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Review

Effects of dietary factors and other metabolic modifiers on quality and nutritional value of meat

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Abstract

A number of technologies that increase feed efficiency and lean tissue deposition while decreasing fat deposition have been developed in an effort to improve profitability of animal production. In general, the mode of action of these metabolic modifiers is to increase muscle deposition while often simultaneously reducing fat deposition. However, there have been some concerns that the focus on increasing production efficiency and lean meat yield has been to the detriment of meat quality. The aim of this review is to collate data on the effects of these metabolic modifiers on meat quality, and then discuss these overall effects. When data from the literature are collated and subject to meta-analyses it appears that conservative use of each of these technologies will result in a 5–10% (0.3–0.5 kg) increase in shear force with a similar reduction in perception of tenderness. However, it should be borne in mind that the magnitude of these increases are similar to those observed with similar increases in carcass leanness obtained through other means (e.g. nutritional, genetic selection) and may be an inherent consequence of the production of leaner meat. To counter this, there are some other metabolic factors and dietary additives that offer some potential to improve meat quality (for example immuncastration) and it is possible that these can be used on their own or in conjunction with somatotropin, approved β-agonists, anabolic implants and CLA to maintain or improve meat quality.

Keywords: Diet; Meat quality; Nutritional value; Metabolic modifiers; Beef; Pork

Contents

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1. Introduction

Genetic selection and increased understanding of nutrition has led to tremendous improvements in the efficiency of animal production and in carcass composition and quality, at least with respect to carcass fatness and muscle yield. In addition, a number of technologies that further increase feed efficiency have been developed, with some of these being used commercially. In general, the mode of action of these metabolic modifiers is to increase protein and muscle deposition while often simultaneously reducing fat deposition. As a result of these technological advancements, producers have benefited because of improved production efficiencies while meat packers have improved processing efficiencies because of increased lean meat yield. Ostensibly, the consumer has also benefited because meat is leaner and less expensive to purchase. However, there have been some concerns that the focus on increasing production efficiency and lean meat yield has been to the detriment of meat quality. For example, in addition to reducing fat in the whole body, genetic selection for leaner meat has also reduced intramuscular (IM) fat levels, and the perception is that meat is now tougher, less moist and has reduced flavour. Indeed, currently the IM fat content of Australian pork is very low and can be as low as 1% (Channon, Reynolds, & Baud, 2001) and given that 2–3% IM fat is necessary for optimum eating quality (Bejerholm & Barton-Gade, 1986; Fortin, Robertson, & Tong, 2005; Savell & Cross, 1986) further modification may be to the detriment of meat quality. Also, generally there is in an increase in shear force and a consumer panel assessed perception of toughness in meat obtained from animals that have been selected to be lean or leaner because of dietary manipulation (Karlsson et al., 1993). While some studies have suggested that meat from animals treated with metabolic modifiers is tougher, there is still much controversy as to whether this is the case and if consumers can detect the differences. In part, this is because there are differences in mode of action of the various metabolic modifiers, even within a class of modifier, dose responses, as well as species, genotype and individual muscle differences. Therefore, the purpose of this paper is to review the effects of metabolic modifiers on meat quality and nutritive value of meat. Where conjecture exists, and where sufficient data are available, data have been collated and meta-analyses performed in an attempt to clarify some meat quality issues.

Not all of the different classes of metabolic modifiers are approved for, or active in, all meat species so by necessity one species may dominate some discussions. Also, the effects of the metabolic modifiers on growth performance and gross chemical carcass composition have been adequately discussed elsewhere and so these effects have only been summarised and only covered where they offer some processing or quality attributes not generally discussed. In the final section of the review, the effects of some dietary additives and vitamins that may, under some circumstances, have some metabolism modifying actions are discussed. However, with the exception of conjugated linoleic acids (CLA), the effects of dietary fatty acids on meat quality are not discussed because this is likely to require a separate review to do this subject justice.

2. Somatotropin

Somatotropin (ST) is a naturally occurring protein hormone produced by the anterior pituitary gland and secreted into the circulation. Somatotropin has several important roles in the regulation of development and growth of skeletal muscle, bone, adipose tissue, and the liver in growing animals and plays an integral role in the coordination of lipid, protein, and mineral metabolism in mammalian species. Elevation of plasma ST redirects nutrients toward increased muscle and bone growth and decreased adipose tissue growth in meat animals (Etherton & Bauman, 1998). In 1994, the FDA approved a prolonged release bST formulation for use in lactating dairy cows but currently no ST products are approved for beef or lamb production. On the other hand, porcine ST is approved for use in 14 countries (Dunshea, Cox, Borg, Sillence, & Harris, 2002a) although not in the USA. As a result of these commercial applications and approvals, most of the data discussed will be from pigs treated with pST although some ruminant data exists, particularly with respect to mechanisms of action.

Exogenous pST treatment consistently improves average daily gain, feed conversion efficiency and protein deposition and reduces fat deposition. Its efficacy is in improving growth performance is unquestioned (Campbell, Johnson, King, & Taverner, 1990a, 1990b; Campbell, Johnson, Taverner, & King, 1991; Campbell et al., 1988, 1989; Etherton et al., 1987; King et al.,

2000). Under commercial conditions, pST is delivered as either a daily, bidaily or thrice weekly injection (ca. 5 mg/day) administered using a propane powered applicator (Dunshea, 2002; Dunshea et al., 2002a). Dose-dependent increases in lean deposition and reductions in feed intake, fat deposition and carcass fat have been observed (Etherton et al., 1987; Evock, Etherton, Chung, & Ivy, 1988; Krick et al., 1992). Qualitatively similar responses occur in ruminants although the responses may not be as marked because the supply of nutrients may be limiting (National Research Council, 1994).

The increase in protein deposition in ST-treated animals is generally considered to be due to an increase in protein synthesis rather than to a reduction in protein degradation, although the responses may differ between species, physiological age in the same species or even between different tissues within the same animal. Both bST and pST increase whole body protein synthesis in growing cattle (Eisemann, 1989; Eisemann et al., 1986; Eisemann, Hammond, & Rumsey, 1989) and finisher pigs (Seve et al., 1993; Tomas et al., 1992), respectively. Boisclair, Bauman, Bell, Dunshea, and Harkins (1994) found that bST increased protein synthesis (+10%) but had little effect on protein degradation (+4%) in the hindlimb of steers. However, given the high rate of protein turnover in skeletal muscle these subtle changes in protein synthesis and degradation were sufficient to account for a 44% increase in hindlimb protein deposition and corresponded to a 40% increase in whole body nitrogen retention (Boisclair et al., 1994). In contrast, Tomas et al. (1992) found that pST increased whole body nitrogen flux (+38%) and both protein synthesis (+55%) and degradation (+60%) resulting in an increased nitrogen balance (+35%). Also, in a recent study with pigs younger than those likely to be commercially treated with pST (ca. 20 kg), the predominant effect of pST was in decreasing protein degradation (−32%) rather than on protein synthesis (+3%; Vann et al., 2000). Although ST increases protein deposition in most muscles in the body there appears to be some variability in how different muscles respond. For example, bST increased both non-collagen and collagen synthesis in *biceps femoris* but not in the *semitendinosus* of lambs (Pell & Bates, 1987). Within skeletal muscle, ST stimulates both collagen and non-collagen protein synthesis (Pell & Bates, 1987). While the ratio of collagen to non-collagen protein is increased in the skin and liver of pigs treated with ST, the ratio is either unchanged in the muscle of lambs (Pell & Bates, 1987), and unchanged (Fabry et al., 1991) or decreased (Caperna, Gavelek, & Vossoughi, 1994) in muscle of pigs.

The increased protein deposition is not restricted to skeletal muscle as ST increases protein deposition in all tissues including skin (Caperna et al., 1994; Caperna & Vossoughi, 1999; Robertson et al., 1997; Suster, Lewis, King, Mottram, & Dunshea, 2004b) and visceral organs (Caperna & Gavelek, 1996; Caperna et al., 1994). Indeed, the proportional increases in protein deposition in skin and viscera may be greater than that in skeletal muscle contributing to a reduction in dressing rate (ca. −1% in pigs). Also, ST can increase bone deposition (Suster et al., 2004b) impacting on boneless meat yield percentage. Therefore, the increases in growth rate observed within the ST treatment needed to be offset against the decreases in dressing and boneless meat yield percentage. It is possible that the increased skin thickness that occurs in pST pigs may influence the amount of force needed to slice skin-on bacon or the quality of roasted "crackling" and pig skin products although these have not been reported.

Slight or no effects of pST on objective and subjective measures of meat tenderness, appearance and shelf life have been reported in some studies (Aalhus, Best, Costello, & Schaefer, 1997; Wander, Clark, Hu, Holmes, & Schrumpf, 1993). However, others reported that pork from pST treated pigs had lower consumer preference scores for tenderness, juiciness and overall acceptability (D'Souza & Mullan, 2002). In order to reconcile many of the, at times, subtle effects of pST on meat quality, the readily available literature on meat quality were collated for a number of muscles from a variety of genotypes treated with a range of doses of pST (Table 1). The data obtained for the loin muscles were then subject to a meta-analysis and the summary is presented in Table 2. The meta-analysis was conducted by using the means from each of the studies cited in Table 2 and assigning equal weighting to each study regardless of the number of replicates in each study. The subjective data were often reported using differing scales and so for the purpose of the analyses were all standardised to a scale of 0–100 before statistical analyses. All analyses were conducted using the multiple experiment residual maximum likelihood (REML) facility in GENSTAT for Windows Version 7.2.0.8 (Payne, Lane, & the Genstat 5 Committee, 2003). The fixed effect was either control or pST regardless of the dose used. This is a powerful statistical tool but it should be borne in mind that it could detect relatively subtle differences if the direction of the response is predominantly the same. These analyses can also hide the range of responses observed and cannot describe the fact that some genotypes or different classes of pigs may behave differently. Therefore, all the collated data are presented in Table 1. From this meta-analysis it is apparent that pST decreases intramuscular fat (−12%), increases shear force (+9%) and reduces drip loss (−6%). There are significant effects of pST on ultimate pH and colour attributes although these are relatively subtle. The limited data on consumer preferences would suggest that there is a decrease in tenderness (ca. −9%), although there is no effect upon juiciness or flavour. Importantly, there may be some

Table 1
Effect of porcine somatotropin on aspects of meat quality (data are expressed as percentage change from the respective control values)

