Modification of the fatty acid composition of dietary oils and fats on incorporation into chylomicrons and chylomicron remnants

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Possible changes in the fatty acid composition of dietary fats and oils which might occur during digestion, absorption and formation of chylomicrons and chylomicron remnants were investigated. Chylomicrons were collected from the thoracic duct of rats tube-fed with olive, maize, palm or fish oil or butter fat, and their fatty acid composition was determined and compared with that of their parent lipids. In turn, these lipoproteins were converted to chylomicron remnants in functionally hepatectomized rats and their composition re-determined. The predominant fatty acids in each of the oils and fats also predominated in their respective chylomicrons, but their proportions were reduced during the processes leading to their formation. Endogenous contributions of linoleic, eicosapentaenoic, and docosahexaenoic acids were particularly noted when these fatty acids were not well-represented in the original oils and fats, suggesting that they may be obligatory constituents in the formation of chylomicrons. The conversion of chylomicrons to remnants further attenuated the extremes in fatty acid composition of the dietary oils and fats. These results indicate that following an acute intake of oil or fat, the resulting chylomicrons and chylomicron remnants presented to the tissues contain a more balanced distribution of saturated, mono- and polyunsaturated fatty acids than the oils and fats from which they were derived.

Fatty acid composition: Dietary fat: Chylomicrons: Chylomicron remnants

Numerous investigations have been made of the relationship between the degree of saturation of dietary fatty acids and the concentration of plasma cholesterol. The main conclusions drawn from these studies are that dietary saturated fatty acids, particularly palmitate, increase plasma cholesterol concentrations, mainly in low-density lipoproteins (LDL), whereas *n*-6 polyunsaturated fatty acids have the opposite effect (Kinsell *et al.* 1952; Ahrens *et al.* 1957; Keys *et al.* 1965). More recently, oleic acid has been reported to be hypocholesterolaemic (Mattson & Grundy, 1985), and long-chain *n*-3 polyunsaturated fatty acids have been found to have variable effects on plasma cholesterol, but to reduce triacylglycerol concentrations, particularly in very-low-density lipoproteins (VLDL; Harris *et al.* 1983). Many of these observations preceded the present detailed understanding of lipoprotein metabolism, so there has been little consideration of the pattern of incorporation of dietary fatty acids into the triacylglycerol-rich chylomicrons and their remnants.

Chylomicrons are formed in enterocytes as a consequence of the uptake of dietary fatty acids and cholesterol, and enter the bloodstream via the lymphatic system. In the circulation, chylomicron triacylglycerol is rapidly hydrolysed by the enzyme lipoprotein lipase (*EC* 3.1.1.34) located on the endothelial surface of capillaries in extrahepatic

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tissues, resulting in the delivery of free fatty acids to the tissues and the formation of chylomicron remnant lipoproteins (Redgrave, 1970). Chylomicron remnants are relatively enriched in esterified cholesterol and have been shown to be atherogenic in experimental animals (Zilversmit, 1979; Melchior *et al.* 1981), and in human subjects (Karpe *et al.* 1994). Ultimately, remnants are removed from the circulation by the liver via a receptor specific for apolipoprotein E (Mahley *et al.* 1989).

Since the type of fatty acid in the diet affects cholesterol metabolism and, therefore, can be considered to be involved in the development of atherosclerosis, it is important to ascertain the extent to which the composition of chylomicrons and their remnants reflects the composition of the dietary lipid from which they are derived. In the present investigation the fatty acid composition of chylomicrons resulting from the ingestion of olive, maize, palm or fish oil, or butter fat in rats was analysed and, on the one hand, compared with the composition of the oils or fat from which they were derived, and on the other, with the composition of their resulting chylomicron remnants, the particles that are ultimately the vehicles for uptake into the liver of dietary fatty acids and cholesterol.

