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Conjugated linoleic acid in meat and meat products: A review

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Abstract

Conjugated linoleic acid (CLA) consists of a group of geometric and positional isomers of linoleic acid to which anticancerogenic, antidiabetic, and antiatherogenic effects, as well as effects on immune system, bone metabolism, and body composition are attributed. CLA is found predominantly in milk and meat of ruminants due to the importance of rumen micro-organism in the formation of CLA and its precursors. This review attempts to give an overview of the available data on intramuscular CLA concentrations in meat and meat products originating from different animal species. The factors influencing these concentrations are discussed and the estimated human daily intakes as well as the percentage provided by meat are reported.

Keywords: Conjugated linoleic acid; CLA; Meat; Meat products; Diet

1. Introduction

In 1979, Pariza, Ashoor, Chu, and Lund (1979) reported the occurrence of antimutagenic substances in pan-fried hamburger, which subsequently were found to inhibit the initiation of mouse epidermal tumors (Pariza & Hargraves, 1985). The fatty acid responsible for this effect was identified as conjugated linoleic acid (CLA) (Ha, Grimm, & Pariza, 1987). Since the publication of these findings more than 15 years have passed and much scientific data is available on the food sources, biosynthesis, and physiological effects of CLA. CLA exerts positive effects on cancer, cardiovascular disease, diabetes, body composition, immune system, and bone health (see reviews of Jahreis, Kraft, Tischendorf, Schöne, & von Loeffelholz, 2000; Khanal, 2004; Kraft & Jahreis, 2004; Larsen, Toubro, & Astrup, 2003; Martin & Valeille, 2002; O'Shea, Bassaganya-Riera, & Mohede, 2004; Pariza, 2004; Terpstra, 2004; Wahle, Heys, & Rotondo, 2004; Wang & Jones, 2004; Watkins, Li, Lippman, Reinwald, & Seifert, 2004). Although data mainly derive from animal trials and are not conclusive for humans, findings so far are encouraging. The interest in CLA research still persists and research efforts will continue, as many questions related to the physiological implications of CLA await answers.

CLA consists of a group of geometric and positional isomers of linoleic acid [*cis*-9, *cis*-12 (*c*9,*c*12)-18:2]. CLA is used as a collective term because all known isomers have double bonds with a single carbon bond in between (=conjugated double bonds) instead of the usual methylene-separation. These double bonds can either be *trans* (*t*) or *cis* (*c*) configured and a wide spectrum of isomers with variations in position (7,9; 8,10; 9,11; 10,12 or 11,13) and geometry (*c*/*c*; *c*/*t*; *t*/*t* or *t*/*c*) exist (Mulvihill, 2001; Martin & Valeille, 2002). In synthetic CLA preparations the *c*9,*t*11 and *t*10,*c*12-18:2 isomers are predominant (often in a 1:1 ratio) (Larsen et al., 2003) whereas in CLA rich sources like beef and dairy products about 80% of the CLA is the *c*9,*t*11-18:2 isomer (Fritsche & Steinhardt, 1998). Food sources originating from ruminants are known to have markedly higher CLA concentration than those from monogastric animals. Fish and some vegetable products also contain low CLA concentrations (Chin, Liu, Storkson, Ha, & Pariza, 1992).

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The aim of the present review is to summarize the published data relating to CLA in meat and meat products. Furthermore, a short overview will be given on CLA biosynthesis, its concentration in meat and meat products, the factors influencing this concentration, and the human dietary intake of CLA through meat and meat products consumption.

2. Biosynthesis of CLA

Naturally occurring CLA originates mainly from bacterial isomerisation or/and biohydrogenation of polyunsaturated fatty acids (PUFA) in the rumen and the desaturation of *trans*-fatty acids in the adipose tissue and mammary gland (Griinari & Bauman, 1999).

The isomerisation/biohydrogenation of PUFA in the lipid metabolism of ruminal micro-organisms delivers directly CLA or important intermediate precursors of CLA on the way to the end product stearic acid. For instance, the predominant pathway of linoleic acid generates *c*9,*t*11-18:2 by isomerisation and *t*11-18:1 (*trans*-vaccenic acid) by further hydrogenation as intermediates. In general, a micro-organism does not cover the full metabolism from the initial PUFA to the end product stearic acid but only part of it. Some bacteria, to which *Butyrivibrio fibrisolvens* belongs, have the capacity to isomerise *cis*-double bonds of PUFA to form conjugated *c*/*t* double bonds and to hydrogenate these conjugated fatty acids because they express the enzymes linoleate isomerase and CLA reductase. The end product of this process is *trans*-vaccenic acid (*t*11-18:1) which is hydrogenated to stearic acid (18:0) by other ruminal bacteria (Harfoot & Hazelwood, 1988; Kepler, Hirons, McNeill, & Tove, 1966). For other PUFA such as α- or γ-linolenic acid, the main sequence also leads to *trans*-vaccenic and then stearic acid but with intermediates other than CLA (Griinari & Bauman, 1999; Harfoot & Hazelwood, 1988; Kepler et al., 1966).

Isomerization and biohydrogenation has been shown to be strongly affected by the rumen pH (Bessa, Santos-Silva, Ribeiro, & Portugal, 2000) as decreased rumen pH can result in a shift of the bacterial population (van Soest, 1994), which then influences the pattern of the fermentation end products (Bauman, Baumgard, Corl, & Griinari, 1999). Griinari and Bauman (1999) proposed putative pathways in this case, leading to *t*10-18:1 instead of *trans*-vaccenic acid. This would generate the *t*10,*c*12-18:2 as an intermediate product. However, the pathways presented do not account for all the various CLA and *trans*-octadecenoic acids found. Double bond migration or the existence of several specific *c*,*t* isomerases in ruminal micro-organisms, with emphasis on the second, could explain the numerous CLA isomers detected in the milk and tissues (Griinari & Bauman, 1999).