Reference	Muscle[d]	Sex	Breed[e]	Dose (mg/day)	IMF[a] (%)	Consumer panel scores[b]					Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
						Odor	Flavour	Off-flavour	Juiciness	Tenderness				L^*	a^*	b^*
Prusa and Love (1989)	LD	Mixed	YxH	4	−27.6		8.8		−7.7	−11.2	−2.6					
				8	−27.6		−0.4		−20.9	−38.5	15.8					
Warner and King (1989)	LD	Boar	LWxL	6.75							4.3	0.2	−12.5	−3.2	−1.8	−13.2
Solomon et al. (1990)	LD	Boar	DxY	7.5												
		Barrow		7.5												
		Gilt		7.5												
Beermann et al. (1990)	LD	Mixed	LxYxD	2.2	−0.6						−8.8	1.9				
				4.4	−33.1						13.2	2.1				
				8.8	−32.5						−4.4	2.6				
				14.6	−32.5						18.6	3.8				
Fabry et al. (1991)	LD	Mixed	L	1.5	4.2						−6.5	1.3	21.3	2.6	0.0	2.1
				3	1.7						5.7	2.3	11.9	−3.4	−1.3	−6.4
				6	5.9						−0.8	3.0	19.2	−2.8	5.3	−4.3
	Gluteus			1.5								0.7				
				3								2.5				
				6								2.1				
Nieuwhof et al. (1991)[g]	LD	Mixed	P	4	−17.1	−1.5	1.2			−3.9	2.5		−24.6			
			YxL	4	−15.1	0.3	−0.1			0.4	7.3		22.0			
			D	4	−10.4	−0.5	1.2			−1.6	7.0		8.9			
Boles et al. (1991a)	LD	Mixed	Dx	4	−31.4		−7.2		−14.0	−10.8				−7.3	2.0	38.8
McPhee et al. (1991)	LD	Mixed	LWxL	6.3							−0.8	−1.6	10.9			
	SM			6.3							7.5	−0.9	−2.0			
	ST			6.3							31.0	−1.4	22.1			
Hagen et al. (1991)	LD	Boar	YxHxD	3.5[h]		−1.6	−4.8		−5.3	−15.3						
				7[h]		1.6	−3.2		1.8	−8.5						
				5			10.9		−7.9							
				5			4.3		−10.5							
Goodband et al. (1990)[i]	LD	Barrow	HxYxC	4	−52.7		−1.3		−13.4	−4.5	35.4	2.5	−50.7			
	SM			4	−19.8						17.7	0.2	−16.8			
	ST			4	−37.0											
Boles et al. (1992)	LD	Mixed	NN	4	−53.8		6.9		−3.2	−14.3	11.3					
			Nn	4	−30.6		−1.3		−26.0	−19.2	11.5					
			nn	4	11.8		−11.4		5.7	−10.5	11.4					
Lefaucheur et al. (1992)[j]	LD	Barrow	LW	7.5	−29.2							−1.1				
				6	−26.9							−0.5				
	SS			7.5	−38.5							0.2				
				6	−50.1							2.2				
Mourot et al. (1992)	LD	Barrow	LW	3	−29.5							−0.2	26.7			
		Gilt		3	−13.0							−1.5	76.2			
	AF	Barrow		3	−36.1							−0.9				
		Gilt		3	−10.3							−2.2				
	SS	Barrow		3								0.2				
		Gilt		3								0.6				

(*continued on next page*)

Table 1 (*continued*)

Reference	Muscle[d]	Sex	Breed[e]	Dose (mg/day)	IMF[a] (%)	Consumer panel scores[b]					Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
						Odor	Flavour	Off-flavour	Juiciness	Tenderness				L^*	a^*	b^*
	LD	Barrow		2[k]	−8.9							4.6	−38.7			
		Gilt		2[k]	−11.0							3.0	4.5			
	AF	Barrow		2[k]	−23.2							1.1				
		Gilt		2[k]	−14.9							4.0				
Nurnberg and Ender (1992)	LD	Boar	L	4	−27.3								12.0			
		Barrow		4	−31.3								−0.8			
		Gilt		4	−25.0								0.0			
Goodband et al. (1993)[l]	LD	Barrow	Crossbred	4	−11.0		5.6		3.1	1.2	9.3	−0.9	−44.7			
				4	−44.9		0.0		−13.8	−8.3	15.0	−0.9	−38.6			
				8	−25.6		1.4		−6.2	−4.8	17.5	−0.7	−35.8			
				8	−55.1		0.0		1.5	−9.5	30.5	−0.9	−36.9			
	SM			4	1.5						7.9		22.3			
				4	−24.3						21.5		61.6			
				8	−22.5						11.8		15.2			
				8	−32.7						14.4		16.6			
	ST			4	−32.0											
				4	−37.0											
				8	−44.1											
				8	−43.5											
Wander et al. (1993)	LD	Barrow		3[m]	−43.9		14.0	7.7	−12.5	−9.8	25.0		−33.0	−0.8	−9.1	0.8
				3[n]	−31.5		4.1	−23.5	−10.2	−10.2	36.7		−26.7	0.2	6.7	−9.1
Oksbjerg et al. (1995)	LD	Gilt	YxL	5.4	−18.6		4.5		−1.4	−8.8	−5.7					
Hansen et al. (1997)	LD	Barrow	DxWc	4							14.0		38.7			
	LD	Barrow	M	4							11.9		4.0			
	LD	Barrow	MxWc	4							19.6		−17.0			
Solomon et al. (1994)	LD	Barrow	YxDxL	4							12.5					
				4							10.8					
				4							22.4					
				4							9.5					
				4							11.0					
Klindt et al. (1995a)	LD	Boar	Xbred	4[o]			6.5	−14.5	1.9	1.0						
				4[p]			4.4	3.6	−0.6	−3.9						
				4[q]			−2.8	16.4	0.2	−9.2						
		Barrow		4[q]			−10.2	12.5	−3.3	−22.4						
Klindt et al. (1995b)[o]	LD	Boar	Lean	2			6.9	−7.7	0.9	10.8	10.9					
				4			4.8	−10.6	0.7	−8.5	14.1					
		Gilt		2			1.4	3.9	10.9	3.7	4.8					
				4			2.6	−5.3	8.2	11.2	−12.9					

		Boar	Obese	2			5.1	0.0	4.4	−4.4	38.1			
				4			2.8	−0.9	0.9	−11.8	35.7			
		Gilt		2			−4.7	−21.1	−0.7	−7.0	25.0			
				4			−4.2	−10.5	−3.8	−15.0	55.0			
		Boar	Lean x	2			−1.3	0.0	−7.0	−6.8	23.2			
			Obese	4			2.0	−26.7	−1.9	4.1	17.9			
		Gilt		2			−4.2	−8.8	8.6	1.5	−3.3			
				4			−4.7	−18.8	2.2	3.1	−1.7			
Aalhus et al. (1997)	SM	Barrow	LaCombe	3							−4.2	1.3	−1.5	−4.1
		Gilt		3							−5.3	−0.4	11.0	2.5
	Psoas	Barrow		3							−2.0	2.6	−17.6	−3.7
		Gilt		3							20.8	−1.3	82.4	6.9
D'Souza and Mullan (2002)	LD	Immuno[r]	50%D	5	−14.3	−8.1	−5.2		−21.8	−25.0		−0.2	−20.5	−3.1
		Barrow		5	7.4	−9.7	−15.6		−23.8	−30.8		−1.9	11.2	4.8
		Gilt		5	0.0	−6.5	8.2		10.9	23.6		4.9	−26.2	−3.5
		Immuno[r]	25%D	5	9.1	−11.5	−15.3		−21.1	−19.0		2.7	−16.6	−6.2
		Barrow		5	−4.3	3.4	−6.6		2.0	0.0		2.2	−15.1	0.4
		Gilt		5	4.5	−4.8	7.4		−4.0	−9.8		2.9	−7.8	1.2

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] LD – *longisimus dorsi*, LT – *longisimus thoracis*, SM – *semimembranosus*, ST – *semitendonosus*, AF – *adductor femoris*, SS- *semi spinalis*.
[e] Y – Yorkshire, LW – Large White, L – Landrace, D – Duroc, P – Pietran, H – Hampshire, C – Chester, NN – halothane negative, Nn – halothane carrier, nn – halothane positive, M – Meishan.
[f] pH taken 24 h after slaughter.
[g] Two injections per week.
[h] Tenderness determined on roast and fried loin.
[i] Control pigs fed diets containing 0.6% lysine and pST treated pigs fed diets containing 1.0% lysine.
[j] Pigs treated with 7.5 and 6 mg/day were treated with 100 μg/kg from 60 and 30 kg, respectively.
[k] Pigs treated with weekly injections of pST.
[l] Control pigs fed diets containing 0.8% lysine and pST treated pigs fed diets containing 0.8% and 1.0% lysine.
[m] Frozen for 0.5 months.
[n] Frozen for 2 months.
[o] Six week implant for 6 weeks.
[p] Six week implants for 12 weeks.
[q] Six week implants for 18 weeks.
[r] Entire boars immunocastrated by vaccination at 8 and 4 weeks before slaughter.

Table 2
Meta–analysis of data collated from the studies presented in Table 1 for the effect of pST on meat quality (data are from studies where meat quality was measured in muscles from the loin)

	IMF[a] (%)	Consumer panel scores[b]					Shear (kg)	pHu[d]	Drip loss (%)	Colour[c]		
		Odor	Flavour	Off-flavour	Juiciness	Tenderness				L^*	a^*	b^*
Control	2.16	64.8	57.9	10.8	54.6	59.7	4.53	5.63	4.78	53.2	4.8	8.8
pST	1.90	64.3	58.3	10.0	54.0	54.6	4.94	5.64	4.48	52.8	4.9	8.3
% Change	−12.0	−0.9	0.7	−7.1	−1.1	−8.5	9.1	0.2	−6.3	−0.6	2.1	−5.7
SED[e]	0.0028	0.37	0.27	0.40	0.59	0.001	0.010	0.0032	0.00057	0.24	0.0004	0.0012
P-value	<0.001	0.12	0.13	0.058	0.33	<0.001	<0.001	0.004	<0.001	0.19	<0.001	<0.001

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] pH taken 24 h after slaughter.
[e] Standard error of the difference.

interactions between muscle types, processing, gender and genotype (Aalhus et al., 1997; D'Souza & Mullan, 2002) and with this limited data set this type of analyses was not able to determine these effects. For example, chops from pST treated pigs received significantly lower scores for initial tenderness, initial juiciness, sustained juiciness, and flavour than chops from control counterparts (Boles, Parrish, Skaggs, & Christian, 1991a). However, there was no effect of pST on the sensory characteristics of the cured and processed semimembranosus obtained from these same pigs (Boles, Parrish, Skaggs, & Christian, 1991b). In general, it appears that pST does cause a small increase in shear force and sensory perceptions of toughness in pork but it is unsure whether this would be consistently detected by consumers as there is no difference in perceptions of flavour or juiciness. Certainly, greater rates of deposition of collagen and other connective tissue proteins into the perimysial connective tissue would be expected to increase sensory toughness and perhaps also shear force (Harper, 1999). There are far fewer studies in ruminants but those that have been conducted suggest similar findings as for pigs, at least with respect to IMF and shear force. In this context, bST treatment was found to decrease IMF in goats by 35% (Kouakou, Gelaye, Kannan, Pringle, & Amoah, 2005) and Friesian heifers by 15% (Vestergaard et al., 1995) and marbling score in steers (Dalke et al., 1992), respectively. While there were no significant effects on shear force, both the magnitude of the increases were similar in the former two studies to that observed in pork from pigs treated with pST.

The majority of studies have reported no effect of pST on fibre type distribution (Aalhus et al., 1997; Beermann et al., 1990; Oksbjerg et al., 1995; Ono, Solomon, Evock-Clover, Steele, & Maruyama, 1995; Rehfeldt & Ender, 1993). However, some authors have reported an increase in the proportion of fast oxidative glycolytic fibres and a decrease in proportion of fast glycolytic fibres in the *longissimus* muscle (Solomon, Campbell, & Steele, 1990, 1991). In contrast, a decrease in the proportion of fast oxidative glycolytic fibres and an increase in the proportion of fast glycolytic fibres were found in another study (Whipple et al., 1992). Solomon et al. (1990) reported that pST administration increased muscle fibre size and subsequent shear force, an objective measure of tenderness, of fresh pork. The use of pST has also been reported to reduce calcium-activated proteolysis in the *longissimus* muscle, thereby preventing improvements in tenderness during the ageing process (Weikard, Rehfeldt, & Ender, 1992).

Another major effect of exogenous pST treatment is a dramatic reduction in de novo fat synthesis (Dunshea, Harris, Bauman, Boyd, & Bell, 1992) and consequently subcutaneous fat depth can be decreased by up to 70% (Krick et al., 1992). While subcutaneous fat is trimmed from many pork cuts (e.g. loin chops), it is still retained in roast portions and skin-on bacon and the nutritive value of these latter products will be enhanced by pST. In addition, these cuts of meat contain more lean since both loin-eye area and ham weight are increased by pST treatment. The level of IM fat is also decreased during pST treatment. This is important because this type of fat cannot be removed by trimming. Subjective fat marbling scores and chemically extractable intramuscular fat in the loin are consistently reduced by pST (Tables 1 and 2). While a reduction in IM fat would likely reduce the intake of saturated fats in the consumed portion of meat, low levels of IM fat can impact negatively on sensory perceptions of meat quality (see above). The poly- and mono-unsaturated fatty acid composition of both subcutaneous and intramuscular fat was significantly increased by pST treatment (Mourot, Bonneau, Charlotin, & Lefaucheur, 1992b; Nurnberg & Ender, 1992; Rehfeldt, Nurnberg, & Ender, 1994). The reduction in intramuscular fat coupled with the favourable fatty acid profile in pork from pigs treated with pST should result in a healthier product, although this may be offset against reduced eating quality (see above). Furthermore, the dramatic reduction in de novo fatty acid synthesis means that proportionately more of the fatty

acids incorporated into newly formed lipids would be of dietary origin and this offers the opportunity to further manipulate fatty acid composition through dietary intervention.

