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Manipulating meat quality and composition

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Meat quality describes the attractiveness of meat to consumers. The present paper focuses on two major aspects of meat quality, tenderness and flavour. Both aspects of quality can be influenced by nutrition, principally through its effects on the amount and type of fat in meat. In several countries, high levels of intramuscular fat (marbling fat), i.e. above 30 g/kg muscle weight in *longissimus*, are deemed necessary for optimum tenderness, although poor relationships between fat content and tenderness have generally been found in European studies, where fat levels are often very low, e.g. below 10 g/kg in UK pigs. Muscle lipid may be a marker for red oxidative (type 1) muscle fibres which are found at higher concentrations in tender muscles and carcasses. Nutritional treatment can be used to manipulate the fatty acid content of muscle to improve nutritional balance, i.e. increase the polyunsaturated (PUFA) : saturated fatty acid value and reduce the *n*-6 : *n*-3 PUFA value. Increasing PUFA levels may also change flavour because of their greater susceptibility to oxidative breakdown and the generation of abnormal volatile compounds during cooking. This situation particularly applies to the *n*-3 PUFA which are the most unsaturated meat lipids. In pigs, a concentration of 3 mg α-linolenic acid (18 : 3)/100 mg in muscle and fat tissue fatty acids can easily be achieved by including whole linseed in the diet. This level has led to abnormal odours and flavours in some studies, but not in others. In cattle and sheep, feeding whole linseed raised 18 : 3 concentrations in muscle fatty acids from about 0·7 mg/100 mg to >1 mg/100 mg. As with pigs, this diet also increased levels of long-chain *n*-3 PUFA formed from 18 : 3, including eicosapentaenoic acid (20 : 5). Although this increase led to greater oxidative breakdown of lipids during storage and the generation of large quantities of lipid-derived volatile compounds during cooking, there were no deleterious effects on odour or flavour. When 18 : 3 levels are raised in lamb and beef because of grass feeding, the intensity of the flavours increases in comparison with grain-fed animals which consume and deposit relatively more linoleic acid (18 : 2). In ruminants, very high levels of 18 : 2 produced by feeding protected oil supplements cause the cooked beef to be described as oily, bland or pork-like.

Meat: Flavour: Fatty acid composition

Sales of meat in many countries have remained static or fallen slightly in recent years; for example, in the UK total meat sales fell by 3·5 % in the 10 years to 1995 (Wood *et al.* 1998). For red meat (beef and lamb) the fall was 19 %, whereas an increase of 8 % was recorded for poultry. This pressure on sales has caused a reappraisal of the factors which influence the appeal of meat to consumers, which together constitute 'quality'.

The list of factors which determine quality in meat, as with other foods, is rather long (Wood *et al.* 1998). It includes freedom from microbiological hazards (food safety) and prevention of animal exploitation (animal welfare). It also includes the sensory appeal of meat, i.e. its taste or eating quality, and perceived healthiness, especially in relation to the amount and type of fat. These aspects of eating quality and composition, their association and manipulation, are the main subject of the present paper.

Tenderness

The three main components of eating quality according to consumer studies are tenderness, juiciness and flavour. Tenderness is the most important, with tough meat being unacceptable. Tenderness variation arises mainly through changes to the myofibrillar protein structure of muscle in the period between animal slaughter and meat consumption. If the carcass is refrigerated too rapidly immediately after slaughter, muscle fibres contract severely, and the result is 'cold shortening' in which the force required to shear the fibres after cooking increases dramatically. This shortening can be prevented in the tender muscles of the hindleg and back by suspending the carcass from the pelvis rather than the achilles tendon, thereby stretching the muscles, preventing contraction. Alternatively, high-voltage electrical stimulation of the carcass depletes energy stores in muscle so that there is none available for contraction. Although the concept of electrical stimulation has been known for many years, it is only relatively recently that it has been widely applied in the UK meat industry.

