The Composition of Triglycerides from Liver, Egg Yolk and Adipose Tissue of the Laying Hen

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The composition of the triglycerides of liver, egg yolk and adipose tissue of laying hens fed on a standard diet were investigated by using argentation thin-layer chromatography to separate the triglycerides according to their degree of unsaturation. About 40% of liver triglycerides consisted of one saturated and two monoenoic fatty acids. Triglycerides containing linoleate were more abundant in adipose tissue than in either yolk or liver. Hydrolysis by pancreatic lipase of the tissue triglycerides and fractions obtained from these triglycerides showed that the triglycerides of adipose tissue had a less ordered arrangement of fatty acids at the 2-position than did either yolk or liver triglycerides. The labelling patterns of triglycerides formed in liver slices incubated in the presence of [1-(3)¹⁴C]glycerol indicated that triglycerides containing four or more double bonds are formed to a greater extent than are other triglyceride fractions. This is evidence for the concept that the type of triglyceride formed depends on the availability of fatty acids to the liver cells.

The lipids found in the yolk of the hen's egg are synthesized in the liver of the laying hen and transported in the blood stream as lipoproteins which are passed more or less intact into the developing ovum in the ovary (Evans & Bandemer, 1961; McIndoe, 1959; Schjiede *et al.* 1963). In contrast, the triglycerides present in adipose tissue are synthesized from fatty acids obtained from plasma lipoproteins hydrolysed by lipoprotein lipase during tissue uptake (Korn & Quigley, 1957; Angervall, 1960). The triglycerides found in the yolk and adipose tissue have been shown by Leclercq, Argot & Blum (1966) to have different distributions of fatty acids at the 2-position of glycerol, the latter having a comparatively random distribution of fatty acids at this position; this has been shown to be true of adipose tissue from several species of birds (Brockhoff, 1966; Brockhoff, Hoyle & Woolmark, 1966). The triglycerides in yolk have a more ordered distribution of the fatty acids between the 2-position and the 1- and 3-positions of glycerol (Leclercq *et al.* 1966). This ordered arrangement was reminiscent of the distribution of fatty acids at the 1-, 2- and 3-positions observed by Slakey & Lands (1968) in rat liver triglyceride. However, no results for the positional distribution of fatty acids esterified to the different hydroxy groups of glycerol in chicken liver triglycerides have been found in the literature and the present work compares the triglyceride composition of hen liver, egg yolk and adipose tissue triglycerides from birds fed on a standard diet.

EXPERIMENTAL

Treatment of the birds. Laying hens of a commercial strain of white Leghorns were maintained on a nutritionally adequate diet for at least 4 weeks before the start of the experiments. The diet contained 2.6% of lipid extractable by chloroform-methanol (2:1, v/v). The fatty acid composition of this dietary lipid was (mol %) 14:0, 0.8; 16:0, 14.6; 16:1, 0.7; 18:0, 3.3; 18:1, 23.4; 18:2, 51.7; 18:3, 2.5; 20:1, 1.0; 20:5, 2.0. The hens were maintained in controlled lighting conditions, with 17 h light in each 24 h and the environmental temperature was maintained at 13-18°C. They were allowed free access to food and water at all times. Egg production was recorded and samples of the eggs laid the day before or on the day of the experiment were used to obtain the yolks analysed. Birds were killed at midday and the livers were immediately excised, cooled on ice and tissue slices prepared. These slices were used immediately for the incubation.

Incubation of liver slices. The liver was sliced by hand with a sharp razor blade. Slices (1.0-1.5 mm thick) were used for incubation in conical flasks containing 7.5 ml of Krebs-Ringer bicarbonate buffer with Ca²⁺ at half concentration (de Luca & Cohen, 1964). The incubation solution also contained ATP (200 µmol), CoA (0.2 mg) and [1-(3)¹⁴C]glycerol (10 µCi). Flasks were shaken at a rate of 60 strokes/min, the atmosphere above the incubation mixture was CO₂+O₂ (5:95) and the temperature was maintained at 38°C. Liver slices were removed at intervals, blotted on filter paper, frozen by contact with solid CO₂ and weighed. At each time-point one slice from each of two flasks was taken. After the last sample had been taken the incubation medium was strained through muslin from the remaining tissue and a sample was taken for lipid extraction and analysis.