Although a strong relationship exists between rumen function and CLA content in the milk and tissue lipids (Griinari & Bauman, 1999) various data suggest (see Griinari & Bauman, 1999) that only a relatively small portion of CLA is directly absorbed from the rumen and small intestine. Thus, there has to be an alternative source for the CLA content in milk and tissue lipids. It was discovered that endogenously the Δ9-desaturase is desaturating *trans*-vaccenic acid to *c*9,*t*11-18:2 (Bauman et al., 1999; Corl et al., 2001; Griinari et al., 2000). Corl et al. (2001) and Griinari and Bauman (1999) estimated that endogenous synthesis is the major source of *c*9,*t*11-18:2 in the milk fat representing 78% and 64% of the total, respectively. Accordingly, Knight, Knowles, and Death (2003) deduced that desaturation of vaccenic acid is the main source of CLA in the muscle lipids based on the high correlations between CLA and *trans*-vaccenic acid. Other CLA isomers eventually derive from other *trans*-18:1 isomers by the action of the Δ9-desaturase (Griinari & Bauman, 1999). Although endogenous synthesis was found both in ruminants and non-ruminants (Gläser, Scheeder, & Wenk, 2000; Loor, Lin, & Herbein, 2002; Salminen, Mutanen, Jauhiainen, & Aro, 1998; Santora, Palmquist, & Roehrig, 2000; Turpeinen et al., 2002) the availability of *trans*-vaccenic acid is higher in ruminants due to ruminal biohydrogenation (Bessa et al., 2000) (Fig. 1). The endogenous synthesis from *trans*-vaccenic acid was also documented in humans but the predominant source of CLA seems to be the dietary CLA intake with meat and meat products as well as milk and dairy products (Adlof, Duval, & Emken, 2000; Kraft & Jahreis, 2001; Salminen et al., 1998; Turpeinen et al., 2002).

3. CLA concentration in meat and meat products

3.1. In meat

Table 1 summarizes the CLA concentration of meat from different animal species usually used in the human diet. Meat from ruminants has higher levels of CLA than meat from non-ruminants. The highest CLA concentrations were found in lamb (4.3–19.0 mg/g lipid) and with slightly lower concentrations in beef (1.2–10.0 mg/g lipid). The CLA content of pork, chicken, and meat from horses is usually lower than 1 mg/g lipid. Interestingly, turkey seems to have a relatively high CLA content (2–2.5 mg/g lipid), but reasons for this are unclear (Chin et al., 1992; Fritsche & Steinhardt, 1998). Some data on CLA meat content of animals less common in human diets like meat from elk (1.3–2.1 mg CLA per gram fatty acid methyl ester (FAME)), bison (2.9–4.8 mg/g FAME), water buffalo (1.83 mg/g fatty acids), and zebu-type cattle (1.47 mg/g fatty acids) are also available (de Mendoza et al., 2005; Rule, Broughton, Shellito, & Maiorano, 2002). The highest CLA concentration of all animals was found in adipose tissue of kangaroos (38 mg/g fatty acids) (Engelke, Siebert, Gregg, Wright, & Vercoe, 2004). Large variations in the CLA content are not only reported between animal species but also within muscles of the same species. Ma, Wierzbicki, Field, and Clandinin (1999) explained the rather low CLA content in beef found in their study (1.2–3.0 mg/g

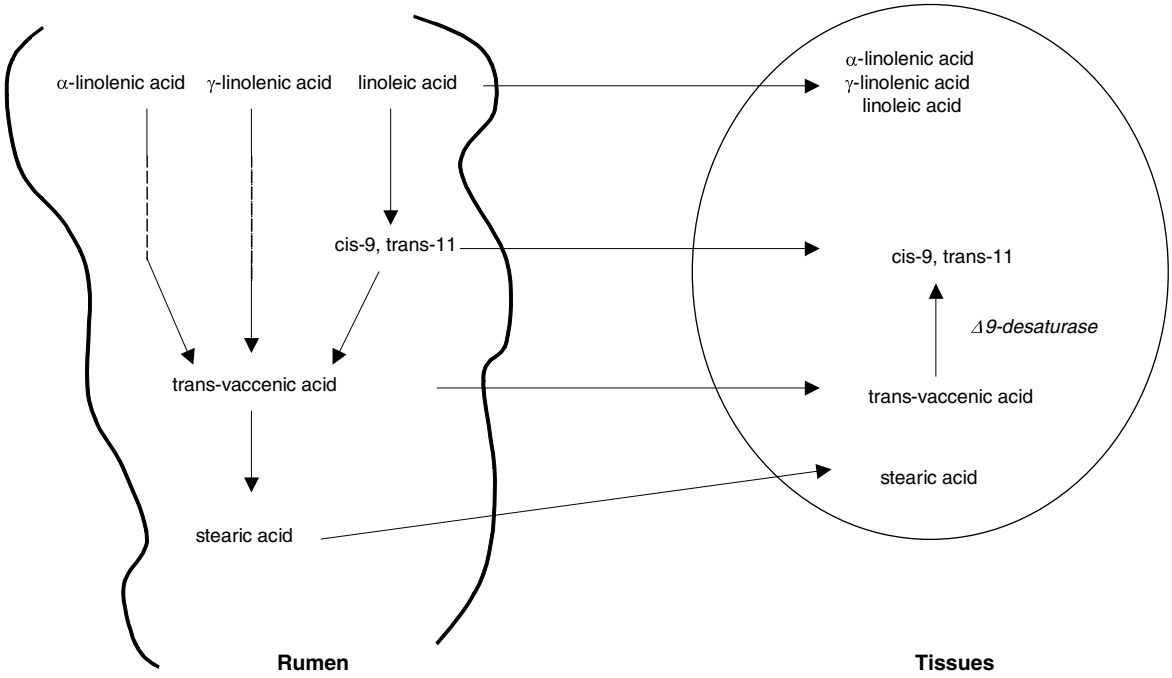

Fig. 1. Biosynthesis of *c*9,*t*11-18:2 ((Griinari & Bauman, 1999) modified).

lipid) with various influencing factors such as seasonal variations, animal genetics, and production practices. The CLA concentrations in beef from different countries reported by Dufey (1999) varied by 70% (3.6–6.2 mg/g lipid) with beef from Argentine and Brazil displaying the highest and that from the US displaying the lowest levels. These findings were ascribed to differences in feeding regime between countries.

The CLA concentrations reported in various studies (Dufey, 1999; Fritsche & Steinhardt, 1998; Knight, Knowles, Death, Cummings, & Muir, 2004; Ma et al., 1999; Raes et al., 2003; Wachira et al., 2002) may be underestimated as only the *c*9,*t*11-18:2 isomer and not the total CLA content was measured. However, Fritsche and Steinhardt (1998) stated that this isomer accounts for more than 80% of the total CLA. Indeed, Chin et al. (1992) reported that between 76% and 92% (depending on the species) of the total CLA was *c*9,*t*11-18:2 while Badiani et al. (2004) documented a value of 78%, and Shantha, Crum, and Decker (1994) a value of about 59%.

