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Proceedings

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Dummerstorf, 1995

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PIGS - RELATION TO MEAT QUALITY - Essén-Gustavsson, Birgitta

urn:nbn:de:hbz:38m:1-30204

EFFECTS OF PHYSICAL STRESS ON MUSCLE FIBRE CHARACTERISTICS IN PIGS - RELATION TO MEAT QUALITY

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Introduction

Skeletal muscles consist of fibres having varying contractile and metabolic characteristics. Histochemical stains for myosin-ATPase identify slow contracting type I and fast contracting type IIA and IIB fibres (Brooke and Kaiser, 1970). Histochemical stains for oxidative and glycolytic enzymes, capillaries, glycogen and lipid content provide information on the metabolic profiles of fibres. In skeletal muscle of pigs, all types of fibres contain glycogen but types I and IIA have a greater lipid content and oxidative capacity and more capillaries per fibre than type IIB fibres (Essén and Lindholm, 1981, Essén-Gustavsson et al., 1992, Essén-Gustavsson et al., 1994). Capillarization of a muscle is of great importance not only for delivery of oxygen and substrates to each fibre but also for elimination of waste products such as lactate. Considerable variations do occur in fibre type composition and metabolic profile of each fibre type in different species and among muscles depending on function. From studies in humans and horses it is known that type I fibres get recruited with light and with prolonged exercise, while with increasing intensity and duration type IIA and IIB fibres become recruited (Saltin and Gollnick 1983, Valberg, 1986).

Not only genetic factors but also environmental factors such as increased or decreased physical activity level, appear to be major determinants of muscle fibre characteristics in the animal kingdom. Studies on trained athletes and on physically active animals such as racehorses, greyhounds and wild animals indicate that the most common adaptation to physical activity is an increase in type IIA/IIB ratio, oxidative capacity and capillary density (Saltin and Gollnick, 1983, Essén-Gustavsson, 1986).

A positive effect of an increased oxidative capacity and capillarization in muscle is a greater resistant to fatigue. Glycogenolysis is lower and less lactate is produced when trained pigs perform similar type of exercise as untrained (Essén-Gustavsson and Lindholm, 1983).

It is well known that muscle performance is not un-limited and that fatigue develops, both in connection with brief intense exercise when the glycogenolysis rate is high and lactate accumulates, and also with endurance type of exercise when the glycogenolysis rate is limited by lack of the substrate glycogen. A similar metabolic response in muscle can be observed when pigs are slaughtered. It is known to give rise to poor meat quality e.g. PSE (pale, soft,

exudative) and DFD (dark, firm, dry) meat. PSE meat is associated with excessive glycogenolysis and lactate formation and lowering of pH at slaughter, whereas DFD meat is associated with low glycogen levels, low lactate concentration and high pH. The proportion of fibre types in a muscle, their metabolic profile and recruitment pattern are probably important factors that determine the extent of glycogenolysis and lactate formation at slaughter.

Effect of physical activity on muscle fibre characteristics

The domestic pigs of today are almost totally physically inactive, as they spend most of their lives indoors, confined in small pens. Through selection and intensive breeding, modern pig breeds are induced to develop rapid muscle growth. Many of their muscles contain a large proportion of large, type IIB fibres, have low oxidative capacity and a low capillary density (Essén et al., 1980, Bader, 1982, Kiessling and Hansson, 1983, Essén-Gustavsson et al., 1992, Karlsson et al., 1993). Many muscles in the pig have a unique distribution of fibres with type I fibres grouped in clusters, type IIA fibres in their close vicinity, and these are surrounded by type IIB fibres (Fig1). Mean fibre areas increase with the age of the animal and most in those fibres having the lowest oxidative capacity (Cooper et al., 1970, Van Den Hende et al., 1974, Klosowska et al., 1985). It has also been shown that fibre area increases with intensity of selection in domestic pigs, while the proportion of oxidative fibres decreases (Rede et al., 1986). The rapid drop in pH and reduced water holding capacity in intensely selected pigs such as Yorkshire and Landrace is said to be related to the large proportion of non-oxidative fibres in these breeds (Rede et al. 1986).