MATERIALS AND METHODS

Animals, diets and chemicals

Male Wistar rats (350–370 g) were used for the preparation of chylomicrons and chylomicron remnants. There were no significant differences in body weight between any of the experimental groups. Before use the rats were fed on a standard commercial rat pellet (low-fat- diet and kept under constant day length (12 h) and temperature (25°). The diet contained soyabean oil as the principal lipid source (2·5% of the total energy intake), with oleic and linoleic acids representing half of the total fatty acids present, and the remainder being associated with small amounts of other saturated, mono- and polyunsaturated fatty acids. Sodium pentobarbital and menhaden fish oil were obtained from Sigma Chemical Co., Poole, Dorset. Palm oil was obtained from Rhone Poulenc, Manchester. Olive oil, maize oil and butter were obtained from domestic suppliers. All other chemicals were obtained from BDH, Dagenham, Essex and Fisons, Loughborough, Leics.

Preparation of chylomicrons and chylomicron remnants

Chylomicrons were prepared according to the methods described by Bollman *et al.* (1948). Briefly, on the morning of the experiment, one rat was tube-fed with either olive, maize, palm or fish oil, or filtered butter fat (0·5 ml); each oil or fat was supplemented with α-tocopherol (4 mg/ml) as an antioxidant. After approximately 1 h the rat was anaesthetized with sodium pentobarbital (60 mg/kg body weight i.p.), the abdominal cavity was opened and the thoracic duct was cannulated with polyethylene tubing (external diameter 1·52 mm) and secured with a ligature. When the chyle was flowing satisfactorily, a further 0·5 ml of the same oil or fat fed initially was injected through the wall of the pyloric region of the stomach. The abdominal wall was sutured and the rat placed in a restraining cage. The animal was allowed to recover, during which time it had access to saline (9 g NaCl/l) for 5 h, and water overnight. Over this period the chyle was collected into a tube containing ampicillin (0·05 mg). Following collection, 2 ml portions of the chyle were layered under NaCl (density 1·006 g/ml) in 6·5 ml polyallomer tubes and ultracentrifuged at 20000 rev./min for 21 min (6×10^5 ***g***.min) in a fixed-angle rotor at a temperature of 12°. This allowed large chylomicrons (diameter > 100 nm) free from intestinal VLDL to float to the tops of the tubes and they were then removed by slicing the top 10–15 mm using a Beckman tube slicer.

Chylomicron remnants were prepared *in vivo* from the chylomicrons, using methods

Table 1. *Fatty acid composition of palm oil, and of the chylomicrons and chylomicron remnants derived from it (g/100 g total fatty acids)*‡

(Mean values with their standard errors for three independent preparations)

	Palm oil					
	Oil		Chylomicrons		Chylomicron remnants	
Fatty acid	Mean	SE	Mean	SE	Mean	SE
10:0	ND		ND		ND	
12:0	ND		ND		ND	
14:0	0·97	0·01	1·10	0·05	1·01	0·04
16:0	44·00	0·22	32·61***	1·22	29·12	0·91
16:1	1·87	0·02	0·99***	0·12	3·02†††	0·18
18:0	4·31	0·03	4·67	0·22	4·99	0·23
18:1	38·66	0·25	36·86	1·00	33·86	0·63
18:2	9·98	0·05	16·91**	1·42	18·14	1·50
18:3	0·23	0·01	0·62*	0·12	0·41	0·07
20:5	ND		0·48**	0·10	0·74	0·04
22:6	ND		1·34**	0·20	2·50†	0·36
Minor unidentified	ND		4·42	0·16	6·21†	0·35
Total identified						
Saturated	49·28	0·29	38·38**	1·44	35·12	1·11
Monounsaturated	40·53	0·28	37·85*	0·93	36·88	0·46
Polyunsaturated	10·19	0·06	19·35**	1·27	21·79	1·81
P:S	0·21		0·50		0·62	

ND, not detected (< 0·2 g/100 g total fatty acids); P:S, polyunsaturated:saturated fatty acid ratio.
Mean values were significantly different from those for palm oil, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
Mean values were significantly different from those for chylomicrons, † $P < 0·05$, ††† $P < 0·001$.
‡ For details of experimental procedures, see pp. 436–439.

