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Regulation of intracellular Ca^{2+} concentration and meat quality in pigs

Dedicated to Prof. Dr. Dr. h. c. Klaus Ender on the occasion of his 60th birthday

Abstract

The meat quality of pigs is essentially dependent on the rate and intensity of energy metabolism after slaughter. The major cellular processes in muscle cells are regulated by the Ca^{2+} concentration in the cytoplasm, stimulating different energy consuming ATPases. The most essential regulator of the Ca^{2+} concentration is the sarcoplasmic reticulum (SR) with its membranes, the SR Ca^{2+} ATPase (Ca^{2+} pump), and the calcium release channel (CRC). Defects of one or more of these elements will be of influence on the metabolism and ultimately on the meat quality. This is widely investigated in pigs with a mutated CRC. However, pigs without a mutation in the CRC also show a wide variability in their meat quality, dependent on other factors e.g. stress or season of the year. The variability in meat quality in these "normal" pigs is at least partly a result of differences in SR Ca^{2+} transport and the resulting metabolism.

Key Words: pig, calcium, sarcoplasmic reticulum, meat quality

Zusammenfassung

Titel der Arbeit: **Regulation der intrazellulären Ca^{2+} Konzentration und die Fleischqualität beim Schwein**

Die Fleischqualität von Schweinen hängt wesentlich von der Geschwindigkeit des Energieumsatzes nach dem Schlachten ab. Die zellulären Prozesse werden vorrangig durch die Ca^{2+} Konzentration im Zytoplasma geregelt wobei verschiedene energieverbrauchende ATPasen aktiviert werden. Der hauptsächliche Regulator für die intrazelluläre Ca^{2+} Konzentration ist das sarkoplasmatische Retikulum (SR) mit dessen Membranen, Kalziumkänalen (CRC) und SR Ca^{2+} ATPasen (Ca^{2+} Pumpen). Defekte an einem oder mehreren dieser Elemente führen zur Beeinflussung des Energiemetabolismus und schließlich der Fleischqualität. Nachweise erfolgten umfassend für Schweine mit mutiertem CRC. Allerdings weisen auch Schweine mit nichtmutiertem CRC eine hohe Variabilität in der Fleischbeschaffenheit auf, beeinflusst durch andere Faktoren wie z.B. nach Einwirkung von Stressoren oder die Jahreszeit. Auch bei diesen Tieren ergibt sich ein Zusammenhang zwischen Ca^{2+} Transport, Metabolismus und Fleischqualität.

Schlüsselwörter: Schwein, Calcium, sarkoplasmatisches Retikulum, Fleischqualität

Introduction

The pig breeding systems aiming for an increase of the lean meat percentage have been very successful in the preceding decades. However, parallel with an increased meat content there was an increasing part of carcasses showing inferior meat quality and also an increase in losses by death during transportation or other kinds of stresses. A major reason for this relationship has been shown to be a mutated calcium release channel (CRC) of the sarcoplasmic reticulum (SR) (MCLENNAN and PHILLIPS, 1992). It turned out, that this mutation causes an insufficient regulation of the intracellular Ca^{2+} concentration, activating metabolic processes not only in the live pig muscle, but also after slaughtering the animals. Currently all major pig producing

nations are taking measures to eliminate this mutation. This will be combined (at least temporarily) with a decreasing lean meat content, however, there are also animal welfare demands to be taken into account because mutated pigs are prone for health problems (MARTENS, 1998). With the elimination of this mutation the question arises: what are the causes for the wide variability of meat quality which occurs even in carcasses of normal pigs. A lot of work has been done to investigate the influence of different kinds of stress on meat quality. The results are not unequivocal, and now there are papers dealing with more basic approaches to this problem (ALLISON et al., 2002; HOPKINS and THOMPSON, 2002; SCHÄFER et al., 2002). The impact of the SR Ca^{2+} transport on meat quality in normal pigs has been the subject of only a small number of investigations. Some basics and some results are summarized in this paper.

Regulation of intracellular Ca^{2+} concentration, muscle activation, and energy metabolism

The most prominent energy consumption in the muscle derives from contraction work. Contractions are initiated by cell membrane depolarisations (action potential). By a not yet fully understood mechanism, the depolarisation of the transverse tubuli of the membrane is followed by a calcium release out of the sarcoplasmic reticulum (SR) through the calcium release channel (CRC). The increasing intracellular Ca^{2+} concentration activates the actin-myosin complex to contract, consuming energy by hydrolysing ATP. At the same time the increased intracellular calcium level initiates the Ca^{2+} ATPase (Ca^{2+} pump) of the SR to sequester Ca^{2+} back into the SR, also hydrolysing ATP.

