UNSATURATED FATTY ACIDS

NUTRITIONAL AND PHYSIOLOGICAL SIGNIFICANCE

The Report of the British Nutrition Foundation's Task Force

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UNSATURATED FATTY ACIDS

BNF TASK FORCE ON UNSATURATED FATTY ACIDS: NUTRITIONAL AND PHYSIOLOGICAL SIGNIFICANCE

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TERMS OF REFERENCE

The Task Force was invited by the Council of the British Nutrition Foundation to:

1. Review the present state of knowledge of:
   (a) the occurrence of unsaturated fatty acids in foods used for human consumption;
   (b) past and present sources and intakes of unsaturated fatty acids;
   (c) the metabolic and physiological functions of unsaturated fatty acids;
   (d) the nutritional requirements for, and desirable intakes of, unsaturated fatty acids.
2. Prepare a report and, should it see fit, to draw conclusions, make recommendations and identify areas for future research.

FOREWORD

The British Nutrition Foundation organises independent 'Task Forces' to review, analyse and report in depth upon specific areas of interest and importance in the field of human nutrition.

These expert committees consist of acknowledged specialists and operate independently of the Foundation.

The Unsaturated Fatty Acids Task Force has reviewed and discussed much published information. This report summarises the deliberations and findings of the Task Force and gives its conclusions and recommendations.

I am most grateful to the members of the Task Force who have contributed their time and expertise so generously. My sincere thanks also go to the Secretariat for their excellent support.

Dr Alan Garton FRS
Chairman of the Task Force

A TRIBUTE TO PRESCIENCE

This Task Force Report would be incomplete if recognition were not accorded to the profound influence of the late Dr Hugh Sinclair (1910–1990) on the development of our understanding of the nutritional and physiological significance of unsaturated fatty acids. In his student days, Sinclair became convinced that many 'diseases of civilization' were, at least in part, due to a chronic relative dietary deficiency of essential fatty acids. At the time, and for many years thereafter, the study of the possible biological functions of lipids and fatty acids was, to say the least, 'unfashionable', but Hugh Sinclair consistently confirmed his conviction and undertook experiments in attempts to validate aspects of his thesis. †he scientific and medical 'establishments' of the day took no notice of him and, even when they did, his views were often dismissed as the ramblings of an eccentric Oxford don.

Nevertheless, Sinclair doggedly persisted and, in due course, he was vindicated when the crucial role which dietary acids play in the maintenance of cellular integrity and in the regulation of metabolic processes became firmly established. In retrospect, a remarkably prophetic letter which Hugh Sinclair wrote to the Editor of *The Lancet* in 1956 probably marked the turning point in attitudes and resulted in stimulating world-wide research. In the letter he elaborated on his contention that degenerative diseases, such as atherosclerosis, are associated with deficiency of unsaturated fatty acids, notably arachidonic acid. It is noteworthy that the letter, the longest ever to appear in *The Lancet*, was selected by *Current Contents* as a 'Citation Classic'.

Hugh Sinclair, Emeritus Fellow of Magdalen College, Oxford, was a memnber of the Council of The British Nutrition Foundation from its establishment in 1967 until his death. He had agreed to advise this Task Force and to comment on the report as it was prepared, but unfortunately his wise counsel was to be denied to us. We trust he would have approved of our conclusions and recommendations in the knowledge that the topics to which he gave so much thought and effort are continuing to attract ever-increasing attention.