As pigs approach maturity, fat deposition is partitioned towards the belly to a greater extent than the rest of the carcass (D'Souza et al., 2004; Shields, Mahan, & Graham, 1983). The increase in fat deposition in the belly may have been accelerated by sustained selection against P2 backfat causing a re-distribution of carcass fat to the belly region. However, pST reduced the amount of fat in the belly of pigs to a greater extent than that found in the whole carcass (Suster, Leury, Hewitt, Kerton, & Dunshea, 2005).

There has been a suggestion that pST treatment may reduce the variation of backfat under commercial conditions. This is an important consideration for producers since a reduction in variation will mean the P2 backfat of all market pigs will be closer to the average, which will help producers to meet market specifications and to predict where the majority of their animals will be on the processor's specification grid. In order to gain some understanding of the effects of pST on variation the original data from Dunshea et al. (2002) was re-examined and it was found that almost three-quarters (74%) of the pigs that had been treated with pST between 80 and 120 kg had a P2 backfat of 14 mm or less, while only 41% of control pigs were under 14 mm (Dunshea & D'Souza, 2003). This corresponds to a reduction in average P2 of 2 mm for pST treated pigs. In addition, the variation in P2 was reduced by pST treatment (6.8 vs. 4.5 mm). To extend this observation, pooled data from 16 on-farm commercial studies was examined and it was found that pST decreased the average, median and maximum P2, P2 deposition and the range in P2 (Dunshea, 2005). Importantly, the variance in P2 was also reduced by pST treatment. The implication for producers is that more pigs will be closer to the required backfat level, and therefore more will fall into the processors required range.

3. β-Agonists

The β-agonist ractopamine has recently been approved for use in many countries as an in-feed ingredient to increase lean tissue growth and improve production efficiency in pigs. Treatment of pigs with β-agonists, particularly ractopamine (RAC), generally has given dose-dependent improvements in ADG, FCR and carcass lean content (see Dunshea & Gannon, 1995). Unlike for pST, feed intake is typically unchanged (Adeola, Darko, He, & Young, 1990; Gu, Schinckel, Forrest, Kuel, & Watkins, 1991b; Yen, Nienaber, Klindt, Crouse, & Effect of ractopamine on growth, carcass traits, & fasting heat production of, 1991) or decreased slightly (Adeola et al., 1990; Mitchell, Solomon, & Steele, 1991; Watkins, Jones, Mowrey, Anderson, & Veenhuizen, 1990) during β-agonist treatment. Other β-agonists that have improved performance in finisher pigs are salbutamol, cimaterol, clenbuterol, Ro16-8714, BRL- 47672 and L-644,969 although none of these other β-agonists have been approved for use in pig production (Dunshea & Gannon, 1995). While there is general agreement that protein deposition is increased during β-agonist treatment, effects on fat deposition have been equivocal. For example, while RAC increased protein deposition in boars, gilts and barrows there was little effect on fat deposition (Dunshea, Eason, King, & Campbell, 1993a). A review of the literature suggests that ractopamine does not appear to decrease backfat measured along the midline (Aalhus et al., 1990; Dunshea et al., 1993a; Dunshea, King, & Campbell, 1993b; Dunshea, King, Eason, & Campbell, 1998a; Gu, Schinckel, Forrest, Kuel, & Watkins, 1991a; Yen et al., 1991) whereas backfat depths measured off the midline have been either decreased (Aalhus et al., 1990; Adeola et al., 1990; Dunshea et al., 1993b; Gu et al., 1991a; Watkins et al., 1990; Yen et al., 1991) or unchanged (Dunshea, King, Campbell, Sainz, & Kim, 1993c; Dunshea et al., 1998a; Mitchell et al., 1991; Sainz, Kim, Dunshea, & Campbell, 1993; Yen et al., 1991). Because ractopamine has been approved in the USA and elsewhere, additional data have become available. A summary of proprietary information from 20 studies conducted in the late 1980s to early 1990s indicated a reduction in backfat at the 10th rib in relatively fat animals (Schinckel, Richert, Herr, Einstein, & Kendall, 2001). In a more recent experiment with leaner pigs, there was a reduction in 10th rib backfat with ractopamine feeding although the response was not as great (Schinckel et al., 2001). However, a summary of a number of recent Australian studies with ractopamine using a variety of treatment regimens in different classes of pigs concluded that although lean meat yield was increased, there were no significant effects of ractopamine on backfat measured at either the P2 site or over the leg (Smits & Cadogan, 2003).

β-Agonists act directly through β-adrenergic receptors on adipocytes and influence cellular metabolism via signalling cascades. In overview, ractopamine or other β-agonists indirectly lead to decreased *lipogenesis* (fat synthesis and storage) and increased *lipolysis* (fat mobilisation and hydrolysis) (Dunshea, 1993; Liu & Mills, 1989; Mersmann, 1998). The rate of fat accumulation in adipocytes or growth of the adipose tissue mass slows, particularly in ruminants, resulting in a leaner animal. The magnitude of these changes is influenced by dose and duration of treatment with the β-agonist, the type of β-agonist, and the species (Beermann, 1993; Mersmann, 1998; Moody, Hancock, & Anderson, 2002). For example, ractopamine and other β-agonists

do not appear to decrease fat deposition in pigs because of a combination of rapid down-regulation of adipocyte β-adrenergic receptors (Dunshea, 1993; Dunshea & King, 1995; Dunshea, Leury, & King, 1998b) and a relative insensitivity of porcine adipocytes to β-agonists (Dunshea & D'Souza, 2003; Pethick & Dunshea, 1996). On the other hand β-agonists have pronounced effects on fat deposition in ruminants (National Research Council, 1994).

Skeletal myocytes also express β-adrenergic receptors, which transduce signal from β-agonist to muscle metabolic enzymes in a dose-dependent manner (Byrem, Beermann, & Robinson, 1996). Direct infusion of the β-agonist cimaterol into the hind limb of growing steers increases the rate of amino acid uptake from the blood and muscle protein accretion (Byrem, Beermann, & Robinson, 1998), independent of any systemic endocrine changes. As with pST, while there is uncertainty as to whether the increased protein deposition is due to changes in synthesis and/or degradation, the majority of the data support increased synthesis (Beermann, 2002). Initial studies in lambs found no significant effects of clenbuterol on skeletal muscle protein synthesis (Bohorov, Buttery, Correia, & Soar, 1987) despite an increase in muscle weight, suggesting reduced protein degradation. On the other hand, feeding clenbuterol for 1 week increased protein synthesis (+45%) in the lamb hindlimb, but had no significant effect on protein degradation (+8%) (McDonagh, Fernandez, & Oddy, 1999). The net result was a 130% increase in hindlimb muscle accretion. Also, in another study dietary ractopamine increased skeletal muscle protein synthesis by 46% (Bergen et al., 1989). In pigs consuming protein-adequate diets, dietary ractopamine increased protein synthesis by 25%, 41% and 41% in *longissimus dorsi*, *biceps femoris* and *gastrocnemius* muscles, respectively (Adeola, Ball, & Young, 1992). Protein degradation also tended to increase by 21%, 43% and 49% in these same muscles. There were small effects on either protein synthesis or degradation in pigs consuming diets that were inadequate in protein (Adeola et al., 1992). The increased protein synthesis occurred primarily in the myofibrillar fraction. Indeed ractopamine tended to decrease protein synthesis in the sarcoplasmic fraction while having no effect on the connective tissue fraction (Adeola et al., 1992), though it should be noted that this fraction is notoriously difficult to measure accurately, presumably as a result of its three-dimensional distribution within muscle (Harper, 1999). In ruminants, it appears that a variety of different β-agonists increase the activity of the major skeletal muscle protease inhibitor calpastatin (Koohmaraie, Shackelford, Muggli-Cockett, & Stone, 1991; Kretchmar, Hathaway, Epley, & Dayton, 1990; McDonagh et al., 1999; Pringle, Calkins, Koohmaraie, & Jones, 1993; Wheeler & Koohmaraie, 1992), further suggesting that β-agonists decrease protein degradation. Some of the discrepancies between studies probably relate to differences in β-agonist studied as well as differences between species. In this context, the pig is less sensitive to β-agonists than ruminants, at least with respect to fat mobilisation (Dunshea & D'Souza, 2003; Pethick & Dunshea, 1996).

Effects of β-agonists on meat quality are equivocal, particularly in pigs. At least some of the confusion must arise from the fact that all β-agonists are not equally potent and also cells, tissues and individual animals vary greatly in expression of β-adrenergic receptors and the metabolic pathways linked to them. In order to reconcile many of the, at times subtle effects of β-agonists on meat quality, the readily available literature on meat quality was collated for a number of muscles from a variety of genotypes treated with a range of doses of various β-agonists (salbutamol, cimaterol, clenbuterol, ractopamine, zilpaterol and L644,969) for ruminants (Table 3) and pigs (Table 4). While there were insufficient data obtained from ruminants to conduct a meta-analysis it seems reasonable to conclude that most β-agonists decrease intramuscular fat and increase shear force, drip loss and pHu. This appears to be the case for loins from cattle treated with cimaterol (for which there is the most data) where the average increase in shear force was approximately 60% (4.1 vs. 6.6 kg). Somewhat surprisingly, there are very few meat quality data for the two β-agonists that are approved for use in cattle; zilpaterol, which is approved in South Africa and Mexico and ractopamine, which is approved in the USA. Dietary zilpaterol did not have any effect on marbling in one study (Plascencia, Torrentera, & Zinn, 1999) but dramatically increased shear force (7.7 vs. 15.9 kg) in another (Morón-Fuenmayor, Zamorano-García, Ysunza, & González-Méndez, 2002). In other studies, zilpaterol had no negative effects on meat quality when fed for 15 or 30 days, whereas feeding it for 50 days resulted in lower sensory tenderness and juiciness ratings for the *longissimus* muscle, and the shear force of the muscle also was negatively affected (Strydom, Osler, Leeuw, & Nel, 1998, 1999). There are even fewer published data on ractopamine but proprietary data suggest a slight decrease in tenderness, measured as trained sensory panel ratings, and increase in mechanical Warner–Bratzler shear force in cooked strip loin steaks, when the highest level (300 mg per head per day) is fed (Schroeder, Polser, Laudert, & Vogel, 2003).