Differences in the CLA content between different animal tissues, between animals of different breeds or upbringing, or between individual animals of the same breed are reported. Due to large animal-to-animal variations, Shantha et al. (1994) and Raes et al. (2003) were not able to show significant differences in the CLA content between breeds or beef muscles. Comparing two beef cattle crossbreds (with and without Wagyu genetics) fed a barley-

Table 1
Mean CLA content in various raw meats

Reference	Lamb	Beef	Veal	Pork	Chicken	Turkey	Horse
				(in mg/g fat)			
Chin et al. (1992)	5.6	2.9–4.3[b]	2.7	0.6	0.9	2.5	
Shantha et al. (1994)		5.8–6.8[b]					
Dufey (1999)	11.0[c]	3.6–6.2[a,c]		0.7[c]			0.6[c]
Ma et al. (1999)		1.2–3.0[b,c]					
Raes et al. (2003)		4.0–10.0[a,c]					
Badiani et al. (2004)	4.32						
				(in mg/g FAME)			
Fritsche and Steinhardt (1998)	12.0[c]	6.5[c]		1.2 / 1.5[b,c]	1.5[c]	2.0[c]	
Rule et al. (2002)		2.7–5.6[a,b,d]			0.7[d]		
Wachira et al. (2002)	8.8–10.8[c]						
Knight et al. (2004)	19.0[c]						

FAME = fatty acid methyl ester.
[a] Meat from different production systems/countries.
[b] Different pieces of carcass (and eventually different animals).
[c] Only *c*9,*t*11-18:2 measured.
[d] Only *c*9,*t*11-18:2 and *t*10,*c*12-18:2 measured.

Table 2
Mean CLA content in meat products (in mg/g FAME) (Fritsche & Steinhardt, 1998; Chin et al., 1992)

Meat product	*N*	CLA content
Salami	2	4.2
Knackwurst	2	3.7
Black pudding	2	3.0
Mortadella	2	2.9
Wiener	4	1.5/3.6
Liver sausage	2	3.3
Cooked ham	2	2.7
Beef frank	2	3.3
Turkey frank	2	1.6
Beef smoked sausage	2	3.8
Smoked bacon[a]	7	0.8–2.6
Smoked bratwurst	3	2.4
Smoked German sausage for spreading	2	4.4
Smoked ham	2	2.9
Smoked turkey	2	2.4
Minced meat	2	3.5
Corned beef	2	6.6
Potted meat	2	3.0

[a] Different brands.

based finishing diet, Mir, Paterson, and Mir (2000a) found similar CLA contents in the *pars costalis diaphragmatic* muscles (1.7 vs. 1.8 mg/g lipid). Since the crossbreds with Wagyu genetics had a higher total lipid content in the muscle the CLA level per dry matter was higher. By contrast total CLA content (mg/g dry matter) did not differ significantly between East Friesian and Romney lambs although Romney lambs had a higher intramuscular fat content (Knight et al., 2004). Wachira et al. (2002) compared the effects of different dietary fat sources and breeds on the CLA content in *longissimus dorsi* muscle of sheep and found among dietary effects a breed effect with Soay lambs having significantly higher CLA tissue concentrations than Suffolk and Friesland lambs.

3.2. In meat products

Little data are available regarding CLA content of meat products. Meat products were analysed by Chin et al. (1992) as well as Fritsche and Steinhardt (1998) and their findings are summarized in Table 2. The CLA content per gram lipid of the meat product is comparable to that of the raw material and seems in general not influenced by the processing method (Chin et al., 1992; Fritsche & Steinhardt, 1998). This might explain why meat products are subjected to the same variations in the CLA content as in the raw meat.

4. Factors influencing CLA content of meat and meat products

Several influencing factors (seasonal variations, animal genetics, and production practices) have already been mentioned. The most important factor is the diet because it provides the substrates for the CLA formation. Besides animal diet – influencing the naturally occurring CLA content – it is interesting to know whether and how CLA is affected by processing.

4.1. Influence of animal diet on CLA content

4.1.1. In ruminants

A variety of dietary components influence the CLA level of meat (Table 3). In general higher CLA concentrations in muscles are associated with a higher intramuscular fat content (Raes, de Smet, & Demeyer, 2004). However, the important question is whether the CLA content expressed in mg/g intramuscular fat can be increased by specific feeding strategies or dietary components. The present knowledge clearly demonstrates that certain feed components are necessary to positively influence CLA content in the meat fatty acids.

4.1.1.1. Pasture feeding. A switch from concentrate-based diet to pasture has been shown to increase CLA content. French et al. (2000) determined in the intramuscular fat of steers (*longissimus dorsi* muscle) increasing CLA contents consistent with increasing intakes of grass. Levels of 5.4, 6.6, and 10.8 mg CLA/g FAME were detected in grazing steers with increasing grass intake compared to 3.7 mg/g FAME in animals fed concentrate. Grass silage also positively influenced CLA content (4.7 g/g FAME) but not to the same extent. Poulson, Dhiman, Ure, Cornforth, and Olson (2004) reported a 6.6 times higher CLA content in the *longissimus* and *semitendinosus* muscle from steers raised only on forages compared to steers fed a common high grain feedlot diet (13.1 vs. 2.0 mg/g FAME). Steers fed a grain based diet in the growing period and grazed on pasture during the finishing period still had a 4 times higher CLA tissue content compared to those fed only the grain based diet (8.0 vs. 2.0 mg/g FAME). That finishing steers on pasture instead of concentrate feeding leads to higher CLA contents in intramuscular fat (5.3 vs. 2.5 mg/g FAME in *longissimus dorsi* muscle) was confirmed by another study (Realini, Duckett, Brito, Dalla Rizza, & De Mattos, 2004). Grazing on pasture for about 200 days and then being shifted to a drylot diet for about 60 days also led to significantly higher CLA concentrations in steers and heifers compared with animals offered only the drylot diet (Sonon, Beitz, Trenkle, Russell, & Rosmann, 2004). Contrary to these results, Nuernberg et al. (2002) found no significant effect of grass feeding on the CLA content in bulls and steers compared with concentrate feeding (5.6/5.2 vs. 6.0/5.5 mg/g FAME in *longissimus dorsi* muscle). However, in a subsequent study Nuernberg et al. (2004) reported significantly higher proportions of the *c*9,*t*11-18:2 isomer in bulls and lambs after pasture feeding compared with concentrate feeding. In agreement, Santos-Silva, Bessa, and Santos-Silva (2002) reported higher CLA concentrations in the *longissimus* muscle of lambs raised on pasture than of lambs fed a