Extraction and analysis of tissues. Samples of liver and subperitoneal adipose tissue were homogenized with 20 vol. of chloroform-methanol (2:1, v/v) (Folch, Lees & Sloane-Stanley, 1957) with a top-drive homogenizer (MSE Ltd., London S.W.1, U.K.) and filtered. To the filtrate was added 0.2 vol. of 0.37% aq. KCl. After being mixed the upper phase was removed and the chloroform layer was washed twice with chloroform-methanol-water (3:48:47, by vol.) (Folch *et al.* 1957). The chloroform layer was then made up to a known volume with chloroform-methanol (2:1, v/v) and stored under N₂ at -20°C until being analysed. Separation of the phospholipids was carried out on thin layers by using the method of Skipski, Peterson & Barclay (1964), and neutral lipids were separated by the method of Hill, Husbands & Lands (1968). Radioactive phosphatidylcholine isolated by these procedures was shown by rechromatography to have over 97% of the radioactivity present as phosphatidylcholine, and triglyceride over 99%.

Triglycerides were separated according to the degree of unsaturation of their fatty acids by t.l.c. on AgNO₃-impregnated-silica gel H. Plates (nominal thickness 0.4 mm) were prepared with 5 g of AgNO₃ and 50 g of silica gel H. The plates were dried in air at 90–100°C and stored in the presence of saturated CaCl₂ in a closed container. The plates were loaded with 5–8 µmol of triglyceride spread over a 14 cm band. They were developed in toluene-diethyl ether (19:1, v/v) at -20°C in a tank containing a curtain. After the solvent had ascended about 16 cm the plate was removed, dried in a current of warm air, sprayed lightly with 2',7'-dichlorofluorescein in methanol and the bands were viewed under u.v. light. The bands were marked and eluted from the adsorbent with diethyl ether after the dichlorofluorescein-silver complex had been broken with 1% NaCl in 90% methanol (Hill *et al.* 1968). The recovery of triglycerides from AgNO₃-impregnated silica gel plates was between 90 and 101% as determined by the 15:0 methyl ester marker technique used.

For counting of the radioactivity the triglyceride solution was transferred to vials, the solvent evaporated, 15 ml of 0.4% 2,5-diphenyloxazole in toluene added and the radioactivity of samples was counted on a Packard model 4322 liquid-scintillation counter with external standardization. For fatty acid analysis of the triglyceride by g.l.c. a known amount (0.5–0.8 µmol) of pentadecanoic acid methyl ester [Sigma (London) Chemical Co. Ltd., London S.W.6, U.K.] was added as internal marker. Glycerol esters were converted into methyl esters by transesterification with sodium methoxide as catalyst. A 2 ml portion of 0.5 M-sodium methoxide in benzene-methanol (1:1, v/v) was added to the sample. After 10 min at room temperature with intermittent shaking 0.2 ml of 6 M-HCl was added followed by 4 ml of light petroleum (b.p. 40–60°C) and 4 ml of water. After mixing and separation the light petroleum layer was removed and dried over anhydrous Na₂SO₄-NaHCO₃ (4:1, w/w) under N₂ for at least 10 min. Samples were stored in this form at -20°C until required for g.l.c. analysis.

Lipase hydrolysis of triglycerides. Lipase hydrolyses were carried out with pancreatic lipase obtained from porcine pancreatin (Koch-Light Laboratories Ltd., Colnbrook, Bucks, U.K.). The enzyme (20 mg) was mixed in a vortex mixer with 2 ml of 0.5 M-NaCl-0.5 M-CaCl₂ and

0.1 mg of sodium deoxycholate (BDH Chemicals Ltd., Poole, Dorset, U.K.) until homogeneous. The reaction mixture contained 7–10 µmol of triglyceride, 380 µmol of NaCl, 380 µmol of CaCl₂, 300 µmol of tris-HCl buffer, pH 8.05, 0.17 mg of sodium deoxycholate and 3 mg of enzyme. The incubation time was 30 min at 39°C and the samples were well shaken on a vortex mixer at the start of the incubation and at 10 min intervals. Control tubes showed that there was no non-enzymic degradation of added triglycerides. At the end of the reaction, 0.6 ml of M-HCl was added to stop the reaction followed by 4.0 ml of chloroform-methanol (2:1, v/v). After shaking and separation the lower layer was removed. A further 1 ml of chloroform was added and the lower phase was removed. The combined lower phases were evaporated to dryness and applied to the base of a thin-layer chromatogram and the triglycerides, free fatty acids, diglycerides and monoglycerides were separated with the light petroleum-diethylether solvent system described above. The fractions were eluted, a known amount of 15:0 methyl ester was added and the samples were methylated with H₂SO₄ as catalyst by the method of Nichols, James & Breuer (1967).