Alan Garton

ABBREVIATIONS USED IN TEXT

ADP	adenosine diphosphate
ATP	adenosine triphosphate
BP	blood pressure
BSA	bovine serum albumin
cAMP	cyclic adenosine monophosphate
CDAGP	cytidyl diacyl glycerophosphate
CHD	coronary heart disease
CHO	carbohydrate
Cho	choline
CM	chylomicrons
CMP	cytidyl monophosphate
CoA	coenzyme A
DAG	diacylglycerol
DGLA	dihomo gamma linolenic acid
DHA	docosahexaenoic acid
DMBA	dimethylbenz-[a] anthracene
DPA	docosapentaenoic acid
DRV	dietary reference value(s)
EAR	estimated average requirement
EC	European Community
ECG	electro-cardiogram
EDRF	endothelium-derived relaxing factor
EFA	essential fatty acids
EPA	eicosapentaenoic acid
EPSO	evening primrose seed oil
Etn	ethanolamine
FAD	flavin adenine dinucleotide
FFA	free fatty acid
FLAP	5-lipoxygenase activity protein
GLA	gamma linolenic acid
GLC	gas liquid chromatography
GP	glycoproteins
HDL	high density lipoproteins
HMWK	high molecular weight kininogen
5-HPETE	5-hydroxyperoxyeicosatetraenoic acid
IDDM	insulin-dependent diabetes mellitus
IDL	intermediate density lipoproteins
Ins	inositol
IP_3	inositol 1,4,5 trisphosphate
IRR	initial rate of response
LCAT	lecithin-cholesterol acyl transferase
LCP	long chain polyunsaturated fatty acid
LDL	low density lipoproteins
LPL	lipoprotein lipase(s)
LT	leukotriene
MCT	medium chain triacylglycerol(s)
MI	myocardial infarction
MS	multiple sclerosis
MUFA	monounsaturated fatty acid(s)
NADH	nicotinamide adenine dinucleotide
NADPH	nicotinamide adenine dinucleotide phosphate
NFS	National Food Survey
NIDDM	non-insulin dependent diabetes mellitus
NSAID	non-steroidal anti-inflammatory drugs
PAF	platelet activating factor
PCTA	percutaneous transluminal coronary angioplasty
PDGF	platelet derived growth factor
PG	prostaglandin
PGI	prostacyclin
PIP_1	phosphatidyl inositol phosphate
PIP_2	phosphatidyl inositol 4,5 bisphosphate
PKC	protein kinase C
PLA	phospholipase A
PLC	phospholipase C
PLG	plasminogen
Ptd	phosphatidyl
PUFA	polyunsaturated fatty acid(s)
RNI	reference nutrient intake
Ser	serine
SFA	saturated fatty acid(s)
SLE	systemic lupus erythematosus
SPE	sucrose polyesters
SRS-A	slow reacting substances A
TBARM	thiobarbituric acid reactive material
TNF	tumour necrosis factor
TDS	Total Diet Study
tPA	tissue plasminogen activator
TPN	total parenteral nutrition
TX	thromboxane
UFA	unsaturated fatty acid
VLC PUFA	very long chain polyunsaturated fatty acid
VLDL	very low density lipoproteins
WHHL	Watanabe hereditary hyperlipidaemia

INTRODUCTION

Lipids containing saturated and unsaturated fatty acids are present in the diet in many forms. They can be overtly present, as in salad oils, butter and margarines or they can be concealed in cooked and processed foods such as biscuits, cakes and confectionery. In whatever form lipids are eaten, they comprise about 40% of the energy value of the average diet – a value which, according to the UK Government's Committee on Medical Aspects of Food Policy (COMA) (Department of Health, 1984), is too high because of the risk of inducing unduly high levels of blood cholesterol thereby increasing the possibility that coronary heart disease may ensue. That Committee concurred with earlier conclusions that high blood cholesterol levels were associated with the intakes of saturated fatty acids and accordingly suggested that the public should be encouraged to eat less fat (less than 35% of energy intake from food) and that not more than 15% should be derived from saturated fatty acids. At the same time, COMA indicated that polyunsaturated fatty acids (P) could, with benefit, be 'substituted' in the diet for saturated fatty acids (S), thereby increasing the 'P/S ratio'. The nature of the polyunsaturated acids was not clearly stated.

Whereas some progress has been made to encourage people to eat less fat and to consume margarines and spreads with a high content of polyunsaturated fatty acids, the public is still confused by much of the dietary information and advice purveyed by the media. Unsaturated fatty acids are sometimes discussed as if they were a group of substances with exactly equivalent nutritional and physiological properties and even the injunction to eat more foods rich in unsaturated fatty acids is called into question in the popular press from time to time because of misunderstandings about increased cancer risk.