Wild pigs, free ranging and therefore having unlimited physical activity during their lifetime, have a higher type IIA/IIB ratio and greater oxidative capacity in most fibres, in comparison with domestic pigs (Rahelic and Puac, 1980, Bader, 1983, Essén-Gustavsson and Lindholm, 1984, Szentkuti and Schlegel, 1985). After the movement of wild pigs was restricted for ten weeks, the proportion of type IIA fibres was still high, while that of type IIB was low, when compared with domestic pigs that had been allowed exercise for 10 weeks (Szentkuti and Schlegel, 1985). The fibre area ratio of type II/I was reduced by exercise and increased by restricted movement of the pigs. Fibre type composition would thus appear to be strictly governed by genetic factors. Free ranging pigs (several generations), crossbreeds of Yorkshire, Landrace, Duroc and Hampshire, have a higher ratio of type IIA/IIB fibres than have domestic pigs (unpublished results). It may be that adaptation becomes evident in different fibre types only after long-term and/or intense exposure to physical activity.

In studies on pigs, breed differences are often evident and one question is whether such variations could affect the proportion of fibre types and the oxidative capacity of muscles. Hampshire was shown in a small material to have a slightly higher oxidative capacity than both Yorkshire and Landrace (Table 1, Essén-Gustavsson and Fjelkner-Modig, 1985). A more recent study on a much larger material has shown that Hampshire pigs also have a higher

capillary density and a greater proportion of type I fibres and a lower proportion of type IIB fibres than either Landrace or Yorkshire and their crossbreeds (Ruusunen, 1994). With the exception of the difference in Hampshire, most breeds and crossbreeds used in pig production appear to have similar muscle characteristics (Essén-Gustavsson and Fjelkner-Modig, 1985, Essén-Gustavsson et al., 1992, Karlsson et al., 1993, Ruusunen, 1994). Individually differences are usually greater within than between breeds.

Adaptation in a muscle as a consequence of exposure to physical activity takes place only in those muscles involved in the work and then only in those fibres that get recruited. Intensity and duration of exercise and the fibre recruitment pattern are therefore important factors to consider when discussing the effects of physical stress on muscles. When pigs were exercised on a treadmill for 12 weeks, oxidative capacity was markedly increased in m. biceps but not in m. longissimus (Table 1, Essén-Gustavsson et al., 1988). This is no doubt due to the fact that m. longissimus is less active during running as is m. biceps. In another study, pigs were allowed moderate exercise indoors during the fattening period by running/walking 5 days a week in the piggery (Enfält et al., 1993). In these pigs the oxidative capacity of both m. longissimus and m. biceps was similar to that in pigs that were kept in pens. The intensity of voluntary exercise was probably too low for any adaptation to have occurred in muscle. But when domestic pigs that had been kept outdoors in rough terrain during the fattening period were compared with pigs kept in pens, a slight increase was found in the former regarding oxidative capacity in both m. longissimus and m. biceps (Table 1, Essén-Gustavsson and Jensen-Waern, 1993). The former no doubt used all their musculature and more often, as they were at liberty to walk and run about and root in the soil. This is probably an important reason why in wild boars and free ranging pigs of various crossbreeds (YxLxDxH) the oxidative capacity of both m. longissimus, m. biceps, m. gluteus and m. semitendinosus is greater than that of these muscles in domestic pigs (Table 1). Most of the fibres have a great oxidative capacity (fig. 1). M. longissimus is a muscle having a low oxidative capacity in comparison to both m. gluteus, m. biceps and m. semitendinosus (Table 1). Exposure to physical activity is an important factor for increasing oxidative capacity in muscles (Table 1).

Physical stress and metabolic response in muscle fibres

In connection with transportation and slaughter, pigs usually undergo handling that must be regarded as both emotionally and physically stressful. They can be forced into unaccustomed physical activity; mixing with unfamiliar animals can result in serious fights and emotional stress. Their response to such stress-situations is believed to be associated with activation of the sympathetic nervous system and an increase in catecholamine levels which stimulates glycogenolysis. Catecholamine levels in pigs are known to be increased by the stress of transportation (Dalin et al., 1993). In pigs carrying the halothane genotype, catecholamine levels were shown to increase markedly on exposure to experimental stress (Häggendal, et al.,

1988). Pigs carrying the halothane genotype are therefore likely to react more strongly to stress-situations prior to slaughter. It is known that exposure of pigs to stressful events can result in death, in many cases correlatable to the porcine stress syndrome and the sensitivity to halothane induced malignant hyperthermia. The porcine stress syndrome appears to follow from a sudden sustained rise in the concentration of calcium due to an abnormality in the calcium release channel of skeletal muscle sarcoplasmic reticulum. An increased calcium level in the muscle fibre will stimulate contractility and glycogenolysis. It has been shown that halothane sensitive pigs have more glycogen depleted type IIB fibres than type IIA and I fibres on exposure to halothane anaesthesia (Essén and Lindholm, 1981).