Gas-liquid chromatography of methyl esters of fatty acids. The methyl esters dissolved in light petroleum were applied to a Pye 104 chromatograph containing a 2.5 m column packed with 80–100 mesh Chromosorb W coated with 10% polyethylene glycol adipate (Pye Unicam Ltd., Cambridge, U.K.). The operational temperature was 190°C, the carrier gas was N₂ and a flame ionization detector was used. Quantitation was achieved by using the method of Carroll (1961). The detector response was checked with a standard containing 16:0, 18:0, 18:1, 18:2 and 18:3 fatty acids (Applied Science Laboratory, College Park, Pa., U.S.A.) and appropriate correction factors were used in calculating the mol % of each fatty acid present. Calculation of the absolute amount of each fraction was made by reference to the quantity of 15:0 fatty acid present in the samples.

RESULTS

The fatty acid composition of the liver triglyceride differed from that of the dietary lipid in that the concentration of linoleate was much lower; it was, however, more abundant in the yolk triglyceride and comprised 25% of the adipose tissue triglyceride fatty acids (Table 1). This unequal distribution of linoleate amongst the three tissue triglycerides was found in all hens studied. The amounts of oleate and saturated fatty acids in liver triglycerides were greater than in yolk and adipose tissue.

The major triglyceride present in the laying hen liver (40%) contained one saturated and two monoenoic fatty acids (011) and this was also the major type in the yolk triglyceride (31%) but in adipose tissue glyceride types containing linoleate were more abundant than the 011 type (Table 1). It is well known that the liver of the laying hen shows a fatty infiltration that consists mainly of triglycerides but it is clear from our results that this

Table 1. *Composition of the triglycerides of liver, egg yolk and adipose tissue*

The results are expressed as mol % and are analyses for a single bird. Samples from two more birds were analysed and essentially similar results were obtained.

Fraction no.	0	1	2	3	4	5	Total (direct)	Total (by addition)
No. of double bonds/ glyceride molecule	0	1	2	2 and 3	3	4 and 5		
No. and type of un- saturated acid present*	—	1	1+1	2 and 1+1+1	1+2	1+1+2; 2+2; and 1+2+2		
Liver								
Yield in fraction (%)	3.0	19.8	40.5	14.8	13.3	8.6	100.0	
Fatty acid composition								
14:0	2.5	1.5	0.3				0.5	0.5
16:0	61.8	45.1	29.5	16.8	23.8	11.9	29.1	29.5
16:1		2.7	5.6	8.4	5.5	6.5	5.3	5.3
16:2								
18:0	30.9	18.8	3.6	5.5	2.7	1.9	7.4	7.4
18:1	4.7	32.0	60.8	57.6	35.8	37.6	47.4	47.6
18:2				11.7	31.6	39.1	10.0	9.3
18:3					0.5	3.1	0.2	0.3
16:0/18:0 ratio	2.0	2.4	8.0	3.1	8.8	6.3		
Egg yolk								
Yield in fraction (%)	1.4	18.2	31.0	14.5	21.6	12.7	99.4	
Fatty acid composition								
14:0			0.5				0.5	0.2
16:0	59.6	39.3	39.6	16.5	26.1	14.3	28.4	32.5
16:1		2.4	7.1	7.5	2.9	5.8	5.0	5.1
16:2								
18:0	30.2	21.0	3.8	6.7	2.8	2.7	6.0	7.3
18:1	10.2	37.4	49.0	56.0	31.9	38.4	45.4	42.0
18:2				13.2	36.3	35.4	14.1	14.3
18:3						3.3	0.6	0.4
16:0/18:0 ratio	2.0	1.9	10.4	2.5	9.3	5.3		
Adipose tissue								
Yield in fraction (%)	0	10.4	19.3	14.8	21.5	34.2	100.2	
Fatty acid composition								
14:0		1.8	0.6	0.7	0.5		0.8	0.5
16:0		52.8	29.3	24.1	21.5	8.2	22.2	22.1
16:1		4.0	8.3	6.4	7.6	6.4	7.8	6.8
16:2						0.6		0.2
18:0		11.6	4.0	4.5	4.1	1.2	4.6	3.9
18:1		29.9	57.8	47.6	35.3	32.8	36.2	40.1
18:2				16.7	30.9	48.1	27.2	25.5
18:3						2.7	1.1	0.9
16:0/18:0 ratio		4.6	7.3	5.4	5.2	6.8		