The apparent virtues of supplementing one's diet with fish oil and/or certain unusual vegetable oils have been widely canvassed, accompanied by somewhat extravagant claims for their potential to cure, alleviate or prevent all manner of conditions ranging from atopic eczema to rheumatoid arthritis. It is not only the public which is confused; many members of the medical profession, nutrition scientists, dietitians and food scientists have voiced their concern over the lack of information on which to base dietary guidance which they would like to be able to provide.

The British Nutrition Foundation commissioned this Task Force to review objectively the present state of knowledge of unsaturated fatty acids. For consistency and convenience, the Report has considered unsaturated fatty acids in three classes: monounsaturated fatty acids, and polyunsaturated fatty acids which are sub-divided into two families, commonly referred to as n-6 polyunsaturates and n-3 polyunsaturates. The monounsaturates can be synthesised in the body, and thus there is no dietary essentiality for them. The parent acids of the two polyunsaturated families cannot be synthesised in the body and must be provided in the diet. The term 'essential fatty acids' has become widely known, prompting the question 'essential for what and for whom?' The Report addresses this question in some detail.

The Report starts by outlining the structure of the different unsaturated fatty acids (Chapter 1). It specifies in what foods they are found, which foods contribute most to intakes (Chapter 2), how much of them are eaten and how this has changed in recent years (Chapter 3). It then discusses how they are digested, absorbed and transported in the body (Chapters 4–6), and what they do (Chapters 7–9). Finally, it examines the role of unsaturated fatty acids in a variety of different disease states (Chapters 10–20) and considers the implications for nutrition labelling (Chapter 21). On the basis of these considerations, the Task Force has put forward its recommendations for intakes of unsaturated fatty acids in the diet (Chapter 22) which complement and extend the conclusions of the COMA 1991 report (DH, 1991) in respect of lipids.

The Task Force hopes that its discussions and conclusions will go some way to create a better general understanding of the nature, nutritional and physiological significance of unsaturated fatty acids. In addition, the Task Force has put forward suggestions for future progress which, if implemented, should shed further light on the metabolic importance of all unsaturated fatty acids and should enable dietary recommendations to be met.

CONTENTS

1

CHEMISTRY OF UNSATURATED FATTY ACIDS

1.1 STRUCTURE AND NOMENCLATURE OF FATTY ACIDS

A fatty acid is made up of a hydrocarbon chain, from which the properties of lipid solubility derive, and a terminal carboxyl group, giving acidic properties. Fatty acids with chain lengths from 2 to over 30 carbon atoms are known, but the commonest are in the range of 12 to 22 carbon atoms (C12–C22). When each of the carbon atoms in the chain, except the two terminal ones, is bonded to two hydrogen atoms, the acids are said to be saturated, since all the bonding capacity of the carbons is saturated with hydrogen. When each of two adjacent carbon atoms is bonded to only one hydrogen, there is an ethylenic double bond between the pair of carbons and the fatty acid is said to be unsaturated. If the chain contains only one double bond, it is a monounsaturated fatty acid (MUFA) and if the chain contains more than one double bond, it is a polyunsaturated fatty acid (PUFA) (Figure 1.1).

Saturated fatty acids are given systematic chemical names that denote the number of carbon atoms (see Table 1.1). Thus the eighteen-carbon, straight chain saturated fatty acid is octadecanoic acid. The presence of a double bond is indicated by the change of the suffix from -anoic to -enoic. Thus monounsaturated and polyunsaturated fatty acids can also be called monoenoic or polyenoic fatty acids (sometimes shortened to monoenes and polyenes). In this Report, we will restrict ourselves to the most familiar terms, saturated and unsaturated. An eighteen-carbon acid with one double bond is octadecenoic acid and with two double bonds, octadecadienoic acid. Table 1.1 lists the commonest saturated and unsaturated fatty acids.