Changes to the myofibrillar proteins in muscle are also caused by proteolytic enzymes during ageing or conditioning. These degrade key minor muscle proteins, thereby fragmenting the muscle structure, which weakens and can be more easily broken down in the mouth. The value of longer conditioning times for meat tenderness has been known for many years. In recent years attention has focused on the calpain (*EC* 3.4.22.17) enzyme system composed of m- and μ-calpain and the inhibitor calpastatin. The importance of the calpain enzyme system can be inferred from the toughening of meat which occurs when the system is inhibited through the administration of β-adrenergic agonists to animals in order to promote lean deposition (Kretchmar *et al.* 1990). Recent research suggests that the tough meat observed in sheep carrying the callipyge gene is also caused by specific changes to calpain enzymes (Koohmaraie *et al.* 1995). This gene improves meat yield and lean content, but clearly reduces tenderness.

The possible links between tenderness and meat composition have been debated for years, with most attention being focused on fat content. As fatness increases in the animal it does so in several body locations simultaneously, which could be important for tenderness. First, it accumulates in subcutaneous and intermuscular sites which could provide insulation for muscles against the effects of refrigeration as the carcass cools. This insulating role of fatness seemed to explain the higher toughness of the leaner lamb carcasses in the studies of Smith *et al.* (1976). Second, it accumulates in muscle (intramuscular or marbling fat) in the perimysial connective tissue. At high levels, e.g. in kobe beef, when the amount of intramuscular fat can exceed 200 mg/g muscle, it is possible that the muscle has a lower resistance to shearing because of the dilution of fibrous protein by soft fat. Also, fat cell expansion in the perimysial connective tissue forces muscle bundles apart, thus opening up the muscle structure (Wood, 1990). In the USA, where marbling fat concentration lies between 20 and 80 mg/g muscle, values above 30 mg/g muscle have been shown to be necessary for optimum tenderness (Smith *et al.* 1984; Dikeman, 1987).

Most speculation over the role of marbling fat in tenderness comes from the UK and Europe, where levels are low and the range so restricted it is statistically difficult to find relationships between the variables. The average current 'extractable lipid' concentration in pork loin (*longissimus*) muscle in the UK, for example, is about 8 mg/g and the range 5–20 mg/g. A mean value of 5 mg/g muscle was recently found in 73 kg Large White carcasses by Wood *et al.* (1996). Some reported studies on pigs show high correlations between marbling fat and tenderness, and others show no correlation at all (Wood, 1990). In beef cattle, values for marbling fat in UK and European literature are also much lower than those in the US literature, and much lower than the 30 mg/g muscle threshold value suggested in USA (Smith *et al.* 1984).

Muscle lipid concentration is generally higher in red muscles than in white muscles. The former have a higher value for red oxidative (type 1) : white glycolytic (type IIB) fibres; for example, in *psoas major* in comparison with the 'white' loin muscle *longissimus*. The *psoas*, like many but not all 'red' muscles, is significantly more tender, suggesting that marbling fat is a marker for muscle fibre type and associated metabolic differences. The combination of redder muscles, higher marbling fat concentration and increased tenderness is illustrated in the Duroc breed of pig. In a comparison of several pig breeds, Warriss *et al.* (1990) showed that the traditional British breeds of pig also tended to have higher muscle lipid concentrations and more tender meat than modern lean breeds. It has been suggested that genetic selection for increased yield and lean content in modern breeds increases the proportion of white glycolytic muscle fibres.

Intramuscular lipid deposition occurs in the later stages of growth and fat deposition, i.e. it is a 'late maturing' fat depot. This process means that feed energy supplied in excess of the requirement for muscle deposition in heavy animals increases the concentration of marbling fat in muscle. When Blanchard *et al.* (1995) fed a high-energy low-protein diet to pigs they produced particularly tender meat which had the highest concentration of marbling fat of several dietary regimens tested. Fast growth, and by implication greater protein turnover (and proteolysis), was one explanation for the improved tenderness, but the higher concentration of marbling fat was another.

Flavour

Flavour is an important part of the eating quality of all foods, including meat. Complaints of blandness are often levelled against modern lean meat, and conversely it is frequently said that meat available many years ago was more strongly flavoured than that available today. Unfortunately, there is little scientific evidence to support or refute these claims.

The meaty flavours of cooked meat are produced in reactions between carbohydrates and proteins, and between breakdown products of these compounds (Mottram, 1992). Inosine, phosphate and ribose are notable flavour precursors (Lawrie, 1998). Heterocyclic, phenolic and S-containing compounds are important flavour-producing endproducts of these reactions. Lipids also contribute to flavour through

their degradation products (e.g. aldehydes, alcohols and ketones), which have direct effects and also participate in these Maillard-like reactions (Mottram & Salter, 1989). Changes in the composition of meat, therefore, can have important effects on flavour.