* 1, monoenoic acid; 2, dienoic acid.

accumulated fat is very different from that found in adipose tissue.

The liver and yolk triglycerides were similar in that the unsaturated fatty acids were concentrated in the 2-position of the triglyceride molecule (Table 2). However, in the adipose tissue triglycerides, the fatty acids esterified to the 2-position were much closer to the average composition of the triglyceride as a whole, although there was some tendency for the more unsaturated fatty acid to be

esterified to the 2-position. This situation is best illustrated by the 001 triglyceride type: that isolated from the adipose tissue has just over 60% of monoenoic fatty acid acids in the 2-position, whereas from both liver and yolk triglyceride the corresponding figure is 90%. Similar results were obtained with the other triglycerides. In the class containing three double bonds, contributed by one monoenoic acid and one dienoic acid, the proportion of linoleic acid esterified to the 2-position was

Table 2. Composition of the fatty acids at the 2-position of glycerol in triglycerides from liver, egg yolk and adipose tissue of a laying hen

Fraction no. No. and type of unsaturated fatty acids in the triglyceride ...	The results are expressed as mol %.											
	1			2			4			5		
	Total triglyceride											
	1			1 + 1			1 + 2			1 + 1 + 2, 1 + 2 + 2 and 2 + 2		
	Liver	Yolk	Adipose tissue	Liver	Yolk	Adipose tissue	Liver	Yolk	Adipose tissue	Liver	Yolk	Adipose tissue
14:0	0.3		1.1									
16:0	5.1	5.5	4.1	1.5	1.3	7.5	5.0	0.5	4.6	3.6	1.1	2.8
18:0	4.5	2.3	3.6	2.2	0.7	3.7	1.6	0.4	1.7	2.1	0.4	2.4
Total saturated	9.9	7.8	7.7	3.7	2.0	11.2	6.6	0.9	6.3	5.7	1.5	
16:1	2.7	3.0	2.5	1.4	2.1	3.8	3.3	1.0	3.1	1.2	1.1	2.3
18:1	65.1	45.2	50.9	94.9	95.9	84.9	33.0	27.0	49.8	26.4	18.7	30.5
Total monoenoic	67.8	48.2	53.4	96.3	98.0	88.7	36.3	28.1	52.9	27.6	19.8	32.8
18:2	22.3	44.1	36.4				57.1	70.1	37.9	63.0	75.9	60.1
18:3			2.5					1.0	2.8	3.7	2.7	2.1

greater in both yolk and liver triglyceride than in adipose tissue. In this class more oleate was esterified to the 2-position in adipose tissue triglyceride than in either yolk or liver triglyceride. Further, nearly all the linoleate present in the yolk triglycerides was esterified to the 2-position whereas that in the adipose tissue was distributed among all the positions of the glycerol. These results were confirmed by the analysis of the fatty acids obtained after hydrolysis by pancreatic lipase, which is not reported here.

The proportions of the individual structures present in the three tissues are shown in Table 3. These results have been calculated from the results after hydrolysis by pancreatic lipase and demonstrate that structures with the saturated acids at the 2-position occur in greater concentration in the adipose tissue triglycerides than in either liver or yolk triglycerides, reflecting the less ordered arrangement of the fatty acids in adipose tissue triglycerides. The amount of the structures containing three double bonds is of interest. In adipose tissue there is less triglyceride type 111 than in either liver or yolk and where a diene is present it is commonly esterified to either the 1- or 3-position in adipose tissue and the 2-position in liver and yolk. This suggests a different metabolic role of linoleate in liver compared with adipose tissue.