based on those of Redgrave (1970). These experiments were performed during the afternoon following chyle collection, to ensure that the rats used were in a post-absorptive state. Rats (four to six animals per chylomicron preparation) were anaesthetized as described previously, and functionally hepatectomized by ligation of the coeliac artery, the anterior mesenteric artery, and the hepatic portal vein. Chylomicrons (containing 30–40 μmol triacylglycerol) and 50 mg glucose in 2 ml 9 g NaCl/l were injected into the left ileolumbar vein. After 45 min the rats were exsanguinated via the abdominal aorta, while a NaCl solution (9 g/l) containing 10 g bovine serum albumin/l was infused into the right ileolumbar vein. The blood removed was allowed to clot for 15 min at 37°, and the serum was separated by centrifugation at 3000 ***g*** for 15 min at 12°. The rat serum was layered (4–5 ml/tube) under NaCl (1·006 g/ml) in 6·5 ml polyallomer tubes and ultracentrifuged for 6×10^7 ***g***.min at 12°. The top fraction (1 ml) from this centrifugation was harvested by tube slicing and further purified by layering (2 ml) under NaCl (1·006 g/ml) and ultracentrifugation for $3·2 \times 10^7$ ***g***.min at 12°. The top fraction (1 ml/tube) was isolated and used as the chylomicron remnant preparation.

The rats employed for the preparation of chylomicron remnants were in a post-absorptive state to ensure that their serum concentrations of VLDL and intermediate-density lipoproteins (IDL) were minimal, and two centrifugation steps were used to reduce further the possibility of contamination. The absence of VLDL and IDL from the remnant preparations was confirmed by SDS-PAGE, which demonstrated the presence of apolipoproteins B-48 and E and the lack of apolipoprotein-B100 (results not shown).

Table 2. *Fatty acid composition of butter fat, and of the chylomicrons and chylomicron remnants derived from it (g/100 g total fatty acids)*‡

(Mean values with their standard errors for three independent preparations)

	Butter fat					
	Fat		Chylomicrons		Chylomicron remnants	
Fatty acid	Mean	SE	Mean	SE	Mean	SE
10:0	2·54	0·09	0·92***	0·11	ND†††	
12:0	4·39	0·02	3·80	0·42	ND†††	
14:0	14·13	0·10	10·31*	0·95	4·84†	1·51
16:0	35·10	0·27	24·66***	0·79	27·98	1·66
16:1	1·87	0·02	2·87**	0·14	3·59	0·72
18:0	12·40	0·07	6·61***	0·24	8·30†	0·30
18:1	16·56	0·12	19·67**	0·66	21·11	0·53
18:2	1·83	0·03	17·02***	2·49	16·51	1·43
18:3	0·42	0·03	1·95	0·09	0·79††	0·22
20:5	ND		0·92	0·22	1·44	0·65
22:6	ND		1·98	0·30	2·64	0·26
Minor unidentified	10·76	0·90	9·29	0·35	12·80††	0·53
Total identified						
Saturated	68·56	0·41	46·30***	2·11	41·12	3·31
Monounsaturated	18·43	0·14	22·54**	0·77	24·70	0·86
Polyunsaturated	2·25	0·06	21·87***	1·79	21·38	2·95
P:S	0·03		0·47		0·52	

ND, not detected (< 0·2 g/100 g total fatty acids); P:S, polyunsaturated:saturated fatty acid ratio.
Mean values were significantly different from those for butter fat, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
Mean values were significantly different from those for chylomicrons, † $P < 0·05$, †† $P < 0·01$, ††† $P < 0·001$.
‡ For details of experimental procedures, see pp. 436–439.