Over the years, a system of trivial names has grown up beside those of the more rigorous chemical nomenclature. Thus the most widespread form of an octadecenoic acid is also known as oleic acid, the most common form of octadecadienoic acid is known as linoleic acid and the most abundant octadecatrienoic acid is alpha linolenic acid. Some fatty acids (DGLA, EPA, DPA and DHA) do not have trivial names and are usually referred to using the abbreviated form of the systematic name.

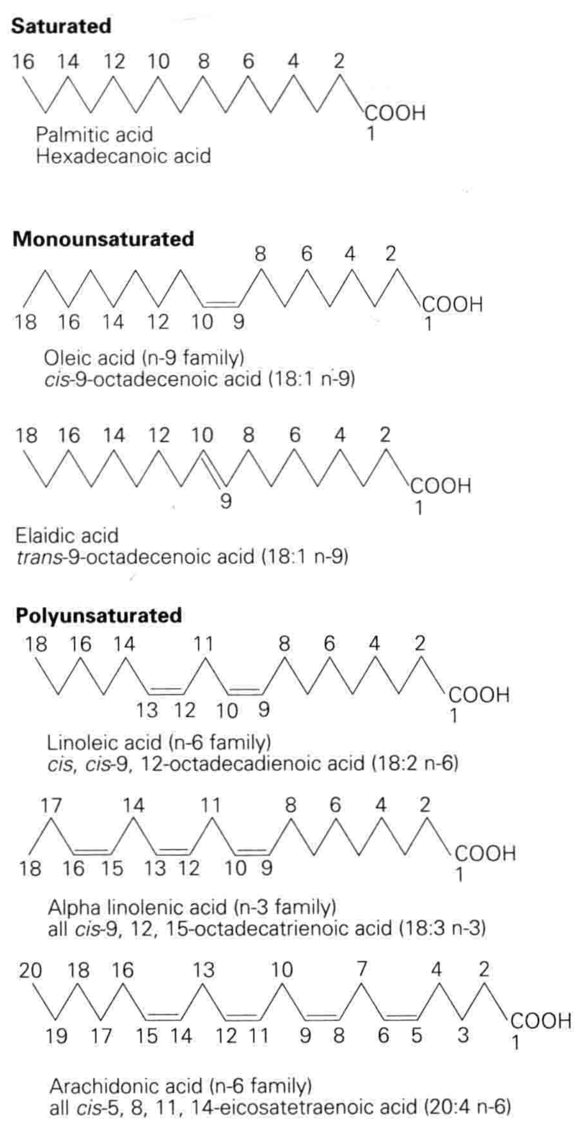

Figure 1.1 Chemistry of unsaturated fatty acids.

Table 1.1 Fatty acid nomenclature

Systematic name	Trivial name/abbreviation	Shorthand notation
Saturated		
dodecanoic	lauric	(12:0)
tetradecanoic	myristic	(14:0)
hexadecanoic	palmitic	(16:0)
octadecanoic	stearic	(18:0)
Unsaturated		
cis-9-hexadecenoic	palmitoleic	(16:1 n-7)
cis-9-octadecenoic	oleic	(18:1 n-9)
trans-9-octadecenoic	elaidic	(18:1 n-9)
cis-11-eicosaenoic	gadoleic	(20:1 n-9)
cis-13-docasaenoic	erucic	(22:1 n-9)
cis-11-docasaenoic	cetoleic	(22:1 n-11)
cis-15-tetracosaenoic	nervonic	(24:1 n-9)
cis,cis,9,12-octadecadienoic	linoleic	(18:2 n-6)
trans-5,*cis*-9,*cis*-12-octadecatrienoic	columbinic	(18:3 n-6)
all *cis*,9,12,15-octadecatrienoic	alpha linolenic	(18:3 n-3)
all *cis*,6,9,12-octadecatrienoic	gamma linolenic	(18:3 n-6)
all *cis*,6,9,12,15-octadecatetraenoic	stearidonic	(18:4 n-3)
all *cis*,11,14,17-eicosatrienoic	Mead	(20:3 n-9)
all *cis*,8,11,14-eicosatrienoic	DGLA	(20:3 n-6)
all *cis*,8,11,14,17-eicosatetraenoic	ETA	(20:4 n-3)
all *cis*,5,8,11,14-eicosatetraenoic	arachidonic	(20:4 n-6)
all *cis*,5,8,11,14,17-eicosapentaenoic	EPA	(20:5 n-3)
all *cis*,7,10,13,16-docosatetraenoic	adrenic	(22:4 n-6)
all *cis*,7,10,13,16,19-docosapentaenoic		(22:5 n-3)
all *cis*,4,7,10,13,16-docosapentaenoic	DPA	(22:5 n-6)
all *cis*,4,7,10,13,16,19-docosahexaenoic	DHA	(22:6 n-3)