The occurrence of triglycerides in the liver with a fatty acid composition dissimilar to that of either adipose tissue or yolk led to the examination of the biosynthesis of lipids by liver slices. The phospholipid incorporating the greatest amount of label was phosphatidylcholine but the major part of the [1-(3)¹⁴C]glycerol was incorporated into triglyceride: there was very little incorporation of [1-(3)¹⁴C]glycerol into either diglycerides or monoglycerides (Table 4). More than 97% of the radioactivity in triglycerides was present in the glycerol portion of the molecule, indicating that little of the glycerol was used in fatty acid synthesis under the conditions of these experiments. The time-course of the incorporation of glycerol into total lipid showed that incorporation proceeded rapidly in the first hour and levelled off between 60 and 90 min. Table 4 shows that the distribution of counts among the lipid classes did not alter with time, indicating that there was no major change in the composition of the newly formed lipid with time in these experiments.

The distribution of counts between the classes of liver triglycerides of differing structures showed that over 50% of the activity was present in fractions 4 and 5, that is in glycerides with three or more double bonds per molecule (Table 5). This proportion contrasts sharply with the mass composition of the liver triglyceride where only 22% of the glycerides were in fractions 4 and 5. Analyses of

Table 3. *Triglyceride structures found in liver, yolk and adipose tissue of a laying hen*

In the structures given, 0 represents a saturated fatty acid, 1 a monoene and 2 a diene. The centre digit represents the fatty acid esterified to the 2-position of glycerol, and the outer two digits those in the 1- or 3-positions.

Structure	% of the total triglycerides of		
	Liver	Egg yolk	Adipose tissue
000	3.0	1.4	0.0
010	18.5	16.5	6.4
001	1.3	1.7	4.0
011	39.0	30.3	17.1
101	1.5	0.6	2.2
002 or 020	1.7	1.9	6.6
111	13.1	12.6	8.2
102	0.9	0.2	1.3
012	4.8	6.0	11.3
021	7.6	15.2	8.1
-3-	0.2	0.5	1.4
Structures with four or more double bonds			
-0-	0.5	0.2	1.8
-1-	2.4	2.5	11.2
-2-	5.4	9.6	20.6

Table 4. *Distribution of radioactivity incorporated into lipids of liver slices incubated with [1(3)-¹⁴C]glycerol*

	Incubation time				Incubation medium
	15 min	30 min	60 min	90 min	
Neutral lipid	89.1	90.0	88.9	84.8	89.3
Phosphatidylethanolamine*	3.8	4.3	4.1	3.4	4.3
Phosphatidylserines and inositol	2.0	1.1	1.4	1.5	1.8
Phosphatidylcholine	4.8	4.4	5.2	4.8	3.3
Sphingomyelin and lysophosphatidylcholine	0.1	0.2	0.2	0.0	0.7
Origin	0.2	0.0	0.3	0.3	0.6
Recovery of radioactivity (%)	74	70	86	84	71

* Including phosphatidic acid.

Table 5. *Distribution of radioactivity incorporated into triglycerides of liver slices incubated with [1(3)-¹⁴C]glycerol*

Fraction no.	Structure	Incubation time				Incubation medium
		15 min	30 min	60 min	90 min	
0	000	0.4	0.3	0.2	0.3	0.3
1	001	4.9	4.3	4.3	4.5	3.7
2	011	24.6	26.5	27.8	26.6	24.9
3	111 and 002	13.1	13.5	17.4	13.9	8.6
4	012	27.9	26.0	25.7	26.6	22.8
5	Four and more double bonds	28.8	29.3	24.5	28.0	39.7
Recovery of radioactivity (%)		82	90	90	100	88

the radioactivity present in the glycerides of the incubation medium after 90 min of incubation showed that the more unsaturated triglycerides in

fraction 5 are preferentially accumulated in the incubation medium (Table 5). In the incubation medium 40% of the total radioactivity was found in

fraction 5 and 23% in fraction 4, whereas 28% of the radioactivity in the slices was in fraction 5 and 27% in fraction 4.