There are much more data for the effects of β-agonists on meat quality in pigs and these have been collated in Table 4 and the data obtained from the studies conducted with pork loins have been subjected to a meta-analysis (Table 5). From this meta-analysis, it appears that there are differences in the responses to the various β-agonists, with cimaterol having the most pronounced effects on decreasing intramuscular fat and increasing shear force and drip loss. On the other

Table 3
Effect of various β-agonists on aspects of meat quality in sheep and cattle (data are expressed as percentage change from the respective control values)

Reference	β-Agonist	Dose (ppm)	Muscle[d]	Sex	Breed[e]	IMF[a] (%)	Consumer panel scores[b]			Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
							Flavour	Juiciness	Tenderness				L^*	a^*	b^*
Sheep															
Hanrahan et al. (1987)	Cimaterol	0.57	LD	Wether	G	−6.7									
		2.29				−20.0									
		11.42				−15.6									
		1.8			BF						2.1				
Shackelford et al. (1992)	L644,969	1	LD	Wether	R	1.3									
Koohmaraie et al. (1996)	L644,969	4	LD	Mixed	Callipyge					32.9	0.7				
Cattle															
Allen et al. (1987)	Cimaterol	33	LD	Steer	F	−42.1					0.2	97.2			
	Cimaterol	49.5				−50.0					−0.5	116.9			
	Cimaterol	66				−55.3					−0.7	108.5			
Boucque, Fiems, Sommer, Cottyn and Buysse (1987)	Cimaterol	4	LD	Bull	WB	−15.8									
Fiems et al. (1990)	Cimaterol	6	LD	Bull	BB	−20.0				31.6	0.0	−3.6	−4.2	3.0	−4.5
		6			C	−44.4				36.2	−1.8	1.9	2.5	−4.5	2.5
		6[g]			BB	−44.4				45.6	1.8	0.0	2.1	−1.3	8.2
		6[h]				−14.8				27.0	1.8	−20.0	−2.3	4.4	2.0
		6[i]				−44.4				30.5	0.0	−20.0	0.5	3.8	2.0
Chikhou et al. (1993)	Cimaterol	4[j]	LD	Steer	F	−52.2				48.9	0.2	7.6			
		4[k]				−40.0				145.5	0.2	47.2			
		4[l]				−57.7				118.3	1.6	2.6			
Miller et al. (1988)	Clenbuterol	10 mg/day	LD	Heifer	CxH					13.5					
Geesink et al. (1993)	Clenbuterol	0.16[m]	LD	Bull	F					51.0	0.5	57.4	9.5	−1.8	8.1
		0.16[n]								19.5	2.2	90.4	7.4	3.0	7.0
		0.16[o]								−1.0	3.2	65.0	13.9	−5.9	8.1
		0.16[m]	SM							4.0		34.7	9.3	−7.7	−4.0
		0.16[n]								12.0		70.2	3.4	−1.2	−8.1
		0.16[o]								−4.0		66.7	6.9	−1.8	0.0
Garssen et al. (1995)	Clenbuterol	1.6	LD	Bull	F	−8.1				41.7	1.8	12.7	3.9	−18.3	−4.5
Garssen et al. (1995)	Salbutamol	60	LD	Bull	F	−18.9				45.3	1.3	2.6	−0.4	−15.0	−5.7
		100				−21.6				44.3	1.6	4.6	1.4	−13.1	−5.1
Wheeler and Koohmaraie (1992)	L644,969	3	LD	Steer	HxAxRP	−10.8				49.2					
Schroeder et al. (2003)	Ractopamine	9.1	LD	Steer	Mixed	−0.6	−1.4	−0.1	−1.3	−1.3	−0. 4				
		18.2				0.4	0.2	1.3	−1.5	2.6	0.0				
		27.3				−0.8	−1.8	−1.2	−6.5	11.5	0.0				
Strydom et al. (1998)	Zilpaterol	45 mg/day[p]	LD	Steer	Crossbred				−10.7						
		45 mg/day[q]	LD	Steer	Crossbred				−10.7						
		45 mg/day[p]	ST	Steer	Crossbred				−5.5						
		45 mg/day[q]	ST	Steer	Crossbred				−9.1						
Plascencia et al. (1999)	Zilpaterol	6	LD	Steer	Crossbred	−1.7									
Morón-Fuenmayor et al. (2002)[r]	Zilpaterol		LD	Heifer	Crossbred					85.2					
			LD[s]	Heifer	Crossbred					136.4					

(*continued on next page*)

Table 3 (*continued*)

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] LD – *longisimus dorsi*, SM – *semimembranosus*, ST – *semitendinosus*.
[e] G – Galway, BF – Blackface, R – Rambouillet, F – Friesian, WB – White Blue, BB – Belgian Blue, C – Charolais, H – Hereford, A – Angus, RP – Red Poll.
[f] pH taken 24 h after slaughter.
[g] Treated for 246 days.
[h] Treated for 127 days.
[i] Treated for 71 days.
[j] Slaughtered at 275 kg.
[k] Slaughtered at 375 kg.
[l] Slaughtered at 475 kg.
[m] Withdrawal period of 8 days.
[n] Withdrawal period of 4 days.
[o] Withdrawal period of 2 days.
[p] Fed for 30 days before slaughter.
[q] Fed for 50 days before slaughter.
[r] No dose level provided.
[s] Zilpaterol and vitamin D.

hand, ractopamine and salbutamol had no effect on intramuscular fat content and had either no effect (ractopamine) or decreased drip loss (salbutamol). Ractopamine and salbutamol both increased shear force by approximately 0.5 kg. In general, β-agonist treatment caused a slight (+0.02) increase in ultimate pH and decreased a^* and b^* values of pork loins, indicating a decrease in redness and yellowness of the meat. The limited data on consumer preferences would suggest that ractopamine causes a decrease in tenderness (−6%), a negligible decrease in flavour (−1%) with no effect on juiciness. In keeping with the lack of effect of ractopamine on intramuscular fat, there is relatively little effect of ractopamine on the fatty acid composition of intramuscular or subcutaneous fat. It should be borne in mind when summarising these effects that most of the data on pork quality from pigs fed ractopamine were obtained in studies where 20 ppm of ractopamine were fed. Under most commercial situations, the levels of ractopamine fed are between 5 and 10 ppm and so effects on meat quality may be less than suggested here.

4. Estrogenic and androgenic implants

Estrogenic and androgenic growth-promoting agents have been widely used in the beef cattle industry for almost 50 years to increase growth performance and profitability. A number of individual compounds are approved for use either alone or in combination and these include naturally occurring steroids such as 17-oestradiol, progesterone and testosterone, and their synthetic counterparts zeranol, melengestrol acetate and trenbolone acetate. Doses of individual compounds vary among the several approved combination implants. Estrogenic products are effective in steers, androgenic products are effective in heifers, and combination products are also effective. Detailed descriptions of the chemistry and mechanisms of action of estrogenic and androgenic compounds have been published (Hancock, Wagner, & Anderson, 1991; Sillence, 2004). These anabolic agents increase rates of muscle protein synthesis and deposition and/or decrease protein degradation and also decrease the amount of fat at a particular live weight. Although implants increase feed intake by 5–10%, they decrease the amount of energy required for maintenance, increasing the amount available for growth thereby improving feed efficiency by 5–15%. Daily gain is improved by up to 25% when aggressive implant strategies are used in cattle fed high-concentrate diets (Bartle, Preston, Brown, & Grant, 1992; Johnson, Anderson, Meiske, & Dayton, 1996; Perry, Fox, & Beermann, 1991). Comprehensive summaries of the effects of implant strategies using various combinations of commercial products indicate that increasing the anabolic implant dose, up to a point, increases the weight at

Table 4
Effect of various β-agonists on aspects of meat quality in pigs (data are expressed as percentage change from the respective control values)

Reference	β-Agonist	Dose (ppm)	Muscle[d]	Sex	Breed[e]	IMF[a] (%)	Consumer panel scores[b]			Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
							Flavour	Juiciness	Tenderness				L^*	a^*	b^*
McKeith et al. (1988)	Ractopamine	20	LD	Mixed	Crossbred	19.3									
		20	SM			−5.6									
Aalhus et al. (1990)	Ractopamine	10	LD	Mixed	Lacombe	14.6				13.7	0.5	2.1	1.6	−7.8	−24. 5
		15	LD			25.3				16.2	0.9	−17.6	1.0	−13.1	−34.2
		20	LD			21.6				15.3	0.4	2.9	1.8	−12.5	−31.0
Anderson et al. (1991)	Ractopamine	10	LD	Mixed	Crossbred		−1.6	2.1	−5.3						
		15	LD				−1.6	4.2	−1.8						
		20	LD				−3.1	6.3	0.0						
Aalhus et al. (1992)	Ractopamine	10	SM	Mixed	Lacombe	1.1				7.6					
		15				16.3				4.5					
		20				2.2				6.7					
		10	Psoas		Lacombe	−9.3									
		15				−5.3									
		20				−12.0									
Dunshea (1993)	Ractopamine	20	LD	boar	LWxL					17.5	0.2	−15.5	−1.5	−5.7	−15.9
		20		Barrow						18.0	0.6	1.5	2.0	−22.4	−20.7
		20		Gilt						−13.3	−0.9	12.7	5.0	0.0	20.5
Uttaro et al. (1993)	Ractopamine	20	LD	Mixed	Crossbred					11.6		−33.3	−1.1	−14.6	−22.9
		20	SM							−2.3			−2.3	−14.1	−23.4
Stites et al. (1994)	Ractopamine	5	LD	Mixed	Crossbred			12.0	0.5	9.2					
		10						9.4	−13.0	7.5					
		20						−3.7	−5.7	10.0					
		5	SM			9.5	−2.5	12.3	−3.5	10.9	0.6				
		10				3.7	−1.2	4.8	−6.6	32.4	0.6				
		20				19.3	−3.7	1.3	−9.7	−2.1	1.3				
Smith et al. (1995)	Ractopamine	5	LM	Boar	LWxL	−14.8				10.2	−1.6	9.3			
		12.5				−11.1				−0.8	2.0	0.0			
		20				−18.5				10.6	−4.1	109.3			
		5		Gilt		−3.6				2.5	3.4	−21.7			
		12.5				−7.1				−5.8	4.8	−21.7			
		20				−25.0				−2.5	6.7	−4.8			
		5		Mixed		16.7				−4.2	0.0	0.0			
		12.5				6.7				8.7	0.5	−14.3			
		20				6.7				−0.7	0.5	14.3			
Stoller et al. (2003)	Ractopamine	10	LM	Mixed	B,D,LxY	−4.0		0.6	−4.0	4.1	0.5	−6.5	0. 6		
Carr et al. (2005)	Ractopamine	10[g]	LD	Mixed	PIC337	−12.7	−1.6	0.8	−7.2	11.7	−0.4	14.8	0.1	−15.9	−16.3
		10[h]			xC22	−18.0	−1.0	−4.3	−4.0	13.6	0.4	14.8	3.4	−9.8	−13.0
		10[i]				−14.5	−0.6	2.5	−9.2	10.0	0.5	2.6	−0.8	−12.8	−15.2
Jones et al. (1985)	Cimaterol	0.25	LM	Mixed	LxHxLW					−8.0					
		0.5								6.4					
		1								13.1					
Bakaert et al. (1987)	Cimaterol	1	LM	Mixed	BL						0.4		0.8	−14.4	−4.2
Walker et al. (1989)	Cimaterol	0.25	LD	Mixed	HxYxD	−6.8				−10.2		82.4			
		0.5	LD			−25.0				15.2		111.8			

(*continued on next page*)

Table 4 (*continued*)

Reference	β-Agonist	Dose (ppm)	Muscle[d]	Sex	Breed[e]	IMF[a] (%)	Consumer panel scores[b]			Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
							Flavour	Juiciness	Tenderness				L^*	a^*	b^*
Thornton et al. (1989)	Cimaterol	0.5	LD	Mixed	LW					17.3	1.7		−6.3		
		1								35.6	1.7		−1.7		
		0.5	SM							9.3	1.7				
		1								−21.7	1.7				
		0.5	ST							4.2	1.6		−4.9		
		1								4.2	1.6		−3.7		
Yen et al. (1990)	Cimaterol	0.69	LD	Barrow	Lean					31.6					
		1.38								34.5					
		0.69			Obese					28.1					
		1.38								37.8					
Cole et al. (1987)	Salbutamol	4	LD	Gilt	LWxL	0.0					0.0				
Warriss et al. (1990a)	Salbutamol	3	LD	Gilt	Hyline	6.2				22.0	0.7	−6.3	1.4	−25.0	−35.6
Warriss et al. (1990b)	Salbutamol	2.7	LD	Gilt	CBxLW					15.2	−0.2		1.1		
		2.7								−2.0	0.0		0.2		
		2.7	SM							8.5	0.9		0.0		
		2.7								4.0	0.5		0.4		
		2.7	SS							−8.1	3.3		−2.6		
		2.7								2.2	1.7		−0.4		
Hansen et al. (1997)	Salbutamol	2.75	LD	Barrow	DxW					0.0		12.9			
		2.75			M					9.1		−32.0			
		2.75			MxW					2.0		−34.0			

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] LD – *longisimus dorsi*, SM – *semimembranosus*, ST – *semitendinosus*.
[e] Y – Yorkshire, LW – Large White, L – Landrace, D – Duroc, CB – Chester Blue, NN – halothane negative, Nn – halothane carrier, nn – halothane positive, M – Meishan; B-Berkshire; Y – Yorkshire, LW – Large White, L – Landrace, D – Duroc, H – Hampshire, C – Chester, M – Meishan PIC – Pig Improvement Company.
[f] pH taken 24 h after slaughter.
[g] Barley-based diet.
[h] Corn-based diet.
[i] Wheat-based diet.