Determination of fatty acid composition

Fatty acid methyl esters were prepared from the parent oils and fats and each of the chylomicron and remnant preparations using the transmethylation method of Morrison & Smith (1964). For the parent oils and fats the results represent the means from three samples, and for the chylomicrons and chylomicron remnants they are the means from three independent preparations. Briefly, the lipids were extracted from each sample using a minimum of 20 volumes of chloroform–methanol (2:1, v/v), and partitioned with 0·4 volumes of 0·03 M-HCl. Following the removal of the aqueous phase, the chloroform layers were dried under N_2, the lipid samples were hydrolysed, and the resulting fatty acids were methylated using 1 ml boron trifluoride-methanol–methanol–hexane (35:30:35, by vol.) at 100° for 45–60 min. When cool, the fatty acid methyl esters were extracted by adding 2 volumes of hexane, then 1 volume of distilled water, shaking briefly, and centrifuging at 3000 *g* for 15 min at 12°. The fatty acid methyl esters from the hexane layer were separated by GC (Shimadzu GC 9A, Shimadzu Seizakusho Co., Kyoto, Japan) using a glass column (1·5 m × 2 mm) packed with GP 3% SP-2310/2% SP-2300 on 100/120 chromosorb WAW (Supelco UK, Poole, Dorset), and using a temperature programme of 190° for 2 min, increasing from 190–220° at a rate of 2°/min, and then maintained at 220° for a further 20 min. Peaks were identified and quantified using known fatty acid methyl ester standards (Supelco UK), and the areas under the peaks were integrated by means of a Shimadzu CR2AX electronic data processor. The results are expressed as a percentage of the total fatty acid mass measured. The method for fatty acid methylation (Morrison & Smith, 1964)

Table 3. *Fatty acid composition of maize oil, and of the chylomicrons and chylomicron remnants derived from it (g/100 g total fatty acids)*‡

(Mean values with their standard errors for three independent preparations)

	Maize oil					
	Oil		Chylomicrons		Chylomicron remnants	
Fatty acid	Mean	SE	Mean	SE	Mean	SE
10:0	ND		ND		ND	
12:0	ND		ND		ND	
14:0	ND		0·27***	0·02	1·01††	0·09
16:0	9·98	0·03	13·27*	0·80	20·25††	0·50
16:1	0·06	0·00	0·91*	0·10	3·97†††	0·05
18:0	1·71	0·01	3·21**	0·07	5·11††	0·24
18:1	27·06	0·02	23·45**	0·65	22·92	0·79
18:2	58·03	0·03	50·02**	1·14	33·02†††	0·85
18:3	1·47	0·01	1·62	0·16	0·71††	0·04
20:5	ND		0·67***	0·08	1·62†	0·31
22:6	ND		1·59**	0·25	2·57	0·80
Minor unidentified	1·69	0·04	4·99***	0·04	8·82†††	0·30
Total identified						
Saturated	11·69	0·03	16·75**	0·87	26·37†††	0·43
Monounsaturated	27·12	0·32	24·36*	0·70	26·89	0·75
Polyunsaturated	59·50	0·04	53·90*	1·36	37·92†††	0·63
P:S	5·09		3·22		1·44	

ND, not detected (< 0·2 g/100 g total fatty acids); P:S, polyunsaturated:saturated fatty acid ratio.
Mean values were significantly different from those for maize oil, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
Mean values were significantly different from those for chylomicrons, † $P < 0·05$, †† $P < 0·01$, ††† $P < 0·001$.
‡ For details of experimental procedures, see pp. 436–439.

used was chosen because of its use in similar studies (Harris & Muzio, 1993), for its rapid methylation of fatty acids from triacylglycerols and esterified cholesterol, and because it has been demonstrated to give recoveries of > 99% for individual saturated and unsaturated fatty acids. Our studies using a mixture of fatty acid standards have confirmed these results.

Significance limits were determined using Student's *t* test.

RESULTS

The fatty acid compositions of the different oils and fats used in the present study, together with the compositions of their respective chylomicrons and chylomicron remnants, are shown in Tables 1–5. Palm oil (Table 1) and butter fat (Table 2) contained mainly saturated fatty acids, maize oil (Table 3) mainly polyunsaturated, and fish oil (Table 4) approximately equal proportions of saturated, mono- and polyunsaturated fatty acids, while olive oil (Table 5) contained mainly monounsaturated fatty acids. The polyunsaturated:saturated fatty acid (P:S) ratio ranged from 0·03 for butter fat to 5·09 for maize oil, representing a 170-fold range between the different oils and fat examined.