If the carbohydrate content of meat is reduced by pre-slaughter stress in which muscle glycogen is totally utilized, the intensity of abnormal or 'off' flavours is increased in beef, lamb and pork (Dransfield et al. 1985; Young et al. 1993). Young et al. (1993) found that the production of S-containing compounds during cooking was greatly increased as the final pH of lamb increased from 5·6 to 6·1, which occurs when animals are stressed and dark cutting meat is produced. Dransfield et al. (1985) believed that the higher water content of dark cutting pork was a further factor in poor flavour development.

Ageing, or conditioning, which results in the gradual breakdown of the myofibrillar protein structure of meat to tenderize it, also changes flavour through the generation of peptides and amino acids. This process increased meat (pork) flavour and reduced abnormal flavour (i.e. had positive effects) during conditioning for between 1 and 10 d at 1° in pork (Table 1), but other authors have referred to the production of bitter flavours arising from peptides during conditioning (Rousset-Akrim et al. 1997). In US work, the recent trend towards conditioning meat in vacuum packs resulted in less favourable flavour development than the previous practice of 'dry ageing' (Warren & Kastner, 1992).

The increased flavour intensity which develops with age in meat animals is assumed to be due to changes in tissue constituents, although there have been surprisingly few detailed studies of these changes. In a study of grazing sheep of different ages, Rousset-Akrim et al. (1997) and Young et al. (1997) found that scores for three odour and flavour descriptors, as given by trained taste panellists to cooked lamb, increased with age. These descriptors were 'sheep meat', 'animal' and 'rancid'. It was assumed that these are the intense flavours of lamb disliked in some markets. Two groups of tissue components were directly related to these descriptors: medium-chain-length (7–10 C) methyl-branched fatty acids and 3-methyl indole (skatole). Branched-chain fatty acids are specific to sheep (Wong et al. 1975) and they have also been implicated in the distinctive flavours of lamb produced on clover (Trifolium spp.) or lucerne (Medicago sativa) diets (Melton, 1990).

Skatole is produced by fermentation in the rumen of sheep and cattle, and in the hindgut of pigs. In pigs it is a major contributor to 'boar taint', which produces abnormal odours and flavours in a small proportion of entire male pigs. Changing fermentation patterns through dietary ingredients affects skatole production and deposition in body fat. Thus, for example, increasing the proportion of sugarbeet feed, rich in pectins, in the pig's diet increases hindgut activity and reduces the skatole concentration in body fat (Wood et al. 1994).

Fatty acids and meat quality

Meat has been criticized on health grounds because of high levels of saturated fatty acids presumed to increase the risk of heart disease. Conversely, polyunsaturated fatty acids (PUFA), which lower blood cholesterol concentrations, are often present at low levels in meat, especially those of the n-3 series which have particularly beneficial effects on health (Department of Health, 1994). For these reasons many workers have sought ways to change meat fatty acid composition, mainly through feeding plant sources of PUFA, particularly those in oil seeds. This dietary regimen can alter meat quality by providing a different mix of reactive ingredients which affect oxidative stability (shelf-life) and flavour.

Pigs

The fatty acid composition of muscle and fat tissues in the pig can be greatly modified by incorporating the appropriate oil source in the feed, since the pig is a single-stomached animal and dietary fatty acids are absorbed intact in the small intestine and then incorporated into tissue lipids.

The main PUFA in plants and oil seeds is linoleic acid (18:2n-6). This fatty acid is now present at approximately 15 mg/100 mg total fatty acids in subcutaneous fat (backfat) and muscle of the average UK pig. This value has gradually increased from about 10 mg/100 mg total fatty acids in the 1970s (Wood et al. 1978), partly because the oil content of feeds has increased since then to produce 'high-energy' diets, and partly because pigs have become leaner (less-fat carcasses). We have shown in several papers (for example, see Wood et al. 1989) that, however lean carcasses are produced (through underfeeding, entire males compared with castrates, or by genetic selection), the proportion of 18:2 is increased and the correlation between this value and indices of body fat is strongly negative.