Table 3
Feeding induced changes in CLA proportions of intramuscular fatty acids

Feed (supplement)	Cattle	Sheep	Pigs	Chicken	Reference(s)
Grass (pasture)	+, ±	+			French et al. (2000), Poulson et al. (2004), Nuernberg et al. (2002), Aurousseau et al. (2004), Nuernberg et al. (2004), Santos-Silva et al. (2002), Sonon et al. (2004), Realini et al. (2004)
Sunflower seeds	+	+			Casutt et al. (2000), Santos-Silva et al. (2003)
Safflower seeds		+			Kott et al. (2003), Bolte et al. (2002)
Linseed	±, +				Casutt et al. (2000), Strzetelski et al. (2001), Stasiniewicz et al. (2000), Wachira et al. (2002), Enser et al. (1999), Demirel et al. (2004)
Rapeseed	(−)				Casutt et al. (2000)
Soybeans	±, +				Madron et al. (2002), Aharoni et al. (2004)
Chickpeas		+			Priolo et al. (2003)
Crushed raw flax	+				Aharoni et al. (2004)
Sunflower oil	+	+			Ivan et al. (2001), Mir et al. (2003), Mir et al. (2002), Noci et al. (2005)
Linseed oil		±			Szumacher-Strabel et al. (2001)
Rapeseed oil	±	±			Strzetelski et al. (2001), Stasiniewicz et al. (2000), Szumacher-Strabel et al. (2001)
Safflower oil		+			Mir et al. (2000b)
Soybean oil	±, −	+			Beaulieu et al. (2002), Griswold et al. (2003), Santos-Silva et al. (2004)
Fish oil	+	±			Enser et al. (1999), Demirel et al. (2004), Wachira et al. (2002)
CLA			+	+	Lauridsen et al. (2005), Bee (2001), Eggert et al. (2001), Joo et al. (2002), Ramsay et al. (2001), Thiel-Cooper et al. (2001), Demaree et al. (2002), Aletor et al. (2003), Du and Ahn (2002), Sirri et al. (2003), Szymczyk et al. (2001)
Partially hydrogenated oil/fat			+		Gläser et al. (2000, 2002)
Ruminally protected lipid supplement	±				Scollan et al. (2003)

+ Means significant increase, − means significant decrease, ± means no effect, brackets mean non-significant changes.

concentrate diet (7.1 vs. 3.2 mg/g FAME). Aurousseau, Bauchart, Calichon, Micol, and Priolo (2004) noted that CLA content in muscle triglycerides depended not only on the diet but also on the growth rate. Again CLA concentration was higher in grass fed lambs compared to those fed the concentrate and was even higher at higher growth rates. This may be due to the higher daily grass intakes of these lambs.

The increased CLA content in meat from animals grazing on pasture is attributed to the high PUFA content of grass (especially *n*-3 18:3 with a *n*-6:*n*-3 ratio of approximately 1:3–5). Although not the only determinant, the amount of dietary PUFA determines the generation of *trans* fatty acids by rumen bacteria as discussed earlier (Lawson, Moss, & Givens, 2001). However, this alone does not explain why hay and grass silage differ in the magnitude of CLA production. This may be related to the reduction of sugar and soluble fibre through the ensiling process which may influence the ruminal environment of the animals consuming the silage (French et al., 2000).

Pasture feeding does not only cause higher CLA concentrations but also influences fatty acid composition. A decrease in the *n*-6:*n*-3 PUFA ratio as well as an increase in the PUFA:saturated fatty acids (SFA) is described in beef adipose and muscle tissue by inclusion of grass in the diet (French et al., 2000; Nuernberg et al., 2002; Realini et al., 2004). In lambs a decrease in *n*-6:*n*-3 PUFA ratio has been documented as well (Aurousseau et al., 2004; Nürnberg et al., 2001; Santos-Silva et al., 2002). These changes in fatty acid composition are favourable in regard to current human dietary guidelines (USDA, 2005).

4.1.1.2. Feeding of oilseeds. Adding oilseeds to the diet has been proven to be an efficient method to increase the CLA content in the muscle lipids. However, not all oilseeds exert the same effect. Casutt et al. (2000) supplemented the concentrate feed of Brown Swiss bulls with either sunflower-, rape-, or linseed (increasing the dietary fat content by 3%). Compared to the control group (5.6 mg/g FAME), the CLA concentration of the subcutaneous fat in the sunflower group was significantly increased (7.8 mg/g FAME) whereas no changes were observed in the linseed group (5.5 mg/g FAME) and in the rapeseed group the CLA content even decreased (4.6 mg/g FAME). Another study was able to confirm the effect of added sunflower seed (Santos-Silva, Bessa, & Mendes, 2003). The authors compared expanded sunflower seed with sunflower meal in lambs raised on pasture with whole corn grain supplements. The CLA content increased significantly by about 70% from 4.1 to 7.0 mg/g total fatty acids in the *longissimus thoracis* muscle. However, with regards to the CLA this feeding strategy was not superior to grass feeding.

Two studies from Poland (Stasiniewicz, Strzetelski, Kowalczyk, Osieglowski, & Pustkowiak, 2000; Strzetelski et al., 2001) investigated the effect of adding linseed (19% of concentrate mixture) to a control diet with concentrate and whole maize plant in Black-and-White Lowland bulls. The CLA levels in the *longissimus dorsi* muscle increased in both studies with the linseed supplementation but only in one study to a significant extent (1.7 vs. 3.7 and 2.1 vs. 2.9 mg/g lipid, respectively). However, the CLA levels were in both studies rather low. Enser et al. (1999) documented markedly higher intramuscular CLA levels in the *longissimus lumborum* muscle of Charolais steers. By feeding them

grass silage and a concentrate containing linseed instead of Megalac (a ruminally protected lipid supplement high in palmitic acid), the CLA content was significantly increased from 3.2 to 8.0 mg/g FAME. In three lamb breeds, Wachira et al. (2002) were also able to increase CLA (on average 10 vs. 16 mg/g fatty acids in the *longissimus dorsi* muscle) by including linseed in the diet. Another study in lambs confirmed the CLA increasing effect of linseed (Demirel, Wood, & Enser, 2004).

In addition to sunflower seed and linseed, safflower seed was also shown to increase the relative CLA content in the muscle tissues of lambs. Kott et al. (2003) fed lambs either a safflower supplemented (containing 6% oil from safflower seeds) or an unsupplemented control diet. The safflower seed supplementation resulted in significantly higher CLA contents in *longissimus lumborum* muscle (4.1 vs. 9.0 mg/g FAME). Similar values were reported by Bolte, Hess, Means, Moss, and Rule (2002). They fed diets with and without cracked high-linoleate or high-oleate safflower seeds (5% additional fat) to lambs. Both safflower seed supplemented diets resulted in significantly higher CLA contents in *semitendinosus* and *longissimus dorsi* muscles compared to the control diet with high-linoleate safflower seeds yielding the highest CLA content (in mg/g FAME; high-linoleate: 9.2, high-oleate: 5.7, and control: 3.7).