In olive oil (Table 5), 75% of the total fatty acid was identified as the monounsaturated fatty acid oleic acid (18:1*n*-9), with the remainder mainly palmitic (16:0; 11%) and linoleic acids (18:2*n*-6; 8%). Palm oil (Table 1) also contained a relatively high proportion of oleic acid (38·7%), and a comparable proportion of linoleic acid (10%) to that found in

Table 4. *Fatty acid composition of fish oil, and of the chylomicrons and chylomicron remnants derived from it (g/100 g total fatty acids)*‡

(Mean values with their standard errors for three independent preparations)

	Fish oil					
	Oil		Chylomicrons		Chylomicron remnants	
Fatty acid	Mean	SE	Mean	SE	Mean	SE
10:0	ND		ND		ND	
12:0	ND		ND		ND	
14:0	7·52	0·09	7·02	0·33	3·04†††	0·51
16:0	19·67	0·25	17·51**	0·40	20·11†††	0·37
16:1	11·86	0·17	11·26	0·48	7·65†	0·65
18:0	3·84	0·04	4·29	0·30	5·12	0·53
18:1	13·33	0·21	12·32	0·10	15·69††	0·63
18:2	1·16	0·02	12·72***	1·43	14·89	1·49
18:3	1·17	0·02	1·76**	0·10	0·60††	0·14
20:5	15·32	0·08	11·98***	0·19	12·75	1·31
22:6	12·07	0·14	8·22***	0·08	7·00†	0·36
Minor unidentified	14·06	1·18	12·92	0·26	12·52	0·86
Total identified						
Saturated	31·03	0·46	28·82	1·00	28·27	0·42
Monounsaturated	25·19	0·44	23·58	0·48	23·34	0·33
Polyunsaturated	29·72	0·23	34·68*	1·58	35·24	0·53
P:S	0·95		1·20		1·25	

ND, not detected (< 0·2 g/100 g total fatty acids); P:S, polyunsaturated:saturated fatty acid ratio.
Mean values were significantly different from those for fish oil, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
Mean values were significantly different from those for chylomicrons, † $P < 0·05$, †† $P < 0·01$, ††† $P < 0·001$.
‡ For details of experimental procedures, see pp. 436–439.

olive oil (8%), although the main fatty acid in this oil was palmitic acid (44%). Palmitic acid was also found to be the main saturated fatty acid in butter fat (35·1%), but in contrast to palm oil this represented only 51·2% of the total saturated fatty acid content, with the remainder comprising the shorter-chain fatty acids myristic (14:0), lauric (12:0), and capric (10:0) acids (Table 2). Maize oil (Table 3) was high in *n*-6 polyunsaturated fatty acids, mainly linoleic acid (58%), while the menhaden fish oil (Table 4) was relatively enriched in the *n*-3 polyunsaturated fatty acids, eicosapentaenoic acid (20:5*n*-3; 15·3%) and docosahexaenoic acid (20:6*n*-3; 12·1%), and poor in linoleic acid (1·2%). Oleic and palmitoleic (16:1*n*-7) acids represented the main monounsaturated fatty acids, and palmitic and myristic acids the main saturated fatty acids in fish oil.

The individual saturated, mono- and polyunsaturated fatty acids present in chylomicrons generally reflected the oils and fats from which they were derived (Tables 1–5), although the proportions of individual fatty acids were altered by the processes of digestion, absorption, and secretion associated with the formation of chylomicrons. When the percentages of saturated, mono- and polyunsaturated fatty acids in chylomicrons were expressed as percentages of those fatty acids in their respective oils and fats, increases in the polyunsaturated fatty acid content of chylomicrons derived from palm oil (1·9-fold), olive oil (2·4-fold), and butter fat (9·5-fold) were found, compared with marginal changes in the composition of maize and fish-oil chylomicrons (Fig. 1(a)). These increases were largely due to an increased content of linoleic acid (1·7–9·3-fold), and to a lesser extent the presence of eicosapentaenoic and docosahexaenoic acids. These *n*-3 fatty acids were present (0·5–2·1%)

Table 5. *Fatty acid composition of olive oil, and of the chylomicrons and chylomicron remnants derived from it (g/100 g total fatty acids)*‡

(Mean values with their standard errors for three independent preparations)