DISCUSSION

The analyses of the triglycerides of the liver of the laying hen show marked differences from those of triglycerides derived from rat liver (Slakey & Lands, 1968). Some of these differences can be accounted for by the different dietary régimes of the experimental animals but differences can also be related to the functional state of the liver tissue. The hen liver contains a higher proportion of its triglycerides with zero, one and two double bonds than does rat liver and lesser amounts of triglycerides with three or more double bonds. The relatively high proportions of these more saturated triglycerides in hen liver is surprising in view of the fatty acid composition of the dietary fat. However, it is known that the liver of the laying hen has a high capacity to synthesize fatty acids from carbohydrate sources and this synthesis must be active in the liver of the laying bird to satisfy the demands for egg production on a diet where only about 6% of the dietary energy is supplied by fatty acids. Moreover, this ability to synthesize fatty acids from carbohydrate sources is confined to the liver in birds as the adipose tissue does not make an appreciable contribution (Goodridge & Ball, 1967). The fatty acids synthesized are saturated and monoenoic acids that would form the triglycerides that are most abundant in hen liver. Linoleate was much more abundant in the triglycerides of adipose tissue than in liver and this is reflected in the relative abundance of triglycerides with a total of three or more double bonds. The fact that adipose tissue contains more linoleate than liver shows that there is no rapid equilibration of fatty acids between adipose tissue and liver. Linoleic acid is obtained from the diet, and during absorption by the intestinal epithelium, is esterified to triglyceride which enters the hepatic portal blood stream as very low density lipoproteins (Noyan, Lossow, Brot & Chiakoff, 1964). Fatty acids from this source must be more available to adipose tissue than to liver suggesting that the lipoproteins containing fatty acids derived from the diet are hydrolysed in the capillary bed of the adipose tissue as they are in mammals (Robinson, 1963), rather than being removed from the circulation by the liver. Laying hen adipose tissue has been shown to contain lipoprotein lipase (Angervall, 1960). The yolk triglyceride shows a composition intermediate between that of liver and adipose tissue. It is known that the yolk lipoproteins carrying the triglyceride are synthesized in the liver (Evans & Bandemer, 1961) and it is noteworthy that the triglycerides contain

appreciably greater amounts of linoleate than do liver triglycerides. This suggests either that a source other than liver synthesis is functioning in supplying triglycerides for yolk or that the liver preferentially secretes the more unsaturated fatty acids. The fatty acids of the 1-, 3- and 2-positions in liver and yolk triglycerides show a similar distribution, suggesting synthesis by enzymes with similar properties whereas the adipose tissue triglycerides have a different pattern implying different synthesizing enzymes. This reasoning suggests that there is no significant contribution of triglycerides from adipose tissue to the yolk.

The distribution of radioactive glycerol in the triglyceride fractions of the laying hen liver slices incubated in the presence of $[1-(3)^{14}\text{C}]$ glycerol was very different from that observed in triglycerides isolated from rat liver slices incubated in a similar medium (Hill, Lands & Slakey, 1968). The amount of $[1-(3)^{14}\text{C}]$ glycerol incorporated into the fractions with three or fewer double bonds was very much more in hen liver slices than in rat liver slices. This is parallel with the greater proportion of the more saturated triglycerides in hen liver than in rat liver. Hawkins & Heald (1966) observed a greater incorporation of $[^{14}\text{C}]$ palmitate into triglycerides in liver slices from laying hens than in liver slices of non-laying hens, and they presented evidence for a 25-fold increase in triglyceride synthetic capacity in laying hens compared with non-laying hens.

The liver is considered to be the site of synthesis of egg-yolk triglycerides (Evans & Bandemer, 1961) and it seemed possible that it was not active in synthesizing triglycerides containing linoleate. Experiments where $[1-(3)^{14}\text{C}]$ glycerol was incubated with liver slices showed that under these conditions synthesis of triglycerides containing three or more double bonds was very active. The triglyceride synthesis recorded in these tissue slices probably does not reflect the physiological conditions as the supply of fatty acids from outside the liver is cut off in this preparation. However, the ability of the liver to synthesize highly unsaturated triglycerides was demonstrated and one would expect that with an active supply of linoleate to the liver triglycerides containing two linoleate groups would be formed. Our experimental results show that the ^{14}C -labelled triglycerides present in the incubation medium have a higher degree of unsaturation than those present in the tissue and this may indicate a preferential secretion of unsaturated triglycerides by liver cells. The low content of linoleate-containing triglyceride in yolk and liver cannot be accounted for by the lack of ability of the liver to synthesize these glycerides but it could be due to a lack of available linoleate for triglyceride synthesis. The higher concentration of linoleate-containing triglycerides in yolk compared with liver may be due to the preferential

secretion by liver cells of the more unsaturated glycerides as lipoproteins.

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