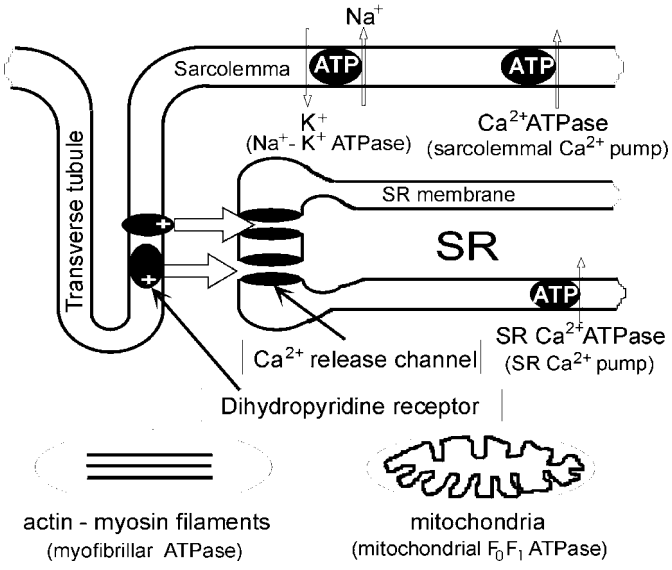

Fig. 1: Energy consuming processes in the live muscle and after slaughter: Activated by membrane depolarisation the dihydropyridine receptor (integrated in the transverse tubule) opens the calcium release channel, releasing Ca^{2+} into the cytosol. The increased intracellular Ca^{2+} concentration activates the actin-myosin filaments to contract, thereby consuming ATP. In the process of relaxation different ATPases are activated: Na^+-K^+ ATPase to restore the membrane potential, the sarcolemmal and the SR Ca^{2+} ATPases to lower the intracellular Ca^{2+} concentration. After slaughter these processes do not stop, the energy consumption by the different ATPases continues until ATP depletion. Whereas in the live animal the mitochondria produce ATP, after slaughter the mitochondrial ATPase can split ATP
(Energie verbrauchende Prozesse in lebenden Muskel und nach dem Schlachten: Der durch die Depolarisierung aktivierte Dihydropyridinrezeptor öffnet den Kalziumkanal (calcium release channel). Die dadurch erhöhte intrazelluläre Ca^{2+} Konzentration führt zu einer Kontraktion der Aktin-Myosin Filamente, verbunden mit ATP

Verbrauch. Zur Muskelrelaxion werden verschiedene ATPasen aktiviert: Na^+-K^+ ATPase zur Membranpolarisierung, Sarkolemm- und SR Ca^{2+} ATPasen zur Absenkung der intrazellulären Ca^{2+} Konzentration. Nach der Schlachtung setzen sich die energieverbrauchenden Vorgänge bis zur ATP Erschöpfung fort. Die im lebenden Tier energieproduzierenden Mitochondrien wirken im Schlachtkörper als ATPase und tragen zum Energieverbrauch bei.)

Figure 1 shows schematically elements of a muscle cell involved in the contraction-relaxation circle, including different ATP consuming ATPases. The largest energy consumer with about 70% is the myofibrillar ATPase (SPRIET, 1989), followed by the SR Ca^{2+} ATPase with about 30%. These relations depend on the muscle activity. The energy consumption by the SR Ca^{2+} ATPase at rest is partly used for "Ca^{2+} -cycling" (SIMONIDES and VAN HARDEVELD, 1988) and partly for heat production (DUMONTEIL et al., 1993).
In the live animal the ATP concentration is restored in different ways:
- in the aerobic way by oxidative phosphorylation by mitochondria
- by conversion of ADP to ATP by adenylate kinase
- ADP phosphorylation by creatine kinase from creatine phosphate
- by glycolysis.

After slaughter the oxygen delivery ceases whereas most biochemical processes in the muscle proceed post mortem. Following a short time interval the only way to regenerate ATP is by glycolysis.

Investigations of muscle Ca^{2+} transport of the sarcoplasmic reticulum

Investigations on the SR Ca^{2+} transport are supported by a very comfortable characteristic of the phospholipid cell membranes. By homogenising muscle tissue the membranes are destroyed. However, the SR membranes readjust themselves to vesicles in a way that the Ca^{2+} pumps are so arranged that the Ca^{2+} will be pumped into the vesicle. About 50% of the produced SR-vesicles contain CRC, derived from the terminal cisterns of the SR, and about 50 % of the vesicles come from the longitudinal SR, not containing calcium channels (KÜCHENMEISTER et al., 1999a; O'BRIEN and LI, 1997). Generally, two ways for determining the Ca^{2+} uptake and the activity of the SR Ca^{2+} ATPase are used. Firstly, the SR is isolated by several steps of centrifugations and the more or less pure SR is used for the measurement procedures. This way is time consuming and includes some uncertainties in the purity of the isolates (purity to be determined by measuring marker enzymes), also dependent on the degree of protein denaturation at the time of sampling the muscle. An easier way is to use the muscle homogenates directly and inhibit unwanted enzyme activities (e.g. mitochondrial ATPase, myofibrillar ATPase, sarcolemmal ATPases) by including biochemical inhibitors in the measuring medium. This has become the mostly used method for determining Ca^{2+} uptake or activity of ATPase (CHEAH et al., 1990; KÜCHENMEISTER et al., 1999a; O'BRIEN and LI, 1997; SIMONIDES and VAN HARDEVELD, 1990). The CRC (ryanodine receptor) can biochemically be closed or opened by incubating the muscle homogenate/isolated SR for different time intervals and with different concentrations of ryanodine (FEHER and LIPFORD, 1985; NAGASAKI and FLEISCHER, 1988; O'BRIEN and LI, 1997). To determine the integrity of the SR membrane, the activity of the Ca^{2+} ATPase has to be measured once with a Ca^{2+} ionophore (e.g. A23187), and once without an ionophore in the

measuring medium. The ratio of these two activities is a measure for the integrity of the membrane (BYRD et al., 1989).