	Olive oil					
	Oil		Chylomicrons		Chylomicron remnants	
Fatty acid	Mean	SE	Mean	SE	Mean	SE
10:0	ND		ND		ND	
12:0	ND		ND		ND	
14:0	ND		0·48	0·19	0·89	0·16
16:0	11·24	0·09	14·39**	0·39	18·53†††	0·23
16:1	0·75	0·01	1·92*	0·30	3·13†	0·24
18:0	2·74	0·03	4·00**	0·24	5·12††	0·33
18:1	75·00	0·05	53·43***	1·07	46·22††	3·80
18:2	8·00	0·02	16·26***	0·59	18·16	1·12
18:3	0·56	0·00	1·16***	0·05	0·71††	0·06
20:5	ND		0·77***	0·07	0·79	0·03
22:6	ND		2·12***	0·11	2·62	0·46
Minor unidentified	1·71	0·11	5·47***	0·36	3·83	1·13
Total identified						
Saturated	13·98	0·14	18·87***	0·50	24·54†††	0·36
Monounsaturated	75·75	0·05	55·35***	1·03	49·35	3·70
Polyunsaturated	8·56	0·02	20·31***	0·69	22·28	1·04
P:S	0·61		1·08		0·91	

ND, not detected (< 0·2 g/100 g total fatty acids); P:S, polyunsaturated:saturated fatty acid ratio.
Mean values were significantly different from those for olive oil, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
Mean values were significantly different from those for chylomicrons, † $P < 0·05$, †† $P < 0·01$, ††† $P < 0·001$.
‡ For details of experimental procedures, see pp. 436–439.

in all the chylomicrons studied, despite their absence from the corresponding dietary oils and fats, except for fish oil. The content of saturated fatty acids increases during the formation of chylomicrons derived from both maize (1·4-fold) and olive oil (1·5-fold), and the content of monounsaturated fatty acids increased in butter-fat chylomicrons (1·2-fold) (Fig 1(a)). These changes were due to an increased content of palmitic and stearic acids in the case of maize and olive oil chylomicrons, and oleic and palmitoleic acids in the case of butter-fat chylomicrons.

Changes in the proportions of saturated and monounsaturated fatty acids were also observed during chylomicron formation, mainly in the predominant fatty acids found in each of the parent oils and fats. Thus, in olive-oil chylomicrons the oleic acid content was reduced to 71% of that observed in olive oil (Table 5), and similar reductions were seen in linoleic acid in maize-oil chylomicrons (86%, Table 3) and in palmitic acid in palm-oil (74%, Table 1) and butter-fat (70%, Table 2) chylomicrons. The contents of the shorter-chain fatty acids, lauric and capric acids, predominant only in butter fat, were reduced to 87% and 36% respectively, in butter-fat chylomicrons (Table 2). The proportions of eicosapentaenoic (78%) and docosahexaenoic acids (68%) in fish-oil chylomicrons were also reduced compared with their proportions in fish oil. These changes, and the more marked increases in polyunsaturated fatty acids which occurred during chylomicron formation, were reflected in a very large decrease in the range of the P:S ratios between the different types of chylomicrons, which was 7-fold compared with 170-fold for the different dietary oils and fats.