Table 5
Meta–analysis of data collated from the studies presented in Table 4 for the effect of various β agonists on meat quality of pork (data are from studies where meat quality was measured in muscles from the loin)

	IMF[a] (%)	Consumer panel scores[b]				Shear (kg)	pHu[d]	Drip loss (%)	Colour[c]		
		Flavour	Off-flavour	Juiciness	Tenderness				L^*	a^*	b^*
Control	4.75					3.75	5.51	1.70	43.2	5.6	16.7
Cimaterol	3.93					4.68	5.53	3.35	41.4	4.8	16.0
% Change	−17.2					25.0	0.4	97.1	−4.0	−14.8	−4.2
Control	3.10	56.0	0.091	50.0	52.9	4.23	5.57	4.21	50.3	8.5	5.3
Ractopamine	3.13	55.4	0.069	50.5	49.6	4.72	5.60	4.48	51.0	7.4	4.5
% Change	1.1	−1.2	−24.1	1.1	−6.3	11.6	0.4	6.4	1.4	−12.5	−13.7
Control	0.81					5.27	5.43	4.30	55.8	6.8	4.6
Salbutamol	0.83					5.61	5.42	3.37	56.1	5.2	3.3
% Change	2.5					6.5	−0.1	−21.7	0.7	−23.6	−29.1
Average SED[e]	0.650	0.26	0.0497	0.95	0.769	0.204	0.0076	0.449	0.72	1.11	1.10
Maximum SED[f]	0.892					0.285	0.0128	0.600	1.44	1.42	1.42
Minimum SED[g]	0.166					0.0004	0.0004	0.281	0.17	0.09	0.0004
BA[h]	<0.001					<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
BA.agonist[i]	0.77	0.011	0.66	0.55	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] pH taken 24 h after slaughter.
[e] Average standard error of the difference.
[f] Standard error of the difference for the lowest number of replicates.
[g] Standard error of the difference for the highest number of replicates.
[h] *P*-value for the comparison between the β-agonists.
[i] *P*-value for the comparisons between the β-agonists and the control.

which animals reach a common body composition or lean-to-fat ratio (Bartle et al., 1992; Guiroy, Tedeschi, Fox, & Hutcheson, 2002). Unlike for ruminant animals, anabolic implants appear to have little effect upon growth performance and carcass quality in pigs and so are not used in pork production.

The effects of estrogenic and androgenic agents on meat quality have been the subject of much debate. For example, a review of possible effects of implant strategies on beef quality concluded that current anabolic implants have subtle, if any; effects on tenderness measured either objectively or subjectively (Nichols, Galyean, Thomson, & Hutcheson, 2002). For example, in one large study with 2748 steers reported that there was no significant effect of moderate implant strategies on shear force in 21 days aged steaks although differences in tenderness were detected by a trained sensory panel but not by an untrained consumer panel (Barham et al., 2003). For steaks that were aged for less than 21 days HGP treatment resulted in increased shear values. Another, comprehensive study conducted at five ranches and looking at implanting at up to five stages through growth, found that implanting at one or more stages had negative effects on meat palatability, marbling scores and shear force (Platter, Tatum, Belk, Scanga, & Smith, 2003). Also, the Meat Standards Australia (MSA) beef grading system, which predicts palatability of individual muscles from a range of production and processing inputs, has recently incorporated a negative effect of anabolic implants into its prediction model. The effect is dependant upon the muscle and can be moderated by aging of the meat and tenderstretch hanging. A number of studies contributed to the MSA decision. Firstly targeted taste panel tests of beef cuts were undertaken using untrained consumers studies. It was concluded that heifers or steers implanted with Revalor –H and –S and slaughtered within the payout period resulted in tougher meat. The greatest response was in those muscles that had the highest ageing rates post-mortem. This was consistent with a mechanism for increased lean deposition being due in part to reduced protein degradation, possibly as a result of increased calpastatin activity in the live animal, which results in lower ageing rates and less tender meat post-mortem. This effect was most evident in those muscles with the fastest ageing rates, as presumably these muscles would respond most to increased calpastatin activity (Thompson, McIntyre, Tudor, Pethick, & Polkinghorne, in press). Those authors also found effects on compressive toughness, consistent with changes in connective tissue structure accompanying changes in calpstatin activity, but having longer half-lives. In a second study, a number of different hormone growth promotant (HGP) implant strategies resulted in a decrease in sensory scores, particularly tenderness (Thompson et al., 2004). Whilst all HGP implant strategies resulted in an increase in ossification scores and a decrease in marbling scores relative to controls the differences in sensory scores were

still apparent after adjustment to the same ossification and marbling scores. Finally, Polkinghorne and Watson, (2004) undertook a meta-analysis on 32 studies with 22 treatment-control comparisons for taste panel tenderness evaluations; and 18 studies, with 24 treatment-control comparisons for the shear-force measurements studies where shear force was measured in control and implanted animals. When all these data were considered, it was concluded that there was a small, but highly significant, increase in shear force of 0.3 kg and a 5% decrease in taste panel tenderness score (Polkinghorne & Watson, 2004). Consistent with earlier analyses, however, more aggressive growth promotion strategies led to greater effects on tenderness.

Toughness in meat derived from the highest value muscles is understood in terms of a dominant effect of the myofibrillar component of muscle and a lesser effect of the connective tissue component. Post-mortem tenderisation occurs through the actions of the calcium-activated proteases, the calpains, and their action is counter-balanced by the specific calpain inhibitor, calpastatin. Most evidence in the literature is consistent with the common anabolic implants having the major proportion of their effect through changes in the expression and/or lifetime of the calpain (μ and m) and calpastatin proteins. A relative increase in the amount of calpastatin reduces the total calpain activity available for intracellular proteolytic degradation of key structural proteins, and hence tenderisation postmortem. On the synthetic side, the data also suggest longer-term changes in the muscle connective tissue structure, and this is indicated in such objective measures as compression. Previous difficulties in measuring repeatable increases in muscle collagen content probably reflect the crudeness of such measures, and we suggest that measures that take into account the complex three-dimensional distribution of connective tissues might be more successful in quantifying the underlying structural changes induced by the more aggressive growth promotant strategies (Harper et al., 2004). Specifically, we would predict measurable changes in the width of perimysial connective tissue seams within hormone-responsive muscles. Whether this synthetic response to anabolic implants is direct (e.g. stimulation of synthesis of collagen type I) or indirect (e.g. stimulation of calpain activity that subsequently influences connective tissue turnover) is yet to be seen, but both mechanisms have been supported by in vitro data.

5. Immunocastration

During sexual development and when mature, entire male pigs accumulate substances in their fatty tissue, predominantly skatole and the pheromone androstenone, that are regarded as the main contributors to boar taint in pork (Bonneau, 1982). To avoid tainting of the meat, entire male pigs destined for fresh meat consumption in Australia and New Zealand have, until recent years, been slaughtered before sexual maturity. In most other countries, taint is overcome by castration of the male pig before weaning. However, castration results in significant reductions in growth performance and excess deposition of fat (Campbell & Taverner, 1988; Dunshea et al., 1993c). Ruminant animals destined for meat consumption are also generally castrated to reduce aggressive behaviours, sexual activity and, particularly in the case of sheep and goats, the accumulation of pheromone taints. Castrated animals also deposit more fat including intramuscular fat and produce meat of a better eating quality than their entire counterparts.

An alternative method of inhibiting sexual development and aggressive behaviours and reducing the accumulation of pheromones in carcass fat, is immunisation against gonadotropin releasing factor (GnRF) resulting in a reduction in plasma gonadotropin and testosterone (Bonneau et al., 1994; Caraty & Bonneau, 1986; Dunshea & McCauley, 2001; McCauley et al., 2003; Oliver et al., 2003). Recently, a vaccine (Improvac) containing a modified form of GnRF in a low reactogenic adjuvant system has been developed to reduce the production and accumulation of both androstenone and skatole in pig carcasses (Dunshea et al., 2001). The vaccine formulation and protocol allows the pigs to receive the secondary immunisation relatively close to slaughter. Any taint substances already present are progressively metabolised, allowing the entire boar to be slaughtered at a higher live-weight without taint and after having earlier benefited from the effects of its own testicular steroids on growth and carcass composition (Dunshea et al., 2001). The decrease in testosterone appears to also have some additional effects on sexual, aggressive and feeding activity with resultant positive effects on growth performance. Immunisation against GnRF is also effective in arresting sexual development in females and a commercial product was released in Australia in the early 1990s to control sexual behaviour and reduce pregnancies in extensively grazed female cattle in Northern Australia (Hoskinson et al., 1990).

In a study involving 200 boars that were slaughtered at two different ages (23 or 26 weeks of age), most of the entire boars treated with either Improvac or a placebo vaccine had appreciable levels of circulating testosterone (>2 nM) at the time of second immunisation (Table 6; Dunshea et al., 2001). At the time of the second treatment, 85% of the boars treated with either vaccine or placebo had a serum testosterone concentration of >2 nM. Within 2 weeks after the second vaccination, there was a marked reduction in testosterone ($P < 0.001$) in the treated boars such that only 6% of animals had testosterone concentrations above 2 nM. Placebo treated boars had fat androstenone levels

almost eight times higher than the immunocastrated boars, which in turn were not significantly different from barrows (Dunshea et al., 2001). When pooled across age groups, 24% of control boars had fat androstenone concentrations between 0.5 and 1.0 while a further 49% had intermediate fat androstenone concentrations greater than 1.0 μg/g. In contrast, only 3% of the immunocastrated boars had intermediate fat androstenone concentrations of between 0.5 and 1.0 μg/g. The remaining vaccinated boars had fat androstenone concentrations well below 0.5 μg/g, with most being below the detection limit. Placebo vaccinated boars had fat skatole levels almost twice as high as the immunocastrated boars (Table 6), which in turn were not significantly different from barrows. The vaccinated boars had no pigs exceeding the fat skatole threshold of 0.25 μg/g, in both age groups, compared to the placebo controls ($P < 0.001$). When pooled across the age groups, 11% of the control boars had skatole above 0.25 μg/g. In contrast, none of immunocastrated boars had skatole above 0.25 μg/g, with most treated boars having skatole levels well below 0.25 μg/g. All barrows had fat androstenone and skatole concentrations below the lower thresholds of 0.5 and 0.25 μg/g, respectively. While, there is some debate regarding the threshold concentrations of androstenone and skatole that are detectable as taint, these levels are close to those suggested by in the USA (Xue, Dial, & Xue, 1997) of 1.0 and 0.25 μg/g and the European Union (Bonneau, Cook, Bonneau, Lundstrom, & Malmfors, 2000) of 1.0 and 0.22 μg/g for androstenone and skatole, respectively. Against these thresholds, the immunocastration vaccine was 99% and 100% effective in suppressing skatole and androstenone, respectively.

