNRG, whichever the diet. The type of dietary fat had no influence on the amount of retroperitoneal fat compared with the total amount of intra-abdominal fat (Table 3).

Discussion

The main finding in the present study was that during weight recovery after a period of undernutrition changes are produced in the distribution of fat, characterized by an increase in lipid content in the intra-abdominal fat tissues, a decrease in intra-muscular lipid content, and a redistribution of the adipose tissue towards the epididymal tissue at the expense of the retroperitoneal tissue. Furthermore, all these changes may be influenced by type of dietary fat.

The catch-up growth seen in our study animals after refeeding is well known in both children and animals and is considered to be a homeostatic phenomenon designed to accelerate the recovery of body structures after a period of undernourishment, especially the protein component of the body (Keys et al. 1950; Waterlow, 1961). This increase in weight is potentially dependent on the amount of food and the initial hyperphagia (Award et al. 1990; Shimomura et al. 1990; Dulloo & Girardier, 1992), the amount of energy eliminated in the faeces (Baba et al. 1982; Su & Jones, 1993), a transitory increase in efficiency of the utilization of the energy (Dulloo & Girardier, 1992, 1993), a shift in energy partitioning in favour of an acceleration for the replenishment of fat stores (Innis, 1991; Takeuchi et al. 1995), the type of dietary fat (Dulloo & Girardier, 1992; Su & Jones, 1993; Dulloo et al. 1995) and the different redistribution of the body fat according to the nutritional state and the type of dietary fat (Ferrrell & Koong, 1986; Belzung et al. 1993; Björntorp, 1997).

Dulloo & Girardier (1992, 1993) found that the refeeding of undernourished rats with a diet containing 30 g fat/kg was accompanied by a 10% reduction in energy expenditure and that virtually all the energy saved as the result of this metabolic adaptation was deposited as fat rather than protein. In our study, energy expenditure was not measured, but the undernourished rats had a lower

### Table 3. Redistribution of body fat index according to group and diet† (Mean values and standard deviations)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group</th>
<th>Olive-oil diet</th>
<th>Fish-oil diet</th>
<th>Soyabean oil + palmitic acid diet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>Intra-abdominal fat:total body fat (×100)</td>
<td>UNRG</td>
<td>3.0 ± 0.6</td>
<td>3.6 ± 0.5</td>
<td>3.0 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>3.1 ± 0.6</td>
<td>3.7 ± 0.6</td>
<td>3.1 ± 0.6</td>
</tr>
<tr>
<td>Epididymal fat:intra-abdominal fat (×100)</td>
<td>UNRG</td>
<td>4.9 ± 0.9</td>
<td>5.5 ± 1.0</td>
<td>4.9 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>3.7 ± 0.8</td>
<td>4.3 ± 0.8</td>
<td>3.7 ± 0.8</td>
</tr>
<tr>
<td>Omental fat:intra-abdominal fat (×100)</td>
<td>UNRG</td>
<td>38.6 ± 3.6</td>
<td>36.9 ± 3.7</td>
<td>38.6 ± 3.6</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>32.9 ± 3.9</td>
<td>31.0 ± 2.9</td>
<td>32.9 ± 3.9</td>
</tr>
<tr>
<td>Retroperitoneal fat:intra-abdominal fat (×100)</td>
<td>UNRG</td>
<td>26.3 ± 3.3</td>
<td>25.5 ± 3.2</td>
<td>26.3 ± 3.3</td>
</tr>
<tr>
<td></td>
<td>NNCG</td>
<td>23.5 ± 2.4</td>
<td>22.8 ± 2.4</td>
<td>23.5 ± 2.4</td>
</tr>
</tbody>
</table>

UNRG, undernourished—refed group; NNCG, normally nourished control group.

*Mean values within a row with unlike superscript letters were significantly different (Duncan’s test) (P<0.01).

†For details of diets and procedures, see p. 116.
metabolizable energy intake than the control rats after refeeding, and a higher feed efficacy, which suggests a transitory increase in efficiency of the utilization of the energy.

The greater weight increase produced during refeeding was initially believed to be at the expense of a positive protein balance (Waterlow, 1961), but it was later seen that in man and other mammals a disproportionate repletion of the fat compartment occurred during the refeeding phase (Lister & McCance, 1967; Ashworth, 1969; Alden, 1970; Harris & Widowson, 1979; MacLean & Graham, 1980). In our study a shift in energy partitioning seems to have occurred between the different fat compartments themselves rather than between the fat and protein compartments, since the lipid content in the muscle tissue was less and the lipid content in the epididymal and omental tissues was greater in the UNRG rats than in the control group.

The lipid content in the tissues during refeeding was not independent of the type of dietary fatty acid. This greater lipid content/tissue unit in the rats fed with fish oils could be due to a lower hydration during the process of refeeding and to the greater lipophilia of the n-3 fatty acids. Although some studies have found that monounsaturated and saturated fatty acids are acylated into triacylglycerols in the adipose tissue faster than other families of fatty acids (Bremer & Norum, 1982) and that the synthesis of fatty acids in the adipose tissue is inversely related to the degree of unsaturation of the fat (Hezberg, 1983), recent studies undertaken by our group suggest that dietary n-3 fatty acids in fact have a greater capacity to become incorporated into the adipose tissue than other families of fatty acids (Soriguer et al. 2000). In the presence of an abundant amount of n-3 fatty acids, as occurs in a diet in which the source of fat is fish oil, this greater lipophilia of the n-3 fatty acids would facilitate the esterification of fatty acids in the adipose tissue and their posterior accumulation.