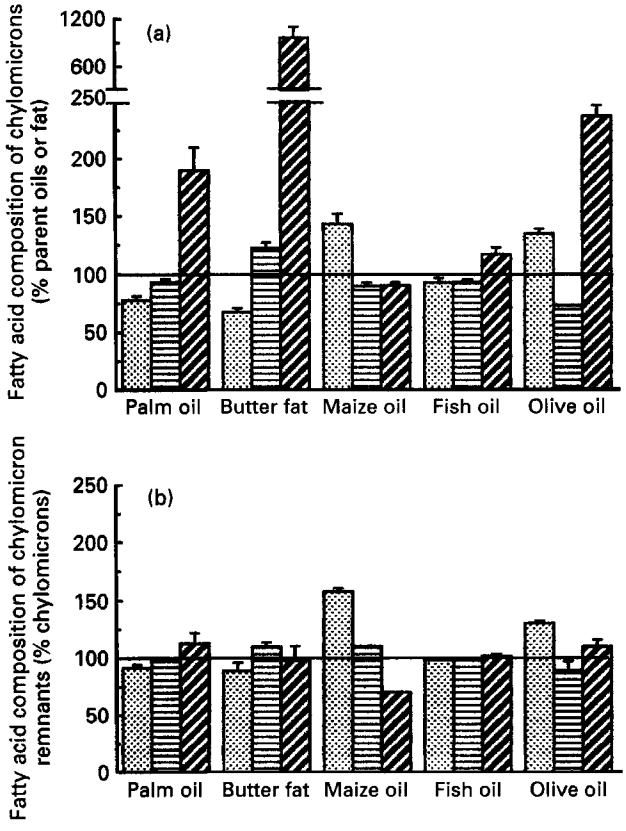

Fig. 1. Changes in the proportions of saturated (⊠), monounsaturated (▤), and polyunsaturated (▨) fatty acids during the formation of chylomicrons and chylomicron remnants from dietary oils and fat. Fatty acid composition of (a) chylomicrons as a percentage of the content of the respective dietary oils and butter fat; (b), chylomicron remnants as a percentage of the content of the respective chylomicrons. Values are means with their standard errors represented by vertical bars for the fatty acid determinations from three separate preparations of chylomicrons and chylomicron remnants. For details of experimental procedures, see pp. 436–439.

The metabolism of chylomicrons to chylomicron remnants resulted in fewer and smaller changes in the proportions of saturated, monounsaturated and polyunsaturated fatty acids than did the formation of chylomicrons from the parent oils (Tables 1–5). The saturated fatty acid content of maize and olive remnants was increased, with a concomitant decrease in polyunsaturated fatty acids in the case of maize oil (Tables 3, 5, Fig. 1(b)). Thus, the range of P:S ratios between the different types of remnants was only 2·8-fold, as compared with 7-fold in the corresponding chylomicrons. The formation of butter fat remnants reduced the proportion of myristic acid to approximately half of that found in the chylomicrons, and 10:0 and 12:0 fatty acids were completely eliminated (Table 2). The proportion of oleic acid in olive-oil remnants was 87% of that found in the chylomicrons, while the content of palmitic acid showed a small decrease (Table 5). A substantial reduction (44%) was observed in the linoleic acid content of maize-oil remnants compared with their chylomicrons, and this was accompanied by increases in the proportions of the saturated fatty acids, palmitic and stearic acids (Table 3). The metabolism of fish-oil chylomicrons to chylomicron remnants resulted in decreases in the proportions of myristic and palmitoleic acids and increases in the proportions of palmitic and oleic acids (Table 4).

DISCUSSION

The present investigation has demonstrated the acute effects of feeding different dietary oils and fats on the fatty acid composition of their triacylglycerol-rich lipoprotein products, the chylomicrons and chylomicron remnants. The similarity between our analyses of the fatty acid composition of the dietary oils and fats used in the present study and those previously reported (Paul *et al.* 1980) provides further evidence for the validity of the method of analysis (Morrison & Smith, 1964) used in this investigation. As this was a study of the effects of fat in the diet on the overall fatty acid composition of the resulting chylomicrons and their remnants, measurements were made on the combined lipid classes. Thus, triacylglycerols, phospholipids, and esterified cholesterols were not separated before analysis. Since triacylglycerol is the predominant class of fatty-acid-containing lipid in chylomicrons (90% by weight) and chylomicron remnants (80%) (Redgrave, 1983), the changes in overall fatty acid composition will reflect much more the changes in triacylglycerol composition than those in the other lipids.

Fish oil contained approximately equal proportions of saturated, mono- and polyunsaturated fatty acids, and the resultant chylomicrons contained a similar balanced distribution of fatty acids in their lipids (Table 4, Fig. 1(a)). This observation suggests that in the case of fish oil there are very few losses or gains of fatty acids during the processes of digestion, absorption and re-esterification which result in the formation of chylomicrons. Our observations are compatible with those of Yang & Kuksis (1991) who used stereospecific analysis and estimated that a maximum of 85% of the predominant dietary fatty acids in fish oil, i.e. *n*-3 polyunsaturated fatty acids, were retained in 2-monoacylglycerols during digestive and absorptive processes associated with chylomicron formation, the greater variation in fatty acid composition being accounted for by the large number of intestinal acyltransferases incorporating fatty acids into chylomicron triacylglycerol in the sn-1 and sn-3 positions. Thus, it would be expected that the greatest opportunities available for randomization of fatty acids from the pool within intestinal cells would occur in the sn-1 and sn-3 positions.