In muscle samples taken immediately after slaughter, carriers of the halothane genotype have not only a lower concentration of glycogen and higher concentration of lactate and lower pH but also lower ATP and CP and higher IMP and ammonia concentrations than non-carriers (Table, 2, Essén-Gustavsson et al., 1991, 1992). It was notable, that high IMP concentrations were only observed when muscle pH was below 6.4. All these pigs had been raised under similar conditions throughout life, fed the same diet and been handled and transported in the same manner up to slaughter. Thus they had been exposed to the same types of physical stress prior to slaughter, with a 2 h lairage, no restrainer and electrically stunning on the floor. Hence the most important factor for the markedly differing metabolic responses seen in these pigs would appear to be their genotype. The fact that carriers of the halothane genotype have twice as many glycogen-depleted type IIA and IIB fibres, larger mean fibre areas and lower capillary density, than non-carriers, is probably a factor contributing to the differing metabolic responses observed in these pigs (Essén-Gustavsson et al. 1992, Fiedler et al. 1993). A sparse capillary density may restrict oxygen supply to the fibres and also hinder the removal of lactate and other waste products and of excess heat. The marked glycogenolysis and also loss of adenine nucleotides in the fibres may be factors of importance for changes in cell membranes which are said to be related to development of PSE-meat. The proportion of glycogen depleted fibres and the IMP concentrations in muscle are also shown to correlate with both reflectance values and drip loss (Essén-Gustavsson et al., 1991, 1992). A great drip loss and a high reflectance value are both indicative of meat of poor quality. These parameters are known to have higher values in *m. longissimus dorsi* in homozygote pigs carrying the halothane genotype, than in non-carriers (Lundström et al., 1989). That study also showed that the meat from heterozygotes was inferior to meat from non-carriers of the halothane genotype, but better than that from homozygote carriers of the halothane genotype.

In another study, crossbreeds of Yorkshire and wild boar were transported 5 km from the research station to the abattoir (Karlsson, 1993). This was evidently a physically stressful experience for these pigs, as they reacted violently. At the abattoir they were not allowed lairage but were immediately electrically stunned, using a restrainer, which is also stressful treatment. Some of these pigs carried the halothane genotype, while others were free from it.

However, the effect of genotype seemed to be of minor importance for the metabolic response in these pigs, as all had low glycogen and ATP concentrations and high lactate and IMP concentrations in the muscle with pH around 6.0, 30-60 min after slaughter (Table 2, Essén-Gustavsson et al. 1994). It is more likely that the metabolic response observed in this study was related to the considerable emotional and physical stress to which all the pigs had been subjected. This is supported by the low glycogen concentration post-slaughter compared to other studies and the marked depletion of glycogen seen in all fibre types (Karlsson, 1993). In samples taken from halothane gene free pigs immediately after slaughter, glycogen depletion was also found in type I and IIA fibres but a great variation was seen within type IIB fibres (0-60% depleted fibres) (Karlsson et al., 1992). The different depletion patterns seen among these pigs is likely related to different recruitment pattern due to physical stress prior to slaughter as these pigs included entire males, which fought during lairage. In both these studies where pigs had been exposed to physical stress pre-slaughter muscles with a marked depletion in type IIB fibres showed a tendency to become DFD. The proportion of glycogen-depleted type IIB fibres was positively correlated to ultimate pH and pH at exsanguination and negatively correlated to drip loss and reflectance values (Karlsson, 1993).

Muscle samples (*m. longissimus*) have been taken from pigs that were raised in pens and free-ranging pigs, both pre-slaughter and 30-60 min after slaughter. All had undergone the same treatment, with 3 hours of lairage and carbon dioxide stunning (Table 2, Essen-Gustavsson and Jensen-Waern, 1993). At exsanguination, blood lactate concentrations were lower (7.7 ± 1.1 mmol/l) in the free-ranging pigs than in those kept in pens (11.9 ± 3.2 mmol/l). This difference was probably due to the greater oxidative capacity of the muscles of free-ranging pigs (Table 1). It was of interest in that study, that glycogen concentrations in muscle biopsies 1 week before slaughter varied widely between all animals. Similar variations were observed in the samples taken after slaughter, though the values were lower. A significant correlation was found between pre and post-slaughter glycogen concentrations. The differences in glycogen concentration (pre vs. post) were correlated to muscle lactate concentration after slaughter, which in turn were correlated to pH (unpublished results). Muscle pH varied among pigs but not between groups. Three of the pigs had high pH-values, over 6.3, and low glycogen content in muscle and they belonged to the group that had been kept in pens.