Apart from the effects of immunocastration on boar taint compounds, there is now evidence that pork from immunocastrated male pigs has higher marbling levels and lower surface exudate compared to pork from entire male pigs (D'Souza, Hennessy, Danby, McCauley, & Mullan, 2000). Also, pork from entire male pigs tended to have poorer odour compared to pork from either barrows or immunocastrates, with the latter having the highest overall acceptability (Table 7; D'Souza, Hagan, Hooper, Nicholls, & Mullan, 1999). In addition, pork from barrows and immunocastrated male pigs had a higher acceptability than that from gilts, although the differences were not as great in animals treated with pST or fed diets containing CLA (D'Souza & Mullan, 2002). Unfortunately, no entire boars were included in this latter study to determine whether immunocastration may offer a means of ameliorating the effects of pST on intramuscular fat and juiciness. The immunocastration vaccine approach has been included in these discussions because it can increase feed intake by up to 35% in the period from 2 to 4 weeks after the second injection (Oliver et al., 2003) with no change in feed efficiency and may offer a means of enhancing intramuscular fat. In boars treated with pST there is usually a reduction in feed intake, which no doubt contributes to the reduction in intramuscular fat. However, the reduction in feed intake in pigs treated with pST is negated by immunocastration (McCauley et al., 2003; Oliver et al., 2003).

Table 6
Effect of sex, age at vaccination and immunocastration vaccine on plasma testosterone, testes weight at slaughter and fat androstenone and skatole at slaughter (Dunshea et al., 2001)

	Early[a]			Late[b]		
	Boar	Immuno-castrate	*P*-value	Boar	Immuno-castrate	*P*-value
Plasma testosterone (nM)						
Secondary dose	13.7	12.7	NS	6.61	8.27	NS
Secondary dose + 2 weeks	8.52	0.51	<0.001	7.03	0.54	<0.001
Secondary dose + 4 weeks	10.5	1.16	<0.001	8.26	0.62	<0.001
Testes weight (g)	421.6	182.6	<0.001	509.6	254.4	<0.001
Fat androstenone (μg/g)	1.21	0.160	<0.001	1.05	0.126	<0.001
Fat skatole (μg/g)	0.133	0.068	<0.001	0.095	0.056	<0.001

[a] Pigs received primary vaccination, secondary vaccination and were slaughtered at 15, 19 and 23 weeks of age, respectively.
[b] Pigs received primary vaccination, secondary vaccination and were slaughtered at 18, 22 and 26 weeks of age, respectively.

Table 7
The effect of sex and immunocastration on eating quality of pork loin steaks (D'Souza et al., 1999b)

Sex	Boar	Barrow	Immunocastrate	LSD[b]	*P*-value
Odour[a]	56	62	62	6.13	0.093
Flavour[a]	58	62	66	7.01	0.101
Tenderness[a]	52	59	62	7.44	0.016
Juiciness[a]	60	59	64	7.05	0.304
Overall acceptability[a]	58	62	67	6.41	0.025

[a] Acceptability score (line scale) for all attributes, 0 = dislike extremely and 100 = like extremely.
[b] Least significant difference.

6. Dietary additives

6.1. Conjugated linoleic acid

Conjugated linoleic acid is a mixture of positional and geometric isomers of linoleic acid with conjugated double bonds located at positions 7,9-, 8,10-, 9,11-, 10,12- or 11,13- on the carbon chain with a number of biological effects. Dietary CLA is normally supplemented as a mix of these isomers with the predominant isomers being the *cis*/*trans*-9,11 and the *trans*/*cis*-10,12 isomers. There is extensive literature that suggests that the *cis*/*trans*-9,11 has anti-cancer and other positive health properties (Pariza, Park, & Cook, 2001; Whigham, Cook, & Atkinson, 2000) while the *trans*/*cis*-10,12 isomer is thought to cause a reduction in lipid deposition in growing animals (de Deckere, van Amelsvoort, McNeill, & Jones, 1999). Dietary CLA supplementation increases live weight gain, feed efficiency and lean tissue deposition and decreases fat deposition in pigs (Ostrowska, Muralitharan, Cross, Bauman, & Dunshea, 1999; Ostrowska et al., 2003b). Dietary CLA supplementation also decreased back fat thickness in most studies (D'Souza & Mullan, 2002; Dunshea et al., 2002b; Thiel, Sparks, Wiegand, Parrish, & Ewan, 1998) although this is not always the case (Dunshea et al., 2002b; Gatlin, See, Larick, Lin, & Odle, 2002; Lauridsen, Mu, & Henckel, 2005). As well as being dose dependent, the reduction in back fat depth in response to supplemental dietary CLA also appears to be related to the initial back fat of the control pigs. Data on the effect of CLA on back fat measured off the midline (either P2 or fat depth at the 10th rib) from a number of studies has been related to the back fat in the control animals (Fig. 1). It is apparent from this relationship that the greater the initial back fat depth the greater the reduction in back fat in response to dietary CLA supplementation (Fig. 1). Therefore, dietary CLA may be more efficacious in decreasing carcass fat in gilts and barrows and pigs of a fatter genotype than it may be in lean boars of an improved genotype. Consequently, the use of dietary CLA may be limited in the genotypes currently being used commercially unless it's use can confer some other positive attributes such as improved meat quality or processing properties. Alternatively, if dietary CLA supplementation can provide a means of improving the fatty acid profile of pork then it offers the potential to develop a value-added pork product for the functional food market.

A number of studies have been conducted to investigate the effect of dietary CLA on pork quality and in general effects have been relatively subtle with few significant effects being seen. However, when the data from these recent studies are collated, some small but consistent responses become apparent (Table 8). For example, in virtually every study there is a reduction in back fat

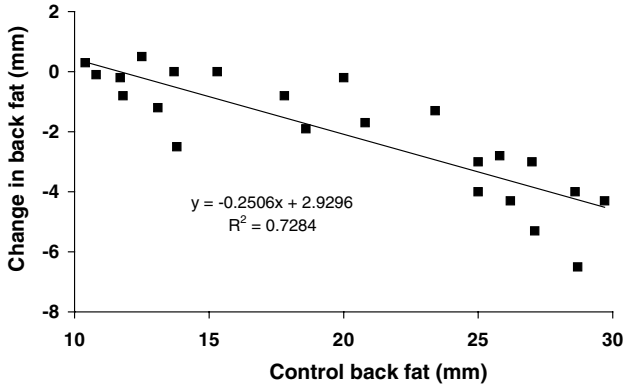

Fig. 1. Relationship between magnitude of the effect of dietary CLA on fat back depth measured at either the last rib (P2) or the tenth rib and fat back depth in the control pigs. No correction made for genotype, sex, length of treatment or dose or type of CLA. Where dose response studies were conducted, the average value was used.

although, as mentioned before, the magnitude of this reduction is dependent upon the initial back fat. To provide some statistical rigour to these responses the collated data were then subject to a meta-analysis (Table 9). This analysis shows that carcass back fat is decreased on average by about 6% (1.2 mm), but intramuscular fat and marbling are increased by 7% and 11%, respectively. Generally back fat and intramuscular fat move in the same direction so these observations are important given that there is a belief that the desire to reduce back fat has resulted in a reduction in intramuscular fat and hence eating quality. Despite the increased intramuscular fat and marbling, there are significant reductions in consumer perception of flavour (−3%), juiciness (−12%) and tenderness (−2.5%) although there are still limited consumer data. The decrease in tenderness is consistent with a 0.3 kg (+6%) increase in shear force, although there is no effect of CLA on firmness of the loin. There appears to be no effect of dietary CLA on pHu of the loin, whereas drip loss is reduced by approximately 5%. There are some slight but significant increases in L^* and a^* colour values indicating an increase in lightness and redness of the loin but no effect on b^* colour value.

Dietary CLA supplementation also results in modified fatty acid composition in pig tissue (D'Souza & Mullan, 2002; Eggert, Belury, Kempa-Steczko, Mills, & Schinckel, 2001; Joo, Lee, Ha, & Park, 2002; O'Quinn et al., 2000; Ostrowska et al., 2005; Ramsay, Evock-Clover, Steele, & Azain, 2001; Wiegand, Parrish, Swan, Larsen, & Baas, 2001; Wiegand, Sparks, Parrish, & Zimmerman, 2002). Dietary CLA is incorporated into adipose tissue and to a lesser extent into intramuscular fat in a dose dependant manner in pigs (Eggert et al., 2001; Ostrowska, Cross, Muralitharan, Bauman, & Dunshea, 2003a), which offers the opportunity to improve the amount of CLA in fat. Although the concentration of individual CLA isomers increases with the

Table 8
Effect of various doses of CLA on aspects of pork meat quality (data are expressed as percentage change from the respective control values)

Reference	Dose (%)	Muscle[d]	Sex	Breed[e]	Backfat	IMF[a] (%)	Marbling	Consumer panel scores[b]			Firmness	Shear (kg)	pHu[f]	Drip loss (%)	Colour[c]		
								Flavour	Juiciness	Tenderness					L^*	a^*	b^*
Thiel-Cooper et al. (1998)	0.12	LD	Barrow	Crossbred	−18.2		0.0	−5.4	−13.1	−5.3	4.6				−2.6	17.5	−6.2
	0.25				−18.2		5.8	−6.3	−3.5	3.1	−9.5				1.9	100.0	0.9
	0.50				−8.7		10.8	−3.7	−7.9	−4.1	−12.2				0.7	92.5	−2.6
	1.00				−10.1		−10.4	−1.7	−6.1	3.9	−27.9				2.7	268.8	1.7
Dugan and Aalhus (1999)	2.00	LT	Mixed	Crossbred		24.6	11.3	1.8	0.2	2.9		−1.2		11.5	0.8		
O'Quinn et al. (2000)	0.50	LD	Barrow	PICL326xC22	−6.5		13.7				−0.9			−6.6	3.4	11.1	12.7
Eggert et al. (2001)	1.00	LD	Gilt	LWx[Lx(DxLW)]	−8.5						1.3		1.1	−7.1			
Wiegand et al. (2001)	0.75	LD	Barrow	Crossbred	−5.6	17.8	15.7	−7.6	−12.7	−12.9	18.6				7.6	−8.4	7.5
	0.75				−14.7	19.2	24.6	−0.8	4.4	3.8	17.2				1.9	5.8	1.6
	0.75				−5.6	16.6	37.0	−6.8	−9.7	−2.5	50.0				4.7	−2.1	4.1
D'Souza and Mullan (2002)	0.50	LD	Gilt	50% D	−4.9	24.0		18.4	−13.0	15.2			1.6	−17.6	−4.8		
	0.50				−5.6	33.3		−21.9	−33.3	−33.8			1.2	9.2	0.8		
	0.50				−4.3	−17.1		−19.0	−32.7	−37.5			−1.4	−12.6	−1.5		
	0.50			25% D	−6.3	0.0		−7.4	−14.0	−11.8			−0.5	6.0	4.2		
	0.50				−6.3	4.3		−3.3	−15.7	−5.5			1.5	−8.8	1.9		
	0.50				−11.9	9.1		−6.8	−19.3	−10.3			3.5	−25.7	−8.3		
Dunshea et al. (2002)	0.15		boar	LWxL	−6.8												
	0.15		Gilt		−9.2												
	0.18	LD	boar		−3.9								0.7	−8.8	−1.6	4.2	−47.6
	0.18		Gilt		5.6								0.4	8.3	−1.8	−2.0	−20.0
Wiegand et al. (2002)	1.25	LD	Mixed	(YxL)x(DxH)	−14.5	9.5	6.9				−3.8						
	1.25				−14.5	18.4	15.2				3.8						
	1.25				−20.6	25.9	13.2	1.5	−1.9	−6.7	5.5		0.0		1.3	6.0	3.3
Gatlin et al. (2002)	1.0	LD	Gilt	Lean	−2.2		14.9										
	1.0				−2.0		35.3										
	1.0				−3.5		6.2										
Tischendorf et al. (2002)	2.00	LD	Mixed	Px(LxLW)	−7.4	4.1		−3.3	−2.6	6.5		8.8	−1.6	7.0	0.4	0.0	0.0
Joo et al. (2002)	1.00	LD	Gilt	LxLWxD		−2.0							1.6	−5.1	−3.2	16.8	−3.5
	2.50					12.3							0.0	−1.4	−1.1	17.9	4.8
	5.00					44.3							0.5	−14.6	−5.7	0.2	−8.3
Migdal et al. (2004)	2.00	LD	Barrow	Px(LxLW)	−5.4	8.5		4.5	−2.2	−0.4			−1.6		11.8	−14.7	7.8
Ostrowska et al. (2005)	0.13	LD	Gilt	LxLW	−7.1	1.4	−5.3				14.9	1.1	−0.2	13.0	−1.6		
	0.25				−17.8	−19.3	−2.6				2.1	0.9	0.0	15.3	−1.4		
	0.50				−17.4	−19.5	0.0				17.0	5.8	0.2	3.8	0.8		
	0.75				−19.1	−10.5	2.6				2.1	−0.9	0.4	14.3	−0.6		
	1.00				−23.7	−42.0	−10.5				10.6	9.7	−0.2	8.7	−1.0		
Sun et al. (2004)	2.00	LD	Barrow	DxLxLW	−5.8	12.5								−5.8			
	4.00				−8.7	29.2								−5.8			
Lauridsen et al. (2005)	0.50	LD		LxYxD	−2.4	−5.8							0.7	−10.1			
	0.50				3.3	−0.2							−0.5	11.4			

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] LD – *longisimus dorsi*, LT – *longisimus thoracis*.
[e] Y – Yorkshire, LW – Large White, L – Landrace, D – Duroc, P – Pietran, H – Hampshire, PIC – Pig Improvement Company.
[f] pH taken 24 h after slaughter.