Extruded full-fat soybeans were also shown to increase the CLA content in muscle fatty acids of crossbred Angus steers (measured in lipids of rib *longissimus*, eye of round, and chuck tender muscles) (Madron et al., 2002). Adding 25.6% of soybeans in the diet, but not 12.7%, significantly increased CLA concentrations (in mg/g FAME; 25.6% soybeans: 7.7, 12.7% soybeans: 6.9, and control: 6.6). However, despite significance, the observed effect was relatively small which may be due to the high CLA content found in the control group. Whole crushed soybeans with crushed raw flax as a supplement in low and high-forage diets for Friesian bull calves showed higher CLA contents with raw flax (2.8 vs. 4.7 and 3.3 vs. 6.3 mg/g FAME in low and high-forage diets, respectively) in the *longissimus dorsi* muscle (Aharoni, Orlov, & Brosh, 2004). In a subsequent experiment a small increase in the CLA content was found when crushed raw flax was added to a low-forage diet (4.6 vs. 5.3 mg/g FAME), but a much larger effect was observed adding raw flax to a high-forage diet (4.0 vs. 6.7 mg/g FAME) (Aharoni et al., 2004). This led to the assumption that there is a synergistic effect of high-forage concentration and dietary supplementation with PUFA.

Using chickpeas to replace soybean meal and corn in the diet of lambs also resulted in higher CLA concentrations in the *longissimus dorsi* muscle regardless of whether the dietary chickpeas concentration was 20% or 42% (in mg/g FAME; control: 4.9, 20% chickpeas: 8.5, and 42% chickpeas: 8.9) (Priolo, Lanza, Galofaro, Fasone, & Bella, 2003).

Compared to the CLA increase in milk fat with sunflower seed or soybean supplementation (Collomb, Sieber, & Bütikofer, 2004; Dhiman et al., 2000; Lawless, Murphy, Harrington, Devery, & Stanton, 1998) the increase in the CLA content in meat with these supplements is relatively low. This may be related to a lower CLA transfer rate into intramuscular lipids than into milk fat or to a lower amount of added oilseeds. Generally, *c*9,*t*11-18:2 levels are much lower in beef and lamb compared to their level in milk (Raes et al., 2004) and increases in CLA concentration are smaller in the lipid fraction of meat than in milk fat with similar diets (Aharoni et al., 2004). The inclusion of linoleic acid-rich oilseeds, such as safflower or sunflower, in the diet of ruminants appears to be most effective for increasing CLA concentration. Dietary oilseed supplementation does not only increase CLA content but has also a modifying impact on the fatty acid composition of adipose tissue. Concentrations of 18:1, 18:2, and 18:3 fatty acids are increased according to the elevated intake of these fatty acids. However, because of ruminal biohydrogenation of unsaturated fatty acids the concentration of saturated fatty acids in animal tissues will be increased at the same time (Casutt et al., 2000).

4.1.1.3. Feeding of vegetable oils. Vegetable oils as equivalent to oilseeds show similar effects on CLA content. In beef cattle the addition of 3% and 6% sunflower oil to a barley based finishing diet resulted in increased CLA contents in *longissimus* muscle: 2.0 vs. 2.6 vs. 3.5 mg/g lipid for control, 3%, and 6% sunflower oil, respectively (Mir et al., 2003). A more substantial increase in the CLA concentration can be expected when sunflower oil is added to both the growing and finishing diet of beef cattle. Added to a barley and hay-based diet sunflower oil supplementation increased the CLA content in the lipids of the *longissimus* muscle to 12.3 compared to 2.8 mg/g FAME in the control group (Mir et al., 2002). Noci, O'Kiely, Monahan, Stanton, and Moloney (2005) documented in their study 4.3, 6.3, and 9.1 mg CLA/g FAME in *longissimus dorsi* muscle lipids of heifers after supplementing the feed with 0, 55, and 110 g sunflower oil per kg of the diet for 142 days before slaughter. In lambs the supplementation of a barley based diet with sunflower oil (6% of dietary dry matter) led to an increase in intramuscular CLA content (in rib muscle: 3.9 vs. 5.2 mg/g lipid) (Ivan et al., 2001).

Rapeseed oil and whole rapeseed do not seem to have positive effects. Of three studies (two in beef cattle and one with lambs) none showed increased CLA concentrations in the *m. longissimus dorsi* after supplementation with rapeseed oil (6% of DM) (Stasiniewicz et al., 2000; Strzetelski et al., 2001; Szumacher-Strabel, Potkanski, Cieslak, Kowalczyk, & Czauderna, 2001).

Results regarding the effect of soybean oil supplementation on CLA content are inconsistent. Supplementing a corn-based diet of Angus-Wagyu heifers with 5% (of dry matter) soybean oil had no effect on the proportion of *c*9,*t*11-18:2 in muscle tissue (Beaulieu, Drackley, & Merchen, 2002). However, in some of the tissues analysed (*semitendinosus* and *triceps* muscle) the *t*10,*c*12-18:2 was increased after the soybean feeding but, as isomers were

not detected consistently, cautious interpretation is necessary. In a study with steers by Griswold et al. (2003), supplementation of 4% soybean oil to a finishing diet based on concentrate and forage (80:20) resulted in a depression of the CLA deposition in muscle tissues (2.5 vs. 3.1 mg/g FAME) compared to the same diet without soybean oil. On the other hand, comparing 4% with 8% added soybean oil in a 60:40 concentrate:forage diet (same study) showed a numerical increase of the CLA content with the higher soybean supplementation (2.8 vs. 3.1 mg/g FAME). CLA concentration of the chuck muscle was affected by dietary treatments whereas the loin and the round muscle were unaffected. Contrary results were documented by Santos-Silva, Mendes, Portugal, and Bessa (2004) in lambs. Inclusion of soybean oil (8%) to a lucerne hay-based diet resulted in an intramuscular (*M. longissimus thoracis*) CLA content of 23.7 compared with 5.5 mg/g FAME in the control group. The difference was smaller – although still significant – when ground and pelleted lucerne was used as basal feed (6.4 vs. 18.3 mg/g FAME).

The intramuscular CLA concentration can also be altered by supplementing 6% (of DM) safflower oil. This was documented by Mir et al. (2000a) in lambs fed a barley and dehydrated alfalfa diet (CLA in rib: 3.13 vs. 8.41 mg/g lipid).

Vegetable oils influence CLA content in meat by supplying PUFA which are substrates for bacterial isomerisation or/and biohydrogenation in the rumen. If the lipid is resistant to ruminal isomerisation or/and biohydrogenation CLA cannot be produced (neither in the rumen nor endogenously) because its precursor is not available as shown by Scollan, Enser, Gulati, Richardson, and Wood (2003) in Charolais steers fed with a grass silage plus concentrate diet. A ruminally protected lipid supplement comprising a mixture of soybean, linseed and sunflower seed oils was compared with the lipid source Megalac. CLA concentration of neutral lipid in muscle tissue of *longissimus thoracis* did not differ between treatments and the CLA content of the phospholipid fraction slightly decreased when the diet with the ruminally protected lipid mixture was given.