Most studies on live pigs show large individual differences in glycogen concentration (Table 2). These could be related to both nutritional and stress factors but also be due to genetic variation. A high glycogen content in muscle has been shown to be related to a specific gene (RN), known to have an effect on meat quality (Sellier and Monin, 1994). It is known that glycogen levels in Hampshire pigs are higher than in other domesticated breeds (Table 2, Essén-Gustavsson and Fjelkner-Modig, 1985). Muscle biopsies taken from live carriers of the halothane genotype also have much higher glycogen levels than non-carriers (Essén-Gustavsson and Lindholm, 1984, Henckel, 1992). The lowest glycogen concentrations are

found in wild pigs (Table 2). This could imply that these animals utilize their substrate stores more efficiently by virtue of their greater muscle oxidative capacity.

Physical stress and giant fibres

Several studies have shown the presence of giant fibres in muscle post-mortem (Cassens et al. 1969, Handel and Stickland, 1986, Klosowska and Klosowski, 1985). Giant fibres are oval or round and are often located near the periphery of the fasciculus (Fig.1). They have been reported to develop more often in stress-susceptible pigs compared to non-stress-susceptible pigs and to occur in PSE-meat. Ultrastructural studies on post-mortem samples have revealed abnormal mitochondria and sarcoplasmic reticulum (Handel and Stickland, 1986). It has been suggested that giant fibres may be pathological fibres, but also that they may develop due to hypercontraction. In the above mentioned study of crossbreeds of Yorkshire and wild boar and a stressful pre-slaughter situation, giant fibres were found in muscle from almost all pigs, of which some carried the halothane genotype, while others did not (Essén-Gustavsson et al., 1994). Furthermore, in another study, giant fibres were found upon slaughter in 3 pigs carrying the halothane genotype. These pigs had the lowest glycogen, ATP and CP concentration and highest IMP and lactate concentration of all pigs in that study (Essén-Gustavsson et al., 1994). Giant fibres thus seem to develop in connection with accelerated energy turnover in fibres caused by stress-situations in connection with slaughter. Development of giant fibres may be one important factor affecting meat quality as a positive correlation was found between the number of giant fibres and the reflectance values of the meat (Essén-Gustavsson et al., 1994).

By reducing the frequency of the halothane gene, and minimize stress-situations pre-slaughter the problem of poor meat quality can be reduced. In the future it may also be worth considering glycogen content, the oxidative capacity and capillary density of muscles in order to obtain good quality meat.