Table 9
Meta–analysis of data collated from the studies presented in Table 8 for the effect of CLA on meat quality (data are from studies where meat quality was measured in muscles from the loin)

	Backfat (mm)	IMF[a] (%)	Marbling	Consumer panel scores[b]			Firmness	Shear (kg)	pHu[d]	Drip loss (%)	Colour[c]		
				Flavour	Juiciness	Tenderness					L^*	a^*	b^*
Control	20.4	2.80	1.96	59.2	60.6	65.2	2.33	4.81	5.47	5.62	51.26	7.02	8.52
CLA	19.2	3.00	2.18	57.5	53.6	63.6	2.40	5.11	5.48	5.32	51.91	7.39	8.52
% Change	−5.9	7.2	11.3	−2.8	−11.6	−2.5	3.0	6.2	0.2	−5.3	1.3	5.3	0.0
SED[e]	0.0004	0.004	0.0004	0.0008	0.0012	0.0014	0.051	0.0005	0.010	0.0006	0.0004	0.0004	0.0013
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.17	<0.001	0.32	<0.001	<0.001	<0.001	0.99

[a] Intramuscular fat.
[b] Consumer panel scores all adjusted to a scale of 1–100 before analyses.
[c] CIE colour scale.
[d] pH taken 24 h after slaughter.
[e] Standard error of the difference.

level of dietary CLA, there is obviously some selectivity in the uptake or incorporation of certain isomers, especially the *cis*/*trans* isomers (Ostrowska et al., 2003a). These authors calculated transfer efficiencies for the individual isomers and showed that the *cis*/*trans*-9,11 isomer was most efficiently incorporated (46.4%) in subcutaneous adipose tissue, whereas in the intramuscular fat, the *cis*/*trans*-11,13 isomer was incorporated most efficiently (0.74%) (Ostrowska et al., 2003a). The preferential enrichment of *cis*/*trans*-9,11 is of particular value with respect to potential health benefits as there is extensive evidence showing anti-cancer properties of this CLA isomer (Pariza et al., 2001; Whigham et al., 2000). The *trans*/*cis*-10,12 isomer, which is thought to be responsible for the reduction in lipid deposition, was incorporated less efficiently, in both subcutaneous and intramuscular fat (13.31% and 0.31%, respectively), than the remaining isomers in the *trans*/*cis* group (Ostrowska et al., 2003a). The implications from these findings are that the levels of CLA can be increased in pig adipose tissue and intramuscular fat to levels similar to those reported for dairy products and beef (typically 2–24 mg/g of fat), which are currently the major sources of dietary CLA, providing approximately 70% and 25%, respectively of CLA intake in the USA (Ritzenthaler et al., 2001). Thus, there is a potential to substantially increase the level of CLA, particularly the *cis*/*trans*-9,11 isomer, which is more readily incorporated into animal fats, through supplementing CLA into animal diets and consequently increase CLA intakes in human diets.

There is also much potential to enrich the CLA content of meat from ruminant animals since CLA occurs naturally in ruminant fat. Trans-vaccenic acid and CLA are products of the normal biohydrogenation of linoleic acid to stearic acid, through trans-vaccenic acid in the rumen. Dietary trans-vaccenic acid is an important source of CLA since humans and other species have the capacity to produce CLA from trans-vaccenic acid. CLA and trans-vaccentic acid production can be further enhanced by a high pasture intake (Aurousseau, Bauchart, Calichon, Micol, & Priolo, 2004; Realini, Duckett, Brito, Dalla Rizza, & De Mattos, 2004) because pasture lipids are abundant in linolenic acid (Garton, 1960), a precursor of both CLA and trans-vaccenic acids. Also, dietary supplementation with fish oils can increase CLA and trans-vaccenic acid production, at least in milk (AbuGhazaleh, Schingoethe, Hippen, & Kalscheur, 2003; Offer, Marsden, Dixon, Speake, & Thacker, 1999; Shingfield et al., 2003), through reducing the ruminal conversion of trans-vaccentic acid to stearic acid (Griinari & Bauman, 1999). Feeding of rumen protected CLA also offers a potential means of increasing the CLA content of ruminant meat products (Gillis et al., 2004). The opportunities that exist for ruminant meats are to, first of all, position intramuscular fat as being excellent sources of CLA and polyunsaturated fatty acids and also to develop markets with products that are further enriched through dietary manipulation.

The effects of dietary CLA on the other fatty acid contents of muscle and fat also depends on the dietary fat that the CLA replaces, because some differences in the fatty acid profiles of the tissue lipids would be due to differences in the fatty acid profile of the diets. Therefore, care should be taken in interpreting effects of CLA supplementation on changes in the profiles of other fatty acids. Despite this caveat, it does appear that some changes in the fatty acid composition of porcine adipose tissue can be attributed to dietary CLA. For example, Ostrowska et al. (2003a) found that the concentrations of palmitoleic (16:1) and palmitic (16:0) acids in both intramuscular and subcutaneous fat increased in a linear fashion with increasing dietary CLA. This was clearly due to an effect of dietary CLA, since the level of dietary palmitic acid decreased with increasing dietary CLA as CLA replaced soy oil in their study (Ostrowska et al., 2003a). Palmitoleic acid was not detected in the diets, therefore, its origin was from desaturation of the respective saturated fatty acid, palmitic acid, which is in turn regulated by the fatty acyl-CoA Δ^9-desaturase complex. The Δ^9-desaturase enzyme complex is also responsible

for desaturation of stearic acid into oleic acid. In the study by Ostrowska et al. (2003a), the concentration of stearic acid was not affected by dietary CLA despite the levels decreasing as the CLA content of the diet increased. However, a significant reduction in oleic acid was detected despite similar levels found in all the six diets. Others have also reported a distinct shift toward lower oleic acid concentrations in pigs fed diets supplemented with CLA (Bee, 2000; Ramsay et al., 2001). This could be due to the depressed synthesis of oleic acid in the adipose tissue lipids, possibly due to decreasing stearoyl-CoA desaturase activity. The resulting increase in the ratio of saturated to unsaturated fatty acids is unfavourable since increased consumption of saturated fatty acids is also associated with increased risk of coronary heart disease. The calculated index of atherogenicity (Ulbricht & Southgate, 1991), which takes into consideration the protective and promoting properties of fatty acids, is also negatively affected by CLA supplementation (Ostrowska et al., 2003a). Therefore, applying nutritional techniques to increase the poly- and monounsaturated fatty acid content of pork to ameliorate for the effects of dietary CLA should be considered. It should also be borne in mind that index of atherogenicity was derived before the potential anti-atherogenic effects of CLA was suggested (Parodi, 2002). From a processing perspective though, the increased saturated fatty acid content and perhaps some of the physical properties of CLA itself makes for harder and firmer bellies that are easier to process (Eggert et al., 2001).

6.2. Magnesium

Magnesium (Mg) has a relaxant effect on skeletal muscle and has been shown to depress skeletal muscle activity by antagonising calcium, which is required for neurotransmitter release and muscle contraction. This reduces the secretion of neurotransmitters by motor-nerve impulses, which in turn reduces neuromuscular stimulation (Hagiwara, Fukuda, & Eaton, 1974; Hubbard, 1973). Studies have since shown that dietary magnesium supplementation alleviates the effects of stress by reducing plasma cortisol, norepinephrine, epinephrine and dopamine concentrations (Kietzmann & Jablonski, 1985; Niemack et al., 1979). Consequently, studies have been conducted to investigate the influence of dietary Mg supplementation on reducing the effects of stress and improving pork quality.

Numerous studies have shown that dietary Mg supplementation in pigs resulted in improved pork quality. In a long-term study, dietary Mg supplementation resulted in slight improvements in pork colour and initial pH (Otten, Berrer, Hartmann, Bergerhoff, & Eichinger, 1992), while short-term dietary magnesium supplementation increased initial pH and reduced % drip loss (Schaeffer, Murray, Tong, Jones, & Sather, 1993). In another short-term study, dietary magnesium aspartate supplementation at 3.2 g elemental Mg for 5 days pre-slaughter significantly improved pork quality in pigs by reducing drip loss and improving pork colour and muscle pH (Table 10; D'Souza, Warner, Leury, & Dunshea, 1998). There were no PSE carcasses in the magnesium supplementation treatment groups, irrespective of the type of pre-slaughter handling (D'Souza et al., 1998). Dietary supplementation using inorganic Mg sources such as MgSO4 and MgCl2 (D'Souza et al., 1999) and magnesium mica (Apple, Maxwell, deRodas, Watson, & Johnson, 2000) have also been shown to reduce drip loss, improve colour and reduce the incidence of PSE pork. The use of dietary organic magnesium supplementation as a viable method to improve meat quality in pigs was also validated under commercial conditions in Victoria, Australia (Hofmeyr, Dunshea, Walker, & D'Souza, 1999). Dietary magnesium supplementation was shown to significantly reduce the incidence of soft, exudative pork in all three replicates of the commercial validation study.

The use of dietary magnesium supplementation has been shown to improve objective measures of pork quality such as drip loss, colour and the incidence of PSE. However, there is no data relating the improvements in objective measures of pork quality with improved pork eating quality. As the relationship between low water holding capacity and increased meat toughness is well established (Lawrie, 1998), it is reasonable to assume that the reduced drip loss and the lower PSE % observed with dietary Mg supplementation could have a positive influence on the eating quality of pork.

Table 10
The effect of dietary magnesium aspartate (MgAsp) supplementation and pre-slaughter handling on meat quality indicators of the *longissimus thoracis* muscle 24 h post-slaughter (D'Souza et al., 1998)

Diet (D):	Control		MgAspartate		Significance[a]
Handling (H):	Minimal	Negative	Minimal	Negative	
Ultimate pH	5.48	5.51	5.61	5.57	D^{***}
Surface lightness L^*	48.7	49.1	45.2	47.4	D^{***}
Drip loss (%)	4.0	6.4	3.5	3.5	D^{***}; H^{**}
PSE (%)	8	33	0	0	D^{**}

Negative handling was induced by use of electrical prodders.
[a] $^{**}P < 0.05$; $^{***}P < 0.01$.

Magnesium supplementation (MgO) has also been shown to reduce the loss of glycogen from muscle in Merino lambs during the post farm period leading up to slaughter (Gardner, Jacob, & Pethick, 2001). This has lead to some supply chains in Australia insisting on high-energy rations containing supplemental MgO being fed to Merino lambs in the 2–4 weeks pre-slaughter. This logic is based on the accepted fact that the Merino breed on average, has a higher incidence of dark cutting (or high pHu meat) due to a greater stress sensitivity and so increased rate of glycogen loss during the post farm gates stressors that occur immediately pre-slaughter (Gardner, Kennedy, Milton, & Pethick, 1998).