In the UNRG rats and the NNCG rats the increase in weight was related to the type of dietary fat. In both groups those rats fed with fish oil had the greatest increase in weight, followed by those fed with olive oil. Others have seen this effect of the type of dietary fat on weight increase in UNRG rats. Though in 7-week-old rats starved for 2 weeks Dulloo & Girardier (1992) did not find that the type of dietary fat had any effect on weight increase, in a later study using the same starvation model (Dulloo et al. 1995), they found that after refeeding with diets containing 50% of the energy from fish the recovery of the body weight was dependent on the type of dietary fat. As with our study, those diets rich in fish or olive oils were more efficient at increasing weight than diets rich in sunflower-seed or coconut oils. In our study there was a control group, lacking in other studies, in which it was possible to verify that the differential effect of the type of dietary fat on the weight increase occurs not only during refeeding after undernourishment, but also in the control rats during spontaneous weight increase, so that the effect does not appear to be specific to refeeding after malnourishment, but rather to the type of dietary fat itself.

The results differ from many other studies in that a diet rich in fish oil generally induces a lower accumulation of fat and a lower weight increase during normal feeding (Cunnane et al. 1986; Parrish et al. 1990; Shimomura et al. 1990; Hill et al. 1993; Su & Jones, 1993). These differences could be explained by the different methodological approaches, the different digestibility and palatability of the diet, the reduction in food intake, the different proportion of body water according to the type of fatty acid, changes in physical activity (which elsewhere have been shown to be of little importance) (Boyle et al. 1981), age, or duration of the diet (Baba et al. 1982; Mercer & Trayhurn, 1987; Shimomura et al. 1990; Hill et al. 1993).

The UNRG in our study had a lower amount of intra-abdominal fat in absolute terms, though only in the groups of rats fed with olive or fish oils. The proportion of intra-abdominal adipose tissue after refeeding, however, was greater in the rats refed with palmitic acid + soyabean oil. On the other hand, within the abdominal tissue after refeeding, the adipose tissue was greater in the epididymal region, the same in the omentum and less in the retroperitoneal region, indicating an anatomic preference for the collection of fat after refeeding, a redistribution which was to a certain extent specific for refeeding, although not wholly independent of the type of dietary fatty acid.

Studies of the size of the visceral organs after undernourishment and refeeding are contradictory, some studies finding a reduction in size (Ferrell & Koong, 1986) but others not (Dulloo & Girardier, 1993). In our study the lower increase in epididymal fat in the animals fed with fish oil, also seen by others (Cunnane et al. 1986; Belzung et al. 1993) was only found in the NNCG animals and relative to the total amount of intra-abdominal fat, but not in the UNRG rats. The relative amount of omental fatty tissue in the NNCG rats fed with fish oil, however, was greater. Olguin et al. (1998) found that saturated fats in normally nourished diabetic animals induced an accumulation of fat in the perirenal tissue but not in the epididymal tissue, the omental tissue not being included in that study.

The metabolic consequences which this effect of refeeding and the type of dietary fatty acid have on the redistribution of intra-abdominal fat could be important. Intra-abdominal adipose tissue is known to possess a very different metabolic behaviour depending on whether it is portal or extraportal fat (Björntorp, 1997).

Lately, the study of the concentration and composition of fats in different tissues has taken on a special interest (Peiris et al. 1986; Murphy, 1990; Borkman et al. 1993). Recent studies have shown that the lipid content in the interior of muscle cells is inversely related to its sensitivity to insulin (Simoneau et al. 1995). Likewise, the increased lipid content has a lipotoxic effect on β cells and heart muscle cells in obese rats (Unger et al. 1999; Zhou et al. 2000). Knowledge of the effects of dietary fatty acids on the lipid content in the cells will afford new opportunities to design diets which enable the lipotoxic effect of an excessive accumulation of cell fat to be avoided. Clinical situations and entities, such as anorexia nervosa, the ‘yo-yo’ effect of slimming diets, or artificial nutrition in potentially recoverable cachetic diseases, in which it is possible to help the patients with suitable refeeding, are becoming more and more common.
Fat redistribution after malnutrition in rats

In summary, the results of the present study suggest that the catch-up growth after a period of undernourishment can be influenced by the type of dietary fatty acid, with a diet rich in fish and olive oil increasing this catch-up growth more than diets rich in saturated fats. This difference cannot be fully explained just by the different amount of food and the differing intestinal absorption of each of the diets involved, though these could be partly involved. The lipid content in adipose and muscle tissues, as well as the distribution of intra-abdominal fat, can be modified by the type of dietary fat.

The extrapolation of the results of these experimental studies to man should be considered with caution. Nevertheless, the variable efficacy of a diet in the process of nutritional rehabilitation after a period of malnourishment opens new possibilities for adequate nutritional advice in malnourished persons, depending on the type of dietary fatty acid and especially on the possibility of influencing the redistribution of body fat in the intra-abdominal area.

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