1.2 STRUCTURAL FEATURES OF UNSATURATED FATTY ACIDS

1.2.1 The chemistry of the ethylenic double bond

The electronic structure of the ethylenic bond, with its so-called *pi*-electrons, gives the double bond much greater chemical reactivity than the single bond. Thus, it can be the site of addition of a number of chemical constituents. Addition of two hydrogen atoms, for example, converts the acid into a saturated fatty acid and this is important in some types of industrial processing ('hardening') of fats and oils. The elements of water can be added to produce hydroxy fatty acids and oils. Most important of all, the double bond is particularly susceptible to attack by oxygen to produce a variety of oxygenated fatty acids, some of which are of considerable biological significance. The presence of double bonds also influences the shape of the molecules, as discussed below.

1.2.2 Geometrical isomerism

The ethylenic double bond can adopt two distinct geometrical configurations, denoted by chemists as the Z and E configurations. An older and more familiar system is the *cis/trans* nomenclature which will be used in this Report. A projection of the *cis* double bond would have the two hydrogens on the same side of the molecule, whilst in the *trans* configuration they are on opposite sides. This has implications for the shape of the molecule. Fatty acids can adopt a large number of configurations or shapes but while it is possible for saturated chains and those containing the *trans* double bond to adopt a straight configuration, the *cis* forms always have a kink in the chain. This influences the physical properties of fatty acids as discussed in Section 1.3.

Cis-double bonds, rather than *trans*-double bonds, are more commonly found in natural lipids. *Trans* bonds do occur sometimes, as intermediates in the biosynthesis of fatty acids, in ruminant fats, in plant leaf lipids and in some seed oils (see Chapter 2).

1.2.3 Positional isomerism

Irrespective of whether double bonds are *cis* or *trans*, they can be located at different positions in the hydrocarbon chain. During biosynthesis, the double bond is introduced between carbon atoms 9 and 10 in the most commonly occurring monounsaturated fatty acid, oleic acid (see Chapter 7).

However, small amounts of monounsaturated fatty acids with double bonds in other positions are known. When a second double bond is introduced in the biosynthetic process, it is usually separated from the first double bond by a methylene (CH_2) group and this pattern is continued with the introduction of subsequent double bonds (Table 1.1). These structures are known as 'methylene-interrupted' polyunsaturated fatty acids. Far less common in natural oils are conjugated, or widely separated, double-bond systems.

During chemical reactions, such as catalytic hydrogenation or oxidation, the double bonds may be shifted along the chain and/or geometrically isomerised to yield a much wider variety of structural isomers than normally occurs in natural oils (see Chapter 7).

The position of double bonds in the hydrocarbon chain of a fatty acid is denoted by a prefix indicating the number of the first of the pair of carbon atoms forming the double bond, starting to number from the carboxyl carbon as carbon atom number one (Figure 1.1 and Table 1.1). Thus, oleic acid is *cis*-9-octadecenoic acid and linoleic acid is *cis*, *cis*-9, 12-octadecadienoic acid. A useful shorthand nomenclature consists of two numbers separated by a colon. The number before the colon gives the carbon chain length while the figure after denotes the number of double bonds. Thus stearic acid is 18:0, oleic acid is 18:1 and linoleic acid is 18:2. When a fatty acid chain is elongated, two carbon atoms are added at the carboxyl end of the chain. Thus the numbering of the double bonds in the systematic name changes each time the chain is elongated (compare arachidonic acid with gamma linolenic acid in Table 1.1).