The fatty acid composition of the other chylomicrons was modified to a greater extent than that of fish-oil chylomicrons compared with the composition of dietary oils and fats from which they were derived. The low proportion of capric acid (10:0) incorporated into butter-fat chylomicrons (36% of that in the parent fat) in our studies is in keeping with the finding that much of the dietary capric acid is absorbed directly into the hepatic portal vein, rather than via the lymphatic system (Pfeffer *et al.* 1977). In chylomicrons derived from butter fat, palm oil and olive oil, there was an increased proportion of linoleic acid, which tended to increase the chylomicron polyunsaturated fatty acid content to a consistent level of about 20% of the total fatty acids present. In addition, although there were no *n*-3 20:5 and 22:6 polyunsaturated fatty acids in palm oil, butter fat, maize oil or olive oil, there was a minimum of approximately 2% of these particular fatty acids in all the chylomicrons. Thus, there appears to be a minimal and specific requirement for *n*-3 polyunsaturated fatty acids as well as linoleic acid in the formation of chylomicrons, suggesting another essential role for these particular polyunsaturated fatty acids.

Endogenous fatty acids present in the intestinal enterocytes at the time of fat absorption and during fatty acid esterification by intestinal acyl-coenzyme A transferases would be expected to influence the fatty acid composition of the chylomicrons being formed. By feeding rats with labelled fatty acids, Whyte *et al.* (1963) demonstrated that unlabelled endogenous fatty acids could represent up to 40% of the esterified fat in chylomicrons. Therefore, under our experimental conditions it appears that chylomicrons formed from butter fat, low in linoleic acid, are placing much greater demands on the endogenous

sources of linoleic acid than those formed from olive or palm oil, both of which contain between 8 and 9% linoleic acid. The sources of these intestinal endogenous fatty acids are not clear, although Shrivastava *et al.* (1967) demonstrated in fasted rats that the fatty acids liberated from biliary phospholipids in the intestinal lumen represent a major contribution to the fatty acids incorporated into chylomicron lipids. These fatty acids may well be the source of the *n*-3 fatty acids, eicosapentaenoic and docosahexaenoic acids, incorporated into all the chylomicron lipids during their formation from palm, maize, and olive oils and butter fat.

The changes in fatty acid composition associated with the metabolism of chylomicrons to chylomicron remnants were less marked than those observed during chylomicron formation (Fig. 1(b)). This reflects the fact that the metabolism of chylomicrons to chylomicron remnants involves a simple hydrolysis of the chylomicron triacylglycerol core rather than the more complicated partial hydrolysis of dietary triacylglycerols followed by re-esterification which occurs when chylomicrons are formed in enterocytes. However, the proportions of the predominant fatty acids in the different chylomicrons were modified in different ways on conversion to remnants. The percentage of linoleic acid in maize oil remnants was reduced considerably, while that of oleic acid in olive-oil remnants was only decreased by a small amount and the palmitic acid content of palm-oil and butter-fat remnants was not significantly changed (Tables 1, 3, 5). These results suggest that linoleic acid may be favoured as a substrate for lipoprotein lipase.

Overall, our findings indicate that the changes in fatty acid composition associated with the processes of digestion, absorption and synthesis which occur during the formation of chylomicrons, and subsequently chylomicron remnants, tend to reduce the extremes of fatty acid composition associated with dietary oils and fats. This is mainly due to a decrease in the proportion of the predominant fatty acids and an increase in the proportion of endogenous *n*-3 and *n*-6 polyunsaturated fatty acids. Thus, the range of P:S ratios for the different remnants is reduced to 2·8-fold, compared with 170-fold in the parent oils and fats, with the mean P:S ratio for all the remnants studied being 0·95. The P:S ratio tends, therefore, to become more balanced during the formation of chylomicron remnants, thereby compensating for the differences in fatty acid composition of different dietary fats. These mechanisms may protect the tissues against sudden changes in the composition of fat in the diet.

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