If 18:2 levels in diets are raised, the concentration in meat is increased, the slope of the regression being higher for this fatty acid than all others. It is effectively conserved in the animal, but is also used as a source of arachidonic acid (20:4) since it is the starting point for the n-6 series of long-chain PUFA.

As the number of double bonds in fatty acids increases, so their melting point and oxidative stability are reduced. Levels of 18:2 exceeding 15 mg/100 mg total fatty acids in backfat produce soft fat, and high levels may cause shelf-life to shorten. This reduction in shelf-life is the result of lipid oxidation products catalysing the oxidation reactions forming dark brown metmyoglobin, and also because these products cause rancidity in cooked meat. In general, pork flavour intensity is reduced and abnormal flavours increase as the concentration of PUFA is raised in meat and that of

Table 1. Effects of 1 or 10 d conditioning at 1° on the eating quality of pork loin steaks (1–8 taste-panel scale) (Adapted from Wood et al. 1996)

Conditioning time (d) . . .	1	10	Statistical significance of difference
Tenderness	4·2	5·2	***
Juiciness	4·1	4·2	NS
Pork flavour	3·6	3·9	***
Abnormal flavour	3·6	3·2	*
Overall liking	3·4	3·9	***

* $P < 0.05$, *** $P < 0.001$.

saturated fatty acids is reduced (Hertzman *et al.* 1988; Cameron & Enser, 1991). However, in pigs, studies show no deleterious effects of high levels of 18 : 2 on flavour. For example, in one study the concentration of 18 : 2 in backfat fatty acids was increased from 11 mg/100 mg total fatty acids in pigs fed on maize only to 29 mg/100 mg total fatty acids in those fed on a high level of peanuts (West & Myer, 1987). Storage of pork for 4 months after cooking increased fatty acid oxidation, but to the same extent in both treatments and flavour scores were similar.

The precursor of the *n*-3 series of PUFA is α-linolenic acid (18 : 3) and its products, eicosapentaenoic acid (EPA; 20 : 5) and docosahexaenoic acid (DHA; 22 : 6), have important metabolic roles. Since nutritional advice indicates that Western diets are low in these PUFA and are unbalanced in *n*-6 : *n*-3 PUFA, attempts have been made to boost levels in feeds and therefore meat. The normal concentration of 18 : 3 in backfat and muscle is about 1 mg/100 mg total fatty acids and this can be raised by feeding linseed, the oil of which is rich in 18 : 3. In a recent study at Bristol, Riley *et al.* (1998*a*) showed that feeding a diet containing 30 g linseed/kg for 65 d raised the concentration of 18 : 3 in backfat lipid from 1·3 to 3·9 mg/100 mg total fatty acids. The concentration of EPA was significantly increased but that of DHA was unchanged. In a subsequent study Riley *et al.* (1998*b*) found that by increasing the dietary concentration of linseed to 110 g/kg, a similar change from control to treated muscle levels (from 1·4 to 4·6 mg/100 mg total fatty acids) could be obtained after only 24 d feeding. Again, the concentration of EPA was increased but not that of DHA.

Linolenic acid is more prone to oxidative breakdown than 18 : 2, so some studies have examined the quality of meat from 18 : 3-treated animals. Rhee *et al.* (1988) showed that thiobarbituric acid-reacting substances in stored frozen ground muscle were increased to levels where off-flavours would be expected when diets containing 100 or 200 g rapeseed oil/kg were fed, raising muscle 18 : 3 to 3 and 4 mg/100 mg muscle fatty acids respectively. Shackelford *et al.* (1990) found that the taste-panel score for off-flavours in cured ham increased significantly when the concentration of 18 : 3 in *longissimus* reached 3 mg/100 mg total fatty acids, again through feeding rapeseed oil. However, in the study of Riley *et al.* (1998*a*) in which the feeding of linseed raised 18 : 3 to 3·9 mg/100 mg backfat fatty acids (this result

was later confirmed in muscle), there were no significant deleterious effects on odours or flavours in grilled loin steaks. Lipid oxidation in meat packed and displayed under simulated retail conditions was slightly increased in the high-linseed treatment, but the breakdown products did not have a negative effect on taste.