Sometimes, to emphasise metabolic relationships, it is helpful to use a shorthand notation which numbers the first double bond from the methyl terminal carbon atom rather than from the carboxyl end. Under this system, the shorthand notation for oleic acid is 18:1 n-9 and that for linoleic acid is 18:2 n-6. Arachidonic acid becomes 20:4 n-6 and gamma linolenic acid is 18:3 n-6 and it is easier to see that the former has been formed from the latter by the addition of two carbon atoms and one double bond.

1.3 TRIACYLGLYCEROLS

Triacylglycerols were previously called triglycerides. Triacylglycerol molecules consist of three fatty acids esterified to a glycerol moiety. In most natural oils and fats, the three constituent fatty acids are not randomly distributed (see Table 1.2). There is a tendency for specific fatty acids to be located at particular positions on the three glycerol carbons (i.e. positions 1, 2 and 3). In cows' milk fat, the characteristic short chain fatty acids are found at position 3, whilst in human milk fat, the saturated acid, palmitic acid is found at position 2 and unsaturated acids at position 1. Animal depot fats have saturated fatty acids mainly at position 1, unsaturated and short chain fatty acids at position 2. Position 3 seems to have a more random population, although polyunsaturated acids tend to accumulate at position 3 in most mammals. Phosphoglycerides usually have a saturated fatty acid at position 1 and an unsaturated fatty acid at position 2.

Table 1.2 Characteristic positioning of fatty acids in triacylglycerol and phosphoglyceride molecules

	Cows' milk fats	**Human milk fats**	**Animal depot fats**	**Phospho-glycerides**
Position 1	Random	Unsaturated fatty acids	Saturated fatty acids	Saturated fatty acids
Position 2	Random	Saturated fatty acids	Unsaturated fatty acids and short chain fatty acids	Unsaturated fatty acids
Position 3	Short chain fatty acids		Random	Phosphate group

These specific distributions are important both in terms of the physico-chemical properties of the lipids and of their metabolic activities, as discussed in Chapters 7 and 8.

1.4 PHOSPHOGLYCERIDES

In mammals, the lipids involved in membrane structures are mainly the phosphoglycerides and unesterified (free) cholesterol (Figure 1.2). Phosphoglycerides belong to a more general class of phosphorus-containing lipids, the phospholipids. Most of the phospholipids considered in this report are phosphoglycerides and the terms may be used interchangeably. The only common phospholipids which are not phosphoglycerides are sphingomyelins and the cerebrosides which are mainly found in nervous tissues (see Figure 1.2). These phospholipids are based on the amino alcohol sphingosine rather than glycerol.

Phospholipids have important properties in membranes and foods because of their amphiphilic nature: i.e they possess chemical groupings that associate with water (hydrophilic groups) in juxtaposition with hydrophobic moieties (amphiphilic is derived from the Greek for 'liking both'). In contrast,