In addition to CLA content, modifications in fatty acid composition in muscle and adipose tissues of beef cattle and lambs are reported when the diet is supplemented with unsaturated fatty acids (Bolte et al., 2002; Casutt et al., 2000; Enser et al., 1999; Kott et al., 2003; Mir, Rushfeldt, Mir, Paterson, & Weselake, 2000b; Mir et al., 2003; Stasiniewicz et al., 2000; Strzetelski et al., 2001; Wachira et al., 2002). Although isomerisation or/and biohydrogenation of unprotected unsaturated fatty acids takes place in the rumen, resulting in a higher ratio of saturated fatty acids in the adipose tissues of cattle than expected from the dietary fatty acid profile, a certain amount of unsaturated fatty acids escapes microbial modification. Therefore, the fatty acid composition in meat is altered according to fatty acid supplementation (Casutt et al., 2000; Raes et al., 2004).

Both oilseeds and free oils affect CLA content and fatty acid composition in the tissues in a similar manner. Free plant oils with high PUFA concentrations are normally not included in ruminant diets as high levels of dietary fat disturb the rumen environment and inhibit microbial activity (Lawson et al., 2001; Raes et al., 2004). Additionally, vegetable oils are a rather expensive dietary supplement for ruminants and are more susceptible to oxidation than seeds. Aharoni, Orlov, Brosh, Granit, and Kanner (2005) compared soybean oil with full fat soybeans as supplements over five months in a high forage fattening diet of Friesian bull calves. Extruded full fat soybeans were about 20% more efficient than free oil in increasing the CLA concentration in intramuscular fat. The full fat soybean supplement also resulted in higher PUFA and lower SFA and monounsaturated fatty acids (MUFA) content in the intramuscular fat than supplementation with soybean oil. This may be due to a partial protection of the oils against ruminal biohydrogenation by roughly crushed seeds (Casutt et al., 2000; Scheeder, 2004). Therefore, using oilseeds instead of free oils may be the preferred option.

4.1.1.4. Feeding of fish oils. Feeding fish oil supplements is another approach to increase CLA. Enser et al. (1999) reported an increase in the CLA concentration from 3.2 to 5.7 mg/g FAME in the *longissimus lumborum* muscles of Charolais steers fed a fish oil supplemented diet but showed simultaneously that whole linseed was more efficient in increasing the CLA concentration. A comparable feeding design used with three lamb breeds documents no effect of fish oil (mean values of 10.0 vs. 11.0 mg/g FAME) but again a significant increase with linseed (Wachira et al., 2002). In both studies combining fish oil with whole linseed let to comparable CLA proportions as with linseed alone but another study (Demirel et al., 2004) with lambs found that the linseed fish oil mixture was more efficient than linseed alone. The comparison of the data is difficult, as the last study reports the CLA content only per 100 g tissue.

The reason for the observed increased CLA levels is not clear yet, as only small amounts of linolenic and linoleic acid are present and the long chain *n*-3 fatty acids are not isomerised/hydrogenated to CLA or *trans*-vaccenic acid. Thus long chain *n*-3 fatty acids present in fish oil may interfere with the biohydrogenation of linolenic or/and linoleic acids or affect Δ9-desaturase activity (Raes et al., 2004). Chow et al. (2004) postulate that fish oil increases ruminal accumulation of *trans*-vaccenic acid by inhibiting the final biohydrogenation step to stearic acid. This would supply more substrate for endogenous CLA synthesis. However, further studies are needed to provide an explanation.

Feeding fish oil also increases the *n*-3 long chain PUFA concentration in the intramuscular fat due to the high eicosapentaenoic (EPA) and docosahexaenoic acid (DHA) content in fish oil. Ruminal biohydrogenation of EPA and DHA is limited, and therefore considerable amounts of these fatty acids are available for incorporation into the adipose tissue (Raes et al., 2004; Scheeder, 2004).

In conclusion, the relative proportion of CLA can be increased by grass feeding or by adding linolenic and linoleic acid rich sources as well as fish oil to high concentrate diets of beef cattle and lambs. Furthermore, the overall fatty acid profile is affected. The changes mainly depend on the supplemented fatty acids and seem to be beneficial from the human health perspective as decreased SFA and increased PUFA tissue concentrations with a lower *n*-6:*n*-3 PUFA ratio were found.