Fish oil contains long-chain *n*-3 PUFA, including EPA and DHA, which are very susceptible to oxidation, producing 'fishy' odours and flavours in stored meat. The results in Table 2 show that the trained taste panel in one study detected off-odours and off-flavours in meat when fish oil reached 10 g/kg diet in growing pigs between 10 and 100 kg live weight. At 30 g/kg, off-odours and off-flavours were unacceptably high.

The use of the antioxidant vitamin E at high levels has been effective in some studies in reducing the off-flavours resulting from lipid oxidation. However, it was not completely effective in preventing oxidation of EPA and DHA in the study of Hertzman *et al.* (1998).

Ruminants

The rumen hydrogenates a high proportion of unsaturated dietary fatty acids so that muscle fatty acids in cattle and sheep are more saturated and less unsaturated than those in pigs (Table 3). In particular, 18 : 2, which is the major plant fatty acid, is much lower in ruminant tissues. This low level causes the PUFA : saturated fatty acid value (an important nutritional index) to be below the recommended value for the diet, which is 0·45 (Department of Health, 1994). On the other hand, the *n*-6 : *n*-3 PUFA value in cattle and sheep is closer to the recommended value (below 4·0) than that in pigs. This difference occurs because 18 : 3 is relatively high in ruminant animals, being the major fatty acid in grass. Although a high proportion is broken down to 18 : 0 in the rumen, significant quantities pass through the rumen to be absorbed in the small intestine.

A further difference between pigs and ruminants is that the long-chain *n*-3 PUFA, including EPA and DHA, are not incorporated into triacylglycerols to any important extent in ruminants. They are restricted to phospholipids (mainly in membranes) and, therefore, are found in muscle but not fat tissue, except at very low levels in the total lipid (Enser *et al.* 1996). This factor has important implications for PUFA supply to the diet in individuals consuming muscle and fat in

Table 2. Muscle (*muscularis longissimus*) fatty acid composition (mg/100 mg fatty acids) and off-flavours and odours in pigs fed on different proportions of soyabean oil (SO) or fish oil (FO) in the diet between 10, 60 and 100 kg live weight* (Adapted from Overland *et al.* 1996)

Dietary treatment (g/kg) at live wt:					
10–60 kg . . .	30 SO	20 SO + 10 FO	20 SO + 10 FO	30 FO	30 FO
60–100 kg . . .	30 SO	30 SO	20 SO + 10 FO	30 SO	30 FO
18 : 2	18·1	15·7	15·2	15·2	12·2
18 : 3	0·3	0·3	0·3	0·3	0·4
20 : 5	0·6	0·8	1·5	1·6	3·8
22 : 6	0·9	1·2	1·8	1·9	2·9
Off-flavours†	2·0	2·7	5·5	5·4	7·1
Off-odours†	2·5	3·0	5·3	5·3	6·5

* All samples were taken at 100 kg live weight.
† After 6 months storage of flank samples at − 20°. Trained taste panel used scales of 1–9.

Table 3. Fatty acid composition of muscle (defatted lean; mg/100 mg fatty acids) in loin steaks or chops purchased from four supermarkets (Adapted from Enser *et al*. 1996)

Fatty acid	Beef	Lamb	Pork
16:0	25·0	22·2	23·2
18:0	13·4	18·1	12·2
18:1*n*-9	36·1	32·5	32·8
18:2*n*-6	2·4	2·7	14·2
18:3*n*-3	0·70	1·37	0·95
20:4*n*-6	0·63	0·64	2·20
20:5*n*-3	0·28	0·45	0·31
22:6*n*-3	0·05	0·15	0·39
P:S*	0·11	0·15	0·58
n-6:*n*-3	2·11	1·32	7·22
Lipid in lean (g/kg)	38	50	22

* Polyunsaturated fatty acids:saturated fatty acids i.e. $\dfrac{18:2\ n\text{-}6 + 18:3\ n\text{-}3}{12:0 + 14:0 + 16:0}$.