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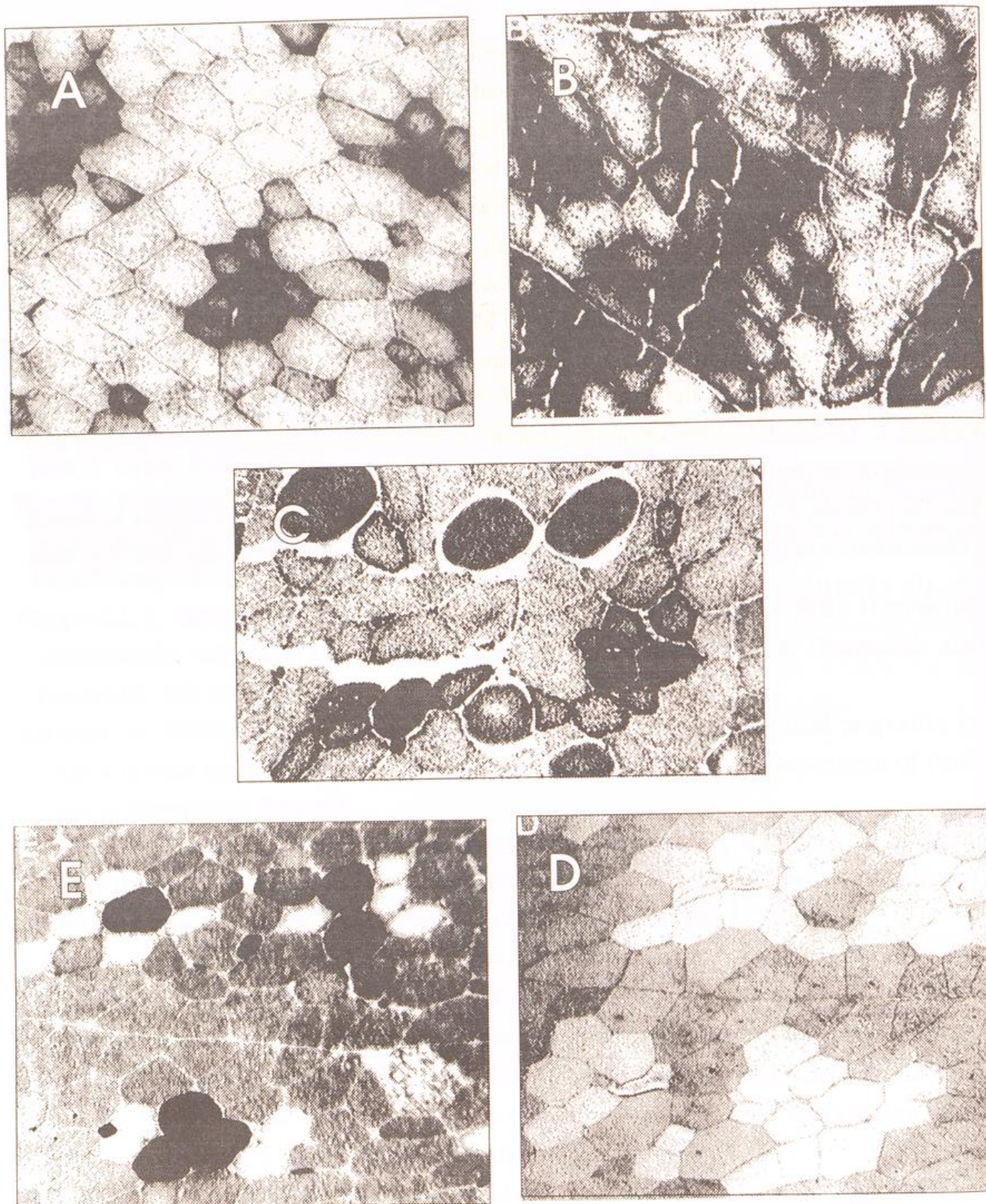


Fig. 1. NADH-stains illustrating the oxidative capacity in samples (*m. longissimus*) obtained after slaughter from a domestic pig (A), a free-ranging pig (B) and a pig having giant fibres (C). Serial cross-sections of a sample obtained after slaughter (*m. longissimus*) illustrating glycogen depleted fibres with the PAS-stain (D) and type I (black), type IIA (white) and type IIB (grey) fibres with the ATPase-stain (pH, 4.6) (E).

Citrate synthase activity ($\mu\text{mol/g/min}$)

	n	m.longis simus.	m.gluteus	m.biceps	m.semite ndinosus	Reference
Hampshire	5	12 $\pm$ 4	16 $\pm$ 3			Essén-Gustavsson and Fjelkner-Modig, 1985
Landrace	5	9 $\pm$ 2	13 $\pm$ 4			
Yorkshire	5	7 $\pm$ 2	12 $\pm$ 3			
Wild Boar	6	14 $\pm$ 1	38 $\pm$ 5		17 $\pm$ 4	Essén-Gustavsson and Lindholm, 1984
Landrace	6	10 $\pm$ 1	17 $\pm$ 5		10 $\pm$ 4	
Landrace (Hal-Nn)	3	8 $\pm$ 1				
Yorkshire	19	8 $\pm$ 1		14 $\pm$ 2		Karlsson et al. 1993
YxL (Hal-NN)	12	8 $\pm$ 2				Lundström et al. 1989
YxL (Hal-nn)	14	9 $\pm$ 2				
YxW (Hal-NN)	10	8 $\pm$ 2		18 $\pm$ 3		Karlsson et al. 1993
YxW (Hal-Nn)	10	8 $\pm$ 3		19 $\pm$ 6		
LxY Kept in pens	10	5 $\pm$ 1		19 $\pm$ 4		Essén-Gustavsson et al. 1988
LxY Trained	10	7 $\pm$ 1		33 $\pm$ 6		
YxLxH Free-ranging	10	9 $\pm$ 1		20 $\pm$ 5		Essén-Gustavsson and Jensen-Waern, 1993
YxLxH Kept in pens	10	7 $\pm$ 1		17 $\pm$ 3		
YxLxDxH Free-ranging	13	16 $\pm$ 4		21 $\pm$ 4	36 $\pm$ 6	Unpublished results
YxL Kept in pens	8	9 $\pm$ 4		10 $\pm$ 2	10 $\pm$ 3	
Wild boar	3	10 $\pm$ 2	27 $\pm$ 4	43 $\pm$ 2	34 $\pm$ 9	Unpublished results
YxLxH Kept in pens	2	9 $\pm$ 1	17 $\pm$ 1	22 $\pm$ 3	23 $\pm$ 6	
HxDxW Free-ranging	8	16 $\pm$ 5		28 $\pm$ 8		Unpublished results
Duroc	2	8 $\pm$ 1	17 $\pm$ 2			Unpublished results