6.3. Selenium

The beneficial effects of selenium supplementation on growth and carcass quality traits in pigs, poultry and cattle are significant and have been reviewed extensively (Close, 1998, 1999; Mahan, 1999). Although the use of inorganic selenium (sodium selenite) in livestock feeds has resulted in tremendous productivity gains, recent research has shown that the use of organic selenium has additional benefits that surpass that of selenite. Results from an experiment evaluating the efficacy of selenite at 0.1 and 0.3 ppm selenium in pigs indicate that yeast-bound selenium supplementation resulted in higher selenium levels in the loin muscle at both 0.1 and 0.3 ppm levels compared to pigs fed the inorganic selenite (Mahan & Kim, 1996).

Selenium, an essential constituent of the antioxidant enzyme glutathione peroxidase (Rotruck et al., 1973), has also been show to significantly improve meat quality by decreasing cell membrane oxidation leading to reduced muscle drip loss. Also, mortality and drip loss was lower when organic selenium rather than selinite was fed to the broilers (Edens, 1996). However, the influence of selenium supplementation on reducing drip loss in pigs is somewhat less clear-cut compared to the reduced drip loss observed in broilers. Studies by Muñoz and his co-workers have shown that dietary yeast-bound selenium supplementation in conjunction with other antioxidants such as vitamin E and C reduced drip loss from the loin muscle of pigs compared to pigs fed a control diet (Table 11; Lyons, 1997). Dietary selenite supplementation resulted in higher drip loss levels and tended to have paler meat for the loin muscle compared to pigs fed the control diet or diets containing yeast-bound selenium (Mahan, Cline, & Richert, 1999).

Selenium deficiency has also been linked with human heart and cellular diseases. Some researchers go as far as suggesting selenium supplementation in humans may prevent some forms of cancer and may also boost the immune status. Hence selenium enriched foods are well placed as a functional food and one on which Korean pork producers have recently capitalised on. Korean pork producers are currently incorporating yeast-bound selenium in pig diets and marketing the selenium-enriched pork as a functional food benefiting human health and nutrition. Consumer feedback also indicates that Koreans regard the selenium-enriched product as being juicier and having better appearance (D.N. D'Souza, personal communication).

6.4. Vitamin E

Dietary vitamin E supplementation (*all-rac*-tocopheryl acetate) in meat animals is perhaps the best known method of improving meat quality by reducing lipid and myoglobin oxidation in fresh meat and meat products. Fresh meat is stored for a very short duration and oxidation of the pigment in meat to a brown colour limits the display life and costs the meat industry millions of dollars per year. In Australia processed meat products are often made from frozen meat that has been stored for extended periods hence making lipid oxidation one of the major quality concerns affecting the shelf life. There are a range of factors that contribute to the deterioration in quality and loss of shelf life as a consequence of lipid and myoglobin oxidation occurring in meat and meat products. These factors include the temperature and duration of storage, the availability of oxygen, the state and content of prooxidants (Fe, myoglobin), level of antioxidants present in muscle (-tocopherol and enzymes such as glutathione peroxidase, superoxide dismutase and catalase) and the composition and amount of muscle lipids.

The major thrust of research involving dietary supplementation of vitamin E has been concerned with its ability to delay lipid oxidation in muscle foods derived

Table 11
Effect of dietary antioxidant[a] supplementation on drip loss % of the *longissimus dorsi* muscle of pigs (Lyons, 1997)

	Group	Time post-mortem (h)			
		24	48	72	120
Whole muscle	Control	2.0	2.7	3.5	4.8
	Treatment	1.6	2.3	3.0	4.1
Steaks	Control	4.7	6.7	8.8	10.7
	Treatment	3.6	5.2	7.5	9.5

[a] 0.1 ppm yeast-bound selenium (SelPlex 50), 20–100 kg body weight; 50 ppm vitamin E, 20–100 kg body weight; 670 ppm vitamin C, 80–100 kg body weight.

from non-ruminant species (Liu, Lanari, & Schaefer, 1995). The effects of supplementation with vitamin E on meat quality were first reported to reduce lipid oxidation in meat from poultry (Bartov, Basker, & Angel, 1983; Marusich et al., 1975) and pigs (Buckley et al., 1989; Tsai, Wellington, & Pond, 1978). A positive effect of feeding vitamin E to beef cattle on meat colour and then on metmyoglobin accumulation in beef meat were reported (Faustman, Cassens, Schaefer, Buege, & Scheller, 1989a; Faustman et al., 1989b) followed by an improvement in retail shelf-life of 1.6–3.8 days in the beef rump and 2.5–4.8 days in the beef loin (Arnold et al., 1992). Ground beef becomes brown and rancid more quickly then unground beef, because grinding exposes more surface to air and microbial contamination. Pigment and lipid oxidation in both fresh and frozen ground beef is delayed if the cattle have been supplemented with vitamin E (Faustman et al., 1989b).

The use of vitamin E supplementation in pig diets to enhance meat quality have been incorporated at levels ranging from 40 to 700 mg *all-rac*-tocopheryl acetate/kg feed. The improvements in meat quality include reduction of thiobarbituric acid reactive substances (TBARS, an indicator of rancidity and off-flavours) scores below 0.50 mg malondialdehyde equivalents (MDA eq.), which is the borderline level for detection of rancidity and off-flavours by trained sensory panellists. Results from a few recent studies using vitamin E supplementation in pigs to improve meat quality are outlined in Table 12. Generally, vitamin E supplementation at doses of 200 mg *all-rac*-tocopheryl acetate/kg of pig feed for periods ranging from 84 to 130 days preslaughter resulted in significantly reduced muscle oxidation levels, improved colour and reduced drip loss of fresh pork and pork products. Vitamin E supplementation at higher doses of 700–800 mg *all-rac*-tocopheryl acetate/kg of pig feed for shorter periods (7 days prior to slaughter) reduced lipid oxidation in the meat but had limited success in improving the colour and drip loss of pork and pork products. The effect of vitamin E supplementation on muscle colour is perhaps more evident in species that have higher levels of myoglobin. Hence the influence of vitamin E supplementation on colour stability is minimal in pork and poultry products while having a significant effect in beef (Chan et al., 1996) and lamb (Guidera, Kerry, Buckley, Lynch, & Morrissey, 1997).

6.5. Chromium

Chromium supplementation in pig diets was found to improve feed efficiency, lean meat yield and reduce backfat thickness (Page, Southern, Ward, & Thompson, 1993). However, limited research has been conducted on the effects of dietary chromium supplementation on pork quality. In one study, dietary chromium propionate supplementation in finisher pigs increased the level of marbling and reduced purge in the loin muscle (Matthews, Higbe, Southern, Coombs, & Bidner, 1999). However, the reasons for the increase in marbling and the reduced purge loss are unknown. In contrast, dietary chromium picolinate supplementation had a detrimental effect on pork colour in another study (O'Quinn et al., 1998). As it is possible that the source of chromium may be responsible for the varied effects of chromium supplementation on pork quality, they should be further investigated. Dietary chromium supplementation is another management strategy to reduce carcass fatness that is widely used by pork producers. Work in sheep has shown that organic chromium supplementation results in reduced subcutaneous fat depth with no effect on muscle glycogen (Gardner et al., 1998).

Table 12
The influence of vitamin E supplementation on pork quality traits of the *longissimus* muscle

Meat product	Vitamin E[a] (mg/kg feed)	Reduced lipid oxidation[b] (%)	Improved colour[c] (%)	Improved drip loss[d] (%)	Reference
Fresh pork					
Steaks	200	73	106		Lanari et al. (1995)
Steaks	100	76	NS		Monahan et al. (1992)
	200	77	44		
Steaks	100	68	33	NS	Asghar et al. (1991)
	200	80	43	40	
Processed pork					
Raw patties	100	39			Asghar et al. (1991)
	200	70			
Raw patties	200	64			Monahan et al. (1990)
Pre-cooked patties	200	20			Monahan et al. (1990)
Bacon	800	NS			Buckley and Connolly (1980)

[a] *All-rac*-α-tocopheryl acetate.
[b] Decrease in TBARS numbers in supplemented group relative to control group.
[c] Increase in *a*-values (red colour) in supplemented group relative to control group.
[d] Decrease in drip loss % in supplemented group relative to control group.

6.6. Betaine

Betaine is an active methyl donor with a lipotropic effect (Barak, Beckenhauer, Junnila, & Tuma, 1993). When incorporated into pig diets, betaine has been reported to improve growth performance by reducing the maintenance energy requirement of the animal, perhaps by reducing the need for ion pumping involved with maintaining intracellular osmolarity (Schrama, Heetkamp, Simmins, & Gerrits, 2003). In addition, dietary betaine has been reported to increase protein deposition and carcass leanness (Fernandez-Figares et al., 2002; Matthews, Southern, Bidner, & Persica, 2001a; Suster et al., 2004b) and to decrease back fat (Cadogan, Campbell, Harrison, & Edwards, 1993). There is evidence that betaine has a more pronounced effect when dietary energy is limiting (Suster, Leury, Hofmeyr, D'Souza, & Dunshea, 2004a) and so it offers a means of improving meat quality through ensuring the provision of additional energy. The additional energy may improve or maintain meat quality in conditions where performance may be limited by energy intake such in genetically improved pigs housed under commercial conditions, in pigs treated with metabolic modifiers such as pST (Suster et al., 2004b) or during heat stress (B.P. Mullan, personal communication). Despite betaine being used quite widely in animal production, there have been relatively few studies investigating effects of betaine on meat quality. In one study, betaine supplementation resulted in improved carcass quality and improved subjective colour and marbling scores (Xu, Huai, & Wang, 1999). Pork from pigs fed betaine was darker and had increased pHu and thaw loss and decreased cooking loss in another study (Matthews, Southern, Higbie, Persica, & Bidner, 2001b). In a companion study, fresh pork from pigs fed betaine had increased initial pH and decreased drip loss (Matthews et al., 2001a). Cooking loss and total loss from frozen pork were decreased in pigs fed betaine with adequate pen space but increased in pigs fed betaine with inadequate pen space. Shear force was not significantly altered in either of these studies (Matthews et al., 2001a; Matthews et al., 2001b). In another study there was no effect of betaine supplementation on objective meat quality (Overland, Rorvik, & Skrede, 1999). Although it is difficult to make any conclusions at this stage on the effects of betaine on meat quality, there do appear to be some benefits in water-holding capacity although there may be some environmental impacts on these qualities.

7. Conclusions

A number of technologies that increase feed efficiency and lean tissue deposition while decreasing fat deposition have been developed in an effort to improve profitability of animal production, with some of these being used commercially. As a result of these technological advancements, producers have benefited because of improved production efficiencies while meat packers have improved processing efficiencies because of increased lean meat yield. An additional driver has been the desire to reduce the fat content of meat and so reduce the fat intake of consumers. However, there have been some concerns that the focus on increasing production efficiency and lean meat yield has been to the detriment of meat quality. This also appears to be the case for. When the data from the literature are collated and subject to meta-analyses, it appears that conservative use of the major classes of metabolic modifiers, somatotropin, approved β-agonists, conjugated linoleic acids and the anabolic estrogenic and androgenic implants will result in a 5–10% (0.3–0.5 kg) increase in shear force with a similar reduction in perception of tenderness. However, it should be borne in mind that the magnitude of these increases are similar to those observed with similar increases in carcass leanness obtained through other means (e.g. increased dietary protein, genetic selection for lean growth) and may be an inherent consequence of the production of leaner meat. To counter this, there are some other metabolic factors, such as immunocastration vaccine, and dietary additives, such as CLA or betaine, that offer some potential to improve meat quality. Some technologies will decrease IM fat (e.g. somatotropin, HGPs) whereas others have no effect (e.g. ractopamine) or increase IM fat (e.g. dietary CLA, immuncastration). It is possible that these latter technologies can be used on their own or in conjunction with somatotropin, approved β-agonists and anabolic implants to maintain or improve meat quality.

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