Table 4. Fatty acid content (mg/g muscle) of 'white' (*longissimus*) and 'red' (*gluteobiceps*) muscle from thirty young bulls fed on concentrates (C) and forty fed on grass (G) (Data from Enser *et al*. 1998)

Fatty acid	Diet	*Longissimus* muscle	*Gluteobiceps* muscle	SED
16:0	G	6·98**	6·84***	0·74
	C	4·88	4·01	0·46
18:0	G	4·56***	4·76***	0·48
	C	2·79	2·49	0·21
18:1*n*-9	G	10·1***	12·3***	1·26
	C	6·22	5·82	0·65
18:2*n*-6	G	0·65***	1·05***	0·05
	C	1·62	2·19	0·11
18:3*n*-3	G	0·33***	0·49***	0·03
	C	0·10	0·11	0·01
20:4*n*-6	G	0·21***	0·39***	0·02
	C	0·44	0·71	0·03
20:5*n*-3	G	0·13***	0·24***	0·01
	C	0·04	0·05	0·003
22:6*n*-3	G	0·02***	0·04***	0·003
	C	0·01	0·02	0·001
Total	G	28·6**	33·9***	3·09
	C	20·7	20·1	1·77

Mean values within muscle were significantly different from those for young bulls fed on C: **$P < 0\cdot01$, ***$P < 0\cdot001$.

the usual proportions. Pigmeat contributes about 80 % of the total PUFA provided by pigmeat, lamb and beef, and about 60 % of the *n*-3 PUFA, 50 % coming from pig fat (Enser *et al*. 1996).

Despite the propensity of the rumen micro-organisms to hydrogenate dietary PUFA, studies have shown important effects of diet on tissue PUFA concentrations. In the study shown in Table 4, bulls fed on grain diets (concentrates) had much higher concentrations of 18:2 and long-chain PUFA of the *n*-6 series in muscle than those fed on grass, which had more 18:3 and its *n*-3 long-chain derivatives. Nutritional effects were clear in both white and red muscles (e.g. *longissimus* and *gluteobiceps* respectively). When cattle and sheep are fed on predominantly grain diets there is a change in rumen microbial populations and hydrogenation

of PUFA is reduced, leading to the absorption and deposition of a lower proportion of saturated fatty acids. On the other hand, although grass (forage) diets increase the deposition of *n*-3 PUFA, the production of saturated fatty acids is also increased and the P:S value in tissues becomes less favourable.

Dietary lipids can be protected from rumen breakdown by encapsulating them so that they pass unchanged to the small intestine for absorption. Effective protection is provided by formaldehyde treatment of feed proteins, which then form a protective barrier around lipid droplets (Scott *et al*. 1971). In this way PUFA concentrations in ruminant tissues can be raised 10-fold very quickly (Scott *et al*. 1971).

In recent work at the Institute of Grassland and Environmental Research, Aberystwyth, Dyfed, and Bristol University, we have studied the natural protection provided by the seed coat of linseed, which is an unusual plant in having a high concentration of 18:3 in its oil (more than 50 g/100 g total fatty acids). An attempt was made to increase protection of the oil by treatment with formaldehyde, although this treatment was only partly successful. Linseed and other oil sources were fed to cattle as part of a mixed forage–concentrate diet in which fat (oil) constituted 30 g/kg DM intake and was provided by linseed, Megalac (Volac Ltd, Royston, South Yorkshire; saturated fatty acids, particularly 16:0) or a 50:50 (w/w) mixture of linseed and fish oil. There were thirty-six steers, half Holstein×Friesian and half Welsh Black. After 90 d on the dietary treatments, the animals were transported to Bristol where three forequarter muscles were combined, minced and analysed. The results (Table 5) show that the linseed treatment almost doubled the concentration of 18:3 in muscle phospholipid-fatty acids and the linseed–fish oil treatment greatly increased the concentrations of EPA and DHA. There was also evidence that feeding linseed promoted the conversion of 18:3 to EPA but not DHA. We have also observed this block on DHA production from EPA in pig studies (Riley *et al*. 1998*a*). There was an interesting breed effect on muscle fatty acid composition. Although Welsh Blacks tended to have a lower concentration of phospholipids in muscle (NS), they had higher concentrations of 18:3 and EPA in phospholipid-fatty acids. Both breeds responded similarly to the dietary fatty acids.