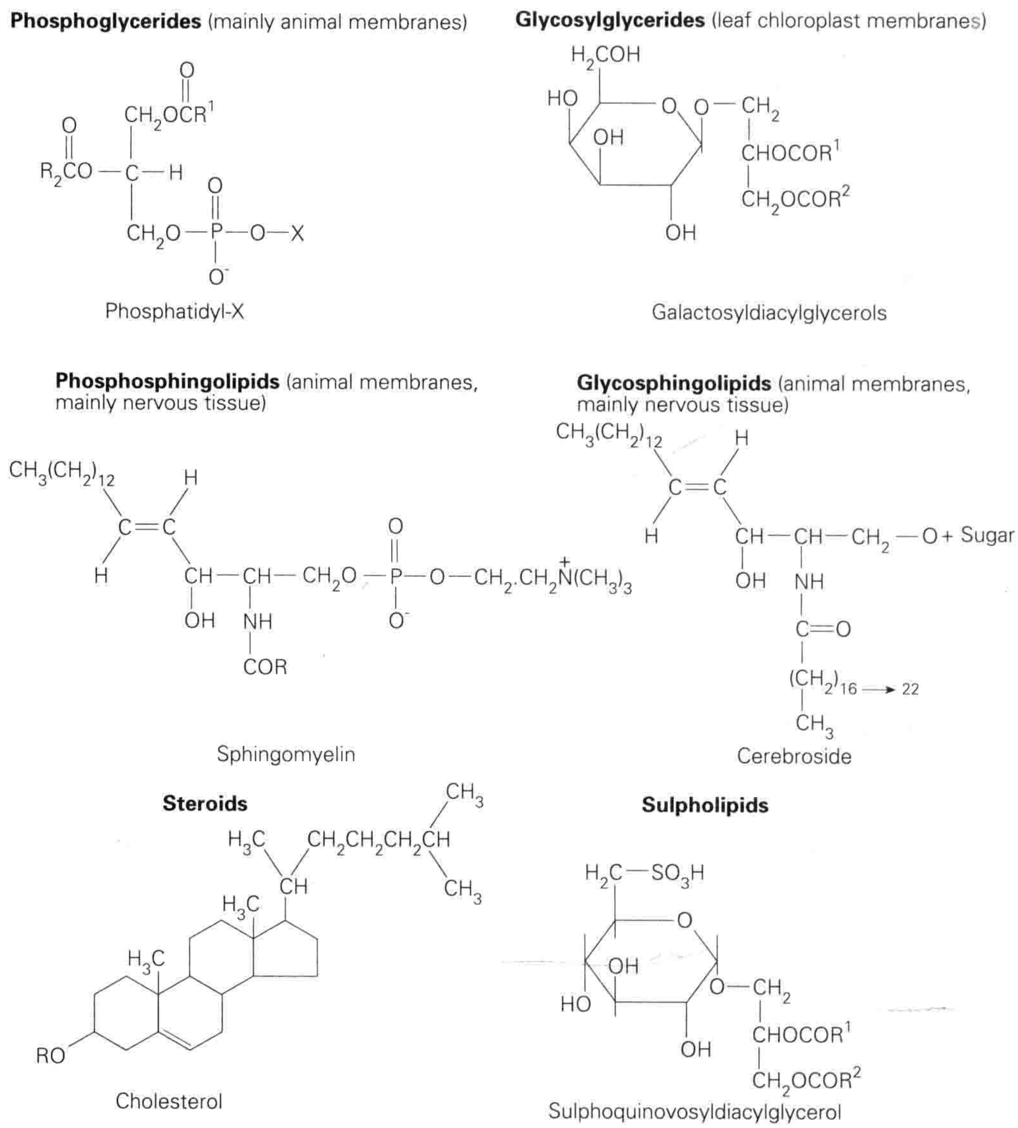

Figure 1.2 Structural lipids in plant and animal membranes.

hydrophobic fats, without polar groups, such as triacylglycerols, wax esters and sterols are often called neutral, apolar or non-polar lipids, but these are imprecise terms.

Phosphoglycerides are amphiphilic lipids in which the polar moiety is an ester of phosphorus with an organic base, such as choline in phosphatidylcholine (PtdCho), ethanolamine in phosphatidylethanolamine (PtdEth), serine in phosphatidylserine (PtdSer) or inositol in phosphatidlyinositol (PtdIns).