4.1.2. In monogastric animals

Compared to ruminants, dietary fats in monogastric animals are unmodified prior to digestion and absorption. Thus, a diet has to contain *trans*-fatty acids (for instance *trans*-vaccenic acid) as substrate for endogenous CLA synthesis or CLA itself in order to elevate the tissue CLA concentration. The CLA supplements used in the studies below consist in general of a mixture of a limited number of CLA isomers (predominantly *c*9,*t*11- and *t*10,*c*12-18:1). Gläser, Wenk, and Scheeder (2002) analysed muscle tissue (*longissimus dorsi* muscle) of Large White pigs after feeding them from 30 to 103 kg live weight a barley–wheat–soybean meal-based diet with either 6% high-oleic sunflower oil or various amounts (1.85%, 3.70%, 5.55%) of partially hydrogenated rapeseed oil (high in *trans* fatty acids). They reported increasing amounts of CLA in the neutral lipids of muscle tissue with increasing amounts of partially hydrogenated rapeseed oil in the diet (3.8, 6.4, and 8.5 mg CLA/g FAME) and 0.9 mg/g FAME in the sunflower oil control group. In the phospholipid fraction the same effects were detected but lower concentrations of CLA (1.3, 3.2, and 5.8 vs. 0 mg CLA/g FAME). Another study by the same investigators found increased CLA concentrations in the adipose tissue of Swiss Large White and Swiss Landrace pigs when 5% partially hydrogenated fat was included in the control diet (barley, wheat, soybean meal) (Gläser et al., 2000). Bee (2001) documented that supplementing the basal diet of Swiss Large White pigs from 70 to 105 kg live weight with a CLA-enriched oil (2%) resulted in a measurable CLA content (14.9 mg/g fatty acids) in the adipose tissue compared with non detectable CLA levels in the groups with linoleic acid-enriched oil or lard supplements. Feeding gilts a conventional corn–soybean meal diet supplemented with either 1% CLA oil or 1% sunflower oil from 75 to 120 kg live weight resulted in a higher CLA concentration in the *longissimus* muscle with the CLA oil (5.5 vs. 0.9 mg/g fatty acids) (Eggert, Belury, Kempa-Steczko, Mills, & Schinckel, 2001). Similar results (4.4 vs. 0.8 mg/g FAME in *M. longissimus dorsi*) were recently published by Lauridsen, Mu, and Henckel (2005) who supplemented the diet of 100 Danish barrows either with 0.5% CLA or 0.5% sunflower oil from 40 to 100/130 kg live weight. Joo, Lee, Ha, and Park (2002) fed 20 crossbred gilts diets supplemented with either 0%, 1.0%, 2.5%, or 5.0% synthetic CLA based on safflower oil for 4 weeks (approximately 105 kg live weight). CLA concentrations in the *longissimus dorsi* muscle increased with increasing CLA percentage in the diet (0.1, 3.7, 10.1, and 11.6 mg/g fatty acids, respectively). Previous studies reported increasing CLA concentrations in muscle and adipose tissue with increasing (0–2%) dietary CLA content in a dose-dependent manner (Ramsay, Evock-Clover, Steele, & Azain, 2001; Thiel-Cooper, Parrish, Sparks, Wiegand, & Ewan, 2001). Ramsay et al. (2001) were able to increase CLA tissue concentration even though pigs were only fed from 20 to 50 kg live weight. Demaree, Gilbert, Mersmann, and Smith (2002) even started at 17 days of age feeding pigs a corn/soybean meal diet supplemented with either tallow or corn oil with or without 3% CLA for 35 days [5.6–26.0 kg body weight (Dugan, Aalhus, & Kramer, 2004)] and documented in *longissimus dorsi* muscle neutral lipids CLA concentrations of 27.3 and 23.0 mg/g fatty acids (corn oil with CLA and tallow with CLA, respectively) compared with 0 mg/g fatty acids without CLA supplementation. The CLA concentration in adipose and muscle tissue may be further enhanced when CLA supplementation is combined with additional dietary fat (Gatlin, See, Larick, Lin, & Odle, 2002).

Supplementing the grower diet of broilers (Cobb 500) from day 22 to slaughtering at day 47 with either 2.0% or 4.0% CLA resulted in higher CLA concentrations in chicken tissues (breast, drumstick meat, skin, and abdominal fat) compared to the control group (in abdominal fat: 51.5, 91.4, and 0.3 mg/g fat, respectively) (Sirri, Tallarico, Meluzzi, & Franchini, 2003). Similar results were reported by Aletor et al. (2003) in Ross broilers. Previously, Szymczyk, Pisulewski, Szczurek, and Hanczakowski (2001), investigated the effects of increasing CLA concentrations (0%, 0.5%, 1.0%, and 1.5%) in starter and grower diet from day 7 to day 42 in Arbor Acres chickens, found a linear increase of CLA in tissue samples associated with CLA supplementation and no CLA in the control group. In abdominal fat the concentrations were 0, 29.4, 66.6, and 102.0 mg/g fatty acids, in breast muscle 0, 28.9, 52.5, and 93.5 mg/g fatty acids for 0%, 0.5%, 1.0%, and 1.5% supplemental CLA, respectively. Supplementing the diet of 3-weeks-old broiler chickens with 0%, 2.0% or 3.0% CLA over a 5 week period resulted in 0, 105.1, and 177.5 mg CLA/g lipids in breast muscle, respectively (Du & Ahn, 2002).

Apart from increased CLA concentrations in the adipose and muscle tissue, the supplementation of CLA influences tissue fatty acid composition in pigs. Several reports indicate that CLA supplementation increases the amount of saturated fatty acids (C14:0, C16:0, and C18:0) and decreases the MUFA fraction (mainly C18:1) in pig tissues by down-regulating the Δ9-desaturase activity (Bee, 2001; Eggert et al., 2001; Gatlin et al., 2002; Joo et al., 2002; Lauridsen et al., 2005; O'Quinn et al., 2000; Ramsay et al., 2001; Smith et al., 2002; Thiel-Cooper et al., 2001; Wiegand, Sparks, Parrish, & Zimmerman, 2002). A higher saturation ratio means firmer bellies and loins and fewer problems with sausage manufacturing but is less desirable from the human health perspective. The same changes in

fatty acid composition are seen in broilers when CLA is supplemented (Aletor et al., 2003; Du & Ahn, 2002; Sirri et al., 2003; Szymczyk et al., 2001).

4.2. Influence of processing and storage on CLA content

CLA concentration of the meat seems not to be affected by cooking or storage. Shantha et al. (1994) found slight increases (not significant except in one meat sample) of CLA (mg/g total FAME) when different raw beef steaks were compared with cooked ones (broiled, 80 °C internal temperature). In ground beef patties cooked either rare (60 °C) or well done (80 °C) using several cooking methods including frying, baking, broiling or microwaving, CLA concentrations did not show large differences, although higher internal cooking temperatures generally resulted in higher CLA concentrations. They concluded that these cooking methods did not cause any major changes in the CLA content when concentrations are compared on a milligram of CLA per gram of fat basis. However, cooking method and degree of doneness did influence the concentration of dietary CLA since fat content and the amount of edible portion were reduced. Another study conducted by Ma et al. (1999) also showed that cooking only altered CLA levels on a per gram of edible sample and not on the % per fat basis. In one meat (sirloin roast tip) there was a strong increase in CLA which though not explained was ascribed to other changes in the edible portion. Both, dry-heat cooking or moist-heat cooking, gave no significant variation in CLA content per gram fatty acids was found by Badiani et al. (2004) in lamb meat. The results support the findings of the previous studies and those of Knight et al. (2004), comparing effects of cooking methods (different preparation and cooking temperatures) on health-promoting fatty acids in lamb meat. Maranesi et al. (2005) reported that both broiling and microwave cooking did not influence total CLA in % of FAME in lamb rib-loins.

Shantha et al. (1994) also examined the effect of storage on CLA concentrations in meat, using the above mentioned ground beef patties cooked by different methods and to two internal temperatures. They stored the cooked beef patties for 7 days at 4 °C and followed CLA concentration and lipid oxidation in the beef patties by analysing for CLA content and thiobarbituric acid reactive substances (TBARS) on days 0, 1, 2, 4, and 7. No changes in the CLA concentration were detected although the stored, cooked beef underwent oxidative deterioration, suggesting a greater stability of CLA compared to other PUFA. Results from storage investigations with dairy products conducted by the same investigators (Shantha, Ram, O'Leary, Hicks, & Decker, 1995) supported this finding. Dairy products also showed no decrease in CLA concentration during storage of up to 6 months.

In conclusion, research to date indicates that cooking and storing does not negatively alter the CLA content of meat.