The minced forequarter muscles were boiled, then packed and stored at 1° for up to 10 d to investigate lipid oxidation measured by the thiobarbituric acid-reacting substances test. Oxidation increased with time stored and was highest in the linseed–fish oil treatment (Fig. 1). However, this increased oxidation had no deleterious effect on the flavour of grilled sirloin steaks. Taste panellists gave similar scores for beef flavour, abnormal flavour and overall liking to meat from all three treatments.

In an earlier study, the same PUFA supplements fed to beef cattle for 120 d increased the concentration of 9-*cis*, 11-*trans*-octadecadienoic acid (conjugated linoleic acid) in *longissimus* muscle (Table 6). Conjugated linoleic acid is derived from linoleic acid, the intake of which was similar for all diets. It seems that the increased concentration of conjugated linoleic acid reflects an inhibition by dietary PUFA of microbial enzymes degrading 18:2 to 18:0. The higher concentration of *trans*-18:1 is a similar indication of

Table 5. Effects of dietary fat source on deposition of selected *n*-3 polyunsaturated fatty acids in forequarter muscle phospholip ids (mg/100mg phospholipid fatty acids) of Hol s t e i× Friesian (HF) and Welsh Black (WB) steers (From Vatansever *et al.* 1999)

Dietary fat sour c e...	Megalac	Linseed	Linseed–fish oil	Overall SED	Statistical significance of feed effect
α-Linolenic acid:					
HF	2·02[a]	3·50[a]	2·98	0·27	***
WB	2·54[b]	4·40[b]	3·25		
Eicosapentaenoic acid:					
HF	2·02[a]	2·70[a]	3·15[a]	0·16	***
WB	2·66[b]	3·39[b]	3·87[b]		
Docosahexaenoic acid:					
HF	0·55	0·70	1·32	0·07	***
WB	0·67	0·69	1·36		
Total phospholipids (mg/g muscle):					
HF	5·66	6·07	5·56	0·23	NS
WB	5·43	5·66	5·57		

[a,b] Means within columns with unlike superscript letters were significantly different between breeds ($P < 0.05$).
The difference between dietary fat sources was significant: ***$P < 0.001$.

Table 6. Effects of dietary fat source on deposition of 9- *cis*, 11-*trans*-octadecadienoic acid (conjugated linoleic acid; CLA) in beef *longissimus* muscle lipids (Adapted from Enser *et al.* 1999)

Dietary fat sour c e ...	Fatty acids (mg/g muscle)				SED	Statistical significance of feed effect
	Megala	Linsee	Fish oil	Linseed–fish oil		
18 : 2	0·81	0·78	0·66	0·64	0·07	NS
18 : 3	0·22	0·43	0·26	0·30	0·04	***
trans-18 : 1	0·63	1·47	1·84	1·73	0·24	**
CLA	0·11	0·36	0·24	0·29	0·06	**

The difference between dietary fat sources was significant: ** $P < 0.01$, *** $P < 0.001$.
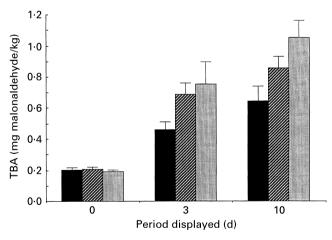

Fig. 1. Effects of dietary feed source on lipid oxidation in boiled beef mince, measured as thiobarbituric acid-reacting substances (TBA), following packaging and simulated retail display for 0, 3 and 10 d. (■), Control; (▨), linseed; (▩), linseed–fish oil. Values are means with their standard errors represented by vertical bars.

impaired rumen metabolism. High muscle concentrations of conjugated linoleic acid may constitute a health advantage to consumers of meat (Enser *et al.* 1999).

The lack of effect of dietary linseed and fish oil on the flavour of beef, as identified by the taste panel, is surprising considering the very different quantities of lipid-derived volatile compounds produced on cooking the modified beef. In ancillary studies to those described previously, Elmore *et al.* (1997) showed that volatile compounds such as aldehydes were much greater with the fish oil and linseed–fish oil treatments than with the Megalac control (Table 7). These authors also confirmed that compounds resulting from reactions between lipid breakdown products and the products of Maillard reactions between sugars and amino groups were important constituents of cooked meat. These compounds included thiazoles and 3-thiazolines, reported for the first time in beef, and again they were greatly increased in animals fed on PUFA supplements. The authors speculated that many of these lipid-derived volatile compounds have high odour thresholds, which explains why the taste panel gave similar flavour scores to the high-PUF beef.