Table 1. Citrate synthase activity in muscles from different studies on pigs.

		Glycogen (mmol/kg)	Glycogen (mmol/kg)	pH	Lactate (mmol/kg)	Reference
	n	Before slaughter	At slaughter or 30-60 min after	At slaughter or 30-60 min after	At slaughter or 30-60 min after	
Hampshire	5	443±127				Essén-Gustavsson and Fjellkner-Modig, 1985
Landrace	5	350±44				
Yorkshire	5	272±30				
Wild Boar	6	281±16				Essén-Gustavsson and Lindholm, 1984
Landrace	6	360±42				
Landrace (Hal-Nn)	3	439±52				
Yorkshire	19		220±11	6.99±0.09		Karlsson et al. 1993
YxL (Hal-NN)	10		232±78	6.62±0.19	90±47	Essén-Gustavsson et al. 1992
YxL (Hal-nn)	9		136±57	6.32±0.07	165±29	
YxW (Hal-NN)	10		94±49	6.11±0.22	189±35	Essén-Gustavsson et al. 1994
YxW (Hal-Nn)	11		103±48	5.98±0.22	220±43	
LxY Kept in pens	10	346±58				Essén-Gustavsson et al. 1988
LxY Trained	10	381±40				
YxLxH Free-ranging	10	422±135	279±113	5.96±0.18	399±111	Essén-Gustavsson and Jensen-Waern, 1993
YxLxH Kept in pens	10	342±129	235±142	6.17±0.27	279±100	
Wild Boar	3		224±22			Unpublished results
YxLxH Kept in pens	2		488±3			
HxDxW Free-ranging	7	424±138				Unpublished results
Duroc	2	322±6				Unpublished results

Table 2. Glycogen concentration, pH and lactate concentration in *m. longissimus* from different studies on pigs.

PERIMORTAL METABOLIC EVENTS AND CONSEQUENCES FOR MEAT QUALITY.

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The development of muscle into meat is an energy requiring proces. Due to the anaerobic condition which exist in the carcass, this production will be based on and depend on the available energy stores at the time of slaughter, and will imply a decrease in pH due to the formation of lactic acid from the break down of glycogen. Monin (1989) has summarized the most important quality traits directly related to the pH decrease. A rapid decrease in pH will lead to PSE meat, which is primarily a problem in pork meat and particular in meat from halothane sensitive individuals. If ultimate pH is too high the meat will be characterized as DFD, which is a problem primarily associated too beef meat, and if ultimate pH is too low, the resulting meat will be characterized as acidic meat or hampshire type meat. Both the rate and the extent of the pH decrease are thus of importance, and only within these borders can we expect an acceptable meat quality to develop.

The pH decrease is unique in the sense, that is the only trait, which is affected by sudden exposure to changes in environmental factors and particularly those imposed on the animals during transport and lairage, and is for the same reason almost impossible to incorporate in any selection schemes. In order to be able to monitor this pH decrease more efficient more information is needed concerning its physiological prerequisites in the live muscles, and the way these prerequisites are effected by the environmental factors, as well as the "energy costs" of slaughter itself.

As stated earlier the pH decrease in the carcass is a result of lactate production and accumulation within the muscles. The lactate production itself is caused by a forced requirement for ATP, that due to the release of large amounts of Ca^{++} , will force the individual fibres to contract.

The ATP can be produced from different sources, either via transfer of phosphate from creatine phosphate (CP) to ADP to yield creatine and ATP, via $\text{ADP} + \text{ADP}$ to form ATP and AMP by the myokinase reaction, or by degradation of glycogen to lactic acid with the release of hydrogen ions, which will accumulate locally in the muscles. Of these reactions the ATP