5. Human dietary intake of CLA

The relatively high CLA content in meat and meat products, especially from ruminants, has led to estimations of the proportion of total human dietary CLA intake attributable to meat and meat products. Data from Germany (Fremann, Linseisen, & Wolfram, 2002; Fritsche & Steinhardt, 1998; Jahreis, 1997), Sweden (Jiang, Wolk, & Vessby, 1999), United States (Ritzenthaler et al., 2001), and Canada (Ens, Ma, Cole, Field, & Clandinin, 2001) are available with calculations of the human daily CLA intake but these reports do not always provide information on the percentages coming from meat and meat products. Fritsche and Steinhardt (1998) estimated the daily intake of *c*9,*t*11-18:2 in Germany based on data from a German nutrition survey and analysis of the CLA content of the food. As no detailed information was available about intake of meat and meat products, they assumed that 40% meat and 60% meat products with a ratio of 80% pork and 20% beef were consumed. Other meat sources were not taken into account. The calculations suggested a total daily CLA intake of 360 mg for women and 440 mg for men in Germany, 25% of this being supplied by meat and meat products. A similar result – 310 mg CLA, one-third coming from meat and meat products – was calculated by Jahreis (1997) based on consumption data of the German "Nationale Verzehrsstudie" and CLA content of food from various literature sources. Fremann et al. (2002) compared the calculations of a 7-day estimated food record with the content of *c*9,*t*11-18:2 in plasma phospholipids and triglycerides in 52 female students in Germany. The estimate of 320 mg CLA intake per day is in accordance with the results of the previous studies. Meat and meat products contributed less than 14% of the daily CLA intake. However, dietary CLA amount seems to differ between countries due to food availability and eating preferences. A Swedish study by Jiang et al. (1999) examined 1-week dietary records (two per person) and 24-h recall interviews of 123 randomly selected men and estimated an intake of 160 mg *c*9,*t*11-18:2 per day, which is only half of that calculated in Germany. The calculations were based on CLA food values given by Chin et al. (1992) which are lower than the German CLA content data of Fritsche and Steinhardt (1998). No information was given on the percentage of CLA coming from meat and meat products. An even lower *c*9,*t*11-18:2 intake was documented in a Canadian study (Ens et al., 2001) which analysed 1-week dietary records (two per person) of 22 Canadians (females and males). The daily *c*9,*t*11-18:2 intake ranged from 15 to 174 mg with an average of 95 mg. An explanation for this may be found in the low consumption of milk products and meat [1.44 and 1.28 servings, respectively (approximately 360 ml milk and 100 g meat)]. CLA values for foods were either based on data from Ma et al. (1999) or estimated according to fat content, serving size and type of fat. A look at the food records showed that the pattern of CLA intake is highly variable between the individual

Table 4
Human total daily CLA intake with food (per person and day)

Reference	Country	Method	Subjects	Daily dietary intake mg (mean ± SD)
Fritsche and Steinhardt (1998)	Germany	1-week dietary records	? men	440 ± ?
			? women	360 ± ?
Jahreis (1997)	Germany	1-week dietary records	? men and women	309 ± ?
Fremann et al. (2002)	Germany	1-week dietary records	57 women	323 ± 79
Jiang et al. (1999)	Sweden	1-week dietary records + 24 h recall interviews	123 men	160 ± 60
Wolff and Precht (2002)	EU	Milk consumption per person and year	? men and women	140–380[a,b]
Ens et al. (2001)	Canada	1-week dietary records	22 men and women	95 ± 41
Ritzenthaler et al. (2001)	US	3-day dietary records	46 men	212 ± 14[c]
			47 women	151 ± 14[c]

?, Data not available.
[a] Intake from dairy products only.
[b] Range of average values obtained in EU countries.
[c] Mean ± SEM.

subjects and varies on a day-to-day basis (Ens et al., 2001). Again no data was given on the CLA amount provided by meat and meat products. Ritzenthaler et al. (2001) calculated a daily intake of total CLA of 210 and 150 mg in the US for men and women, respectively. The intake of the *c*9,*t*11-18:2 isomer was slightly lower (190 and 140 mg/day). This result was the most accurate comparing different written dietary assessment methods in 93 adults. Meat and meat products supplied about 37% of total CLA. Finally, Wolff and Precht (2002) evaluated the daily CLA intake from dairy milk consumption in 15 countries of the European Union. They estimated average daily intakes varying from 140 mg (in Spain) to 380 mg (in Ireland) per person. Since the data are based only on milk products without taking meat and other food into consideration, the actual intake is certainly higher.

The average total CLA intakes estimated so far range between 95 and 440 mg (Table 4), differing from country to country due to different food patterns and variable CLA values in food.

Optimal dietary intake remains to be established. At the present time there are wide variations in the suggested daily intakes. It was hypothesised that 95 mg CLA per day is enough to show positive effects in the reduction of breast cancer in women; calculations were based on epidemiological data linking increased milk consumption with reduced breast cancer (Enser et al., 1999; Knekt, Jarvinen, Seppanen, Pukkala, & Aromaa, 1996). On the other hand, Ha, Grimm, and Pariza (1989) extrapolated from rat studies that 3.5 g/day were needed to promote human health benefits and Ip, Singh, Thompson, and Scimeca (1994) suggested 3 g/day on the same basis. Ritzenthaler et al. (2001) calculated the CLA intake with a cancer protective effect to be 620 mg/day for men and 441 mg/day for women, also by projecting animal data. However, all these values represent rough estimates and are mainly based on extrapolations from animal data. Hence, they should be interpreted cautiously until experimental human data are available.

6. Conclusion

Conjugated linoleic acids are predominantly present in products from ruminants because of the action of rumen micro-organisms in fatty acid biohydrogenation. CLA concentration per gram FAME varies substantially not only between species but also from animal to animal and within an animal in different tissues. The diet has a strong influence on CLA content. As has been shown in many studies, there are several ways to increase CLA levels in meat from ruminants. In monogastric animals only the supplementation of CLA itself or its precursor *trans*-vaccenic acid are effective in elevating CLA contents. Diet modifications aimed at CLA increases also influences fatty acid composition in the animal tissue.

Meat and meat products contribute about 25–30% of the total human CLA intake in Western populations. This intake could be increased with a stronger orientation on CLA containing foodstuffs and by enhancement of the CLA content in meat through specific feeding strategies. To date, statements about health promoting effects of CLA are mainly based on animal trials and remain to be proven in humans. In human trials synthetic CLA supplements are usually used and these do not reflect natural isomer composition in foodstuffs. Whether natural CLA sources (meat and milk from ruminants) have a similar impact on human health warrants further research.

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