Although we have seen few effects on beef flavour of changes in muscle *n*-3 PUFA concentrations, important effects of changing the *n*-6 : *n*-3 PUFA value by feeding grass or grain diets have been observed in other work. Larick & Turner (1990), in a US study, showed that the scores for flavour descriptors changed when previously-grazed cattle were introduced to a grain (maize) diet in a feedlot. As the period of grain feeding increased, the concentration o f 18:3 in muscle phospholipids declined and that of 18 : 2 increased. Flavours identified as 'sweet' and 'gamey' declined, whereas 'sour', 'blood-like' and 'cooked beef fat' increased. In other work, Larick *et al.* (1987)

Table 7. Aldehydes isolated from the volatiles of cooked beef from animals fed on different dietary fat sources (From Elmore *et al.* 1997)

Dietary fat source . . .	Amount in extract (ng)			
	Megalac	Linseed	Fish oil	Linseed–fish oil
3-Methylbutanal	833	987	3861	4106
2-Methylbutanal	366	871	1812	1742
Pentanal	144	221	1011	640
Hexanal	212	527	1486	816
Heptanal	109	625	1843	1344
Octanal	84	286	681	478
Nonanal	128	307	428	380

Table 8. Effects of feeding a protected sunflower-seed supplement to lambs for different periods of time on fatty acid composition and meat flavour (From Park *et al.* 1975)

Period of feeding the supplement (weeks) . . .	0	2	4	6
18:2 in carcass fat (mg/g)	20	95	162	205
Meat aroma*	3·6[b]	3·5[b]	3·2[a]	3·2[a]
Meat flavour*	3·9[b]	3·8[b]	3·2[a]	3·0[a]
Different aroma*	1·4[a]	1·6[a]	2·5[b]	3·0[b]
Different flavour*	1·3[a]	1·6[a]	2·8[b]	3·6[b]

[a,b] Mean values with unlike superscript letters were significantly different ($P < 0.05$).
* 0–8 intensity scores of twenty taste panellists.

showed that lipid breakdown products such as aldehydes and ketones were more apparent in volatile compounds from beef produced on grass rather than on grains. Terpenoids derived from chlorophyll were also detected and correlated with flavour changes.

In US and Canadian studies such as those of Larick & Turner (1990), the intense flavours of grass-fed beef are generally presumed to be disliked by consumers. In a study conducted jointly by the Universities of Bristol and Zaragoza, grass-fed British and grain-fed (and less heavy) Spanish lamb were compared. Taste panels in both countries agreed that the British lamb had more intense lamb flavour, but whereas the British panellists gave a higher 'flavour liking' score to British lamb, the Spanish panellists preferred the flavour of the grain-fed Spanish lamb (Sanudo *et al.* 1998). Correlations between the concentration of 18:3 and the flavour intensity score were positive and high for both panels (r 0·68 and 0·44 for the British and Spanish panels respectively). However, whereas the correlation between 18:3 and flavour liking was positive for the British panel (r 0·61), it was negative for the Spanish panel (r −0·67). These results show that flavour intensity and flavour preference are not the same, the latter depending to some extent on previous experience.

Further support for the importance of the *n*-6:*n*-3 PUFA value for flavour development in ruminant meats comes from studies in which protected lipid supplements have been used to raise PUFA levels in tissues. In one study with sheep, Park *et al.* (1975) increased the concentration of 18:2 in carcass fat from 2 to 20 mg/100 mg total fatty acids by feeding protected sunflower seeds for 6 weeks (Table 8). This reduced 'meat' aroma and flavour and increased 'different' aroma and flavour. The panellists described the high-18:2 meat as having a 'sweet' and 'oily' flavour. Analysis of the volatile compounds produced during cooking showed higher concentrations of a lactone compound and aldehydes derived from linoleic acid.

The results for ruminants therefore show that fatty acid composition can be manipulated by diet to affect the shelf-life and flavour of meat. It appears that changes in the fatty acid composition of relatively-saturated ruminant meats affect meat quality more than in more-unsaturated pigmeat.

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