1.5 PHYSICAL PROPERTIES OF FATS AND OILS AND THEIR CONSTITUENT FATTY ACIDS

The physical properties of food fats (triacylglycerols) are influenced largely by the nature of their constituent fatty acids, although the presence of minor components such as sterols and phospholipids can also be important. Table 1.3 shows that in general, the higher the chain length, the higher the melting point (compare 12:0 and 16:0); the greater the number of double bonds, the lower the melting point (compare 18:1, 18:2 and 18:3). However, because fatty acids with *trans* unsaturation have melting points higher than the corresponding acids with *cis*-unsaturation (compare *trans* 18:1 with *cis* 18:1), the total degree of unsaturation can sometimes be an unreliable guide to physical properties. As discussed above, the physical properties of triacylglycerols are also dependent on the distribution of fatty acids on the three positions of the glycerol backbone, so that interesterification can also modify physical properties. In most foods, fats and oils are not present in isolation from other components. Physical properties of fats and oils can be markedly influenced by the formation of water-in-oil or oil-in-water emulsions exemplified by margarine and mayonnaise respectively.

Table 1.3 The melting points of some fatty acids

Chain length	Fatty acid	Melting point (°C)
12	12:0	44.2
16	16:0	62.7
18	18:0	69.6
18	c-18:1	13.2
18	t-18:1	44.0
18	c,c-18:2	−5.0
18	t,t-18:2	28.5
18	c,c,c-18:3	−11.0
18	t,t,t-18:3	29.5

2

SOURCES OF UNSATURATED FATTY ACIDS IN THE DIET

The raw materials from which food fats are derived are mainly the storage fats of land and marine mammals and fish and the seed oils of plants. To convert them into a suitable condition for food use, various extraction and purification processes are used that may modify the composition to some degree. More extensive compositional changes are brought about by other specific processes such as industrial hydrogenation which affects particularly the unsaturated fatty acids. These manufacturing processes are described in Section 2.4.

2.1 NATURALLY OCCURRING STORAGE FATS FOR FOOD USE

2.1.1 Storage lipids of land animals

2.1.1.1 Pigs and poultry

The composition of the adipose tissue of simple-stomached animals, of which pigs and poultry are economically the most important, is markedly affected by the fat in the diet. When these species are given low fat, cereal-based diets, as in traditional farming practice (columns A and D in Table 2.1), the adipose tissue fatty acids are synthesised in the body from dietary carbohydrates and the storage fat is composed mainly of saturated and monounsaturated fatty acids (MUFA). However, cereals contain structural lipids that influence storage fat composition to some extent, depending on the type of cereal.

Inclusion of vegetable oils, such as soya bean oil, in the diet (columns B and E) results in higher proportions of linoleic acid and lower proportions of oleic acid than the inclusion of tallow (column C) which tends to give a storage fat similar in composition to that of animals fed on cereals (column A).

2.1.1.2 Ruminants

The adipose tissue of ruminants is less variable than that of simple-stomached animals because about 90% of the unsaturated fatty acids originally present in the animals' diet are hydrogenated (i.e. converted into relatively more saturated fatty acids)

Table 2.1 The fatty acid composition of some animal storage fats used in human foods showing the influence of different feeding practices

Fatty acid (g/100g total fatty acids)		Pig (lard)			Poultry		Beef (suet)		Lamb	
		A	B	C	D	E	F	G	H	I
Myristic	(14:0)	1	1	1	1	1	3	3	3	4
Palmitic	(16:0)	29	21	21	27	22	26	20	21	19
Stearic	(18:0)	15	12	17	7	6	8	10	20	16
Palmitoleic	(16:1)	3	3	4	9	5	9	4	4	6
Oleic	(18:1)	43	46	54	45	27	45	33	41	37
Linoleic	(18:2)	9	16	3	11	35	2	23	5	12
Long chain MUFA	(20:1, 22:1)	0	0	0	0	0	0	0	0	0
Long chain PUFA	(20:5, 22:5, 22:6)	0	0	0	0	0	0	0	0	0
Others		0	1	0	0	4	7	7	6	6

A, pig fed low fat cereal-based diet; B, pig fed high fat diet containing soyabean oil; C, pig fed high fat diet containing beef tallow; D, poultry fed low fat cereal-based diet; E, poultry fed high fat diet containing soyabean oil; F, cattle fed diet based on hay; G, cattle fed diet containing 'protected' safflower oil; H, lambs fed cereal-based concentrate diet; I, lamb fed diet containing 'protected' safflower oil (Adapted from Gurr, 1984)