Figure 2 depicts schematically a model of a SR vesicle with essential elements responsible for the Ca^{2+} transport: SR membrane, CRC, and SR Ca^{2+} ATPase. A disturbance of one or more of these elements results in a disturbed regulation of intracellular Ca^{2+} concentration.

These different possibilities leading to an increased (disturbed) intracellular Ca^{2+} concentration are:

- the efflux through the CRC is higher than the activity of the Ca^{2+} ATPase can cope with to sequester the Ca^{2+} into the SR.
- the Ca^{2+} ATPase is disturbed/inactivated and is unable to pump the Ca^{2+} back into the SR even with normal efflux.
- the phospholipid membrane is destroyed so that there is no way to hold the Ca^{2+} in the SR.

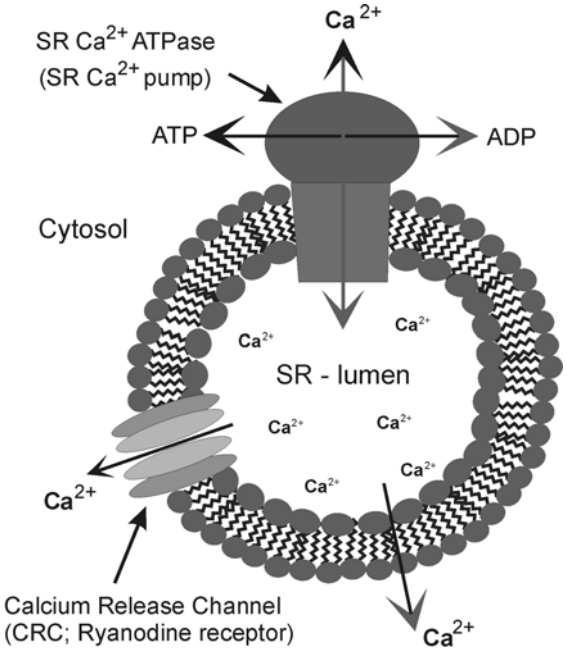

Fig. 2: Model of an isolated SR (sarcoplasmic reticulum) vesicle, consisting of SR membrane, calcium release channel (CRC; ryanodine-receptor RyR), SR Ca^{2+} ATPase (Ca^{2+} pump) (Modell eines isolierten SR (sarkoplasmatisches Retikulum) Vesikels, bestehend aus der SR-Membran, dem Calcium Release Channel (CRC; Ryanodin-Rezeptor RyR) und der SR Ca^{2+} ATPase (Ca^{2+} Pumpe))

Mutation of the CRC, Ca^{2+} transport and meat quality

Especially in pigs with a high muscle meat content it turned out that there is a defect in the calcium release channel (CRC) causing inferior meat quality (MCLENNAN and PHILLIPS, 1992; REMPEL et al., 1995). By a mutation in the CRC-protein the efflux of Ca^{2+} is facilitated compared to a normal CRC. At rest and without additional stress the appearance and the muscle contractions of pigs with mutated CRC are inconspicuous. However, physical stress like transportation, stunning, mixing with unknown pigs etc. can cause that the Ca^{2+} efflux can not be compensated by the Ca^{2+} pump and will result in a lasting increased intracellular Ca^{2+} concentration and lasting muscle contractions. These effects do not only happen in the live animal but also after

slaughter in the carcass, often evidenced by muscle twitches up to one hour p.m. and an early rigor.

Investigations with normal (MHR = malignant hyperthermia resistant = normal CRC) and mutated (MHS = malignant hyperthermia susceptible = mutated CRC) pigs have consistently shown the development of inferior meat quality of MHS pigs (KÜCHENMEISTER et al., 1999a; REMPEL et al., 1995). These differences are related to changes in the SR Ca^{2+} transport. Immediately after slaughter the SR Ca^{2+} uptake did not differ between MHS and MHR muscles, however in the time course p.m. the decrease of uptake occurs at a much higher rate in MHS pigs (Fig. 3). Four hours p.m. the uptake rate has been shown to be decreased (in vitro) to about one third in MHS, but only by about 15% in MHR (KÜCHENMEISTER et al., 1999a). Though the CRC can biochemically be opened and closed even 4 h p.m. (KÜCHENMEISTER et al., 1999a), without manipulating the CRC of MHS muscle is (in vitro) almost fully open. Interestingly, the SR Ca^{2+} ATPase activity has been shown to be higher immediately after slaughter in MHS muscle, but the activity decreased much faster than in MHR muscle (Fig. 4), showing similarities with the shape of uptake decrease in MHS as well as in MHR (KÜCHENMEISTER et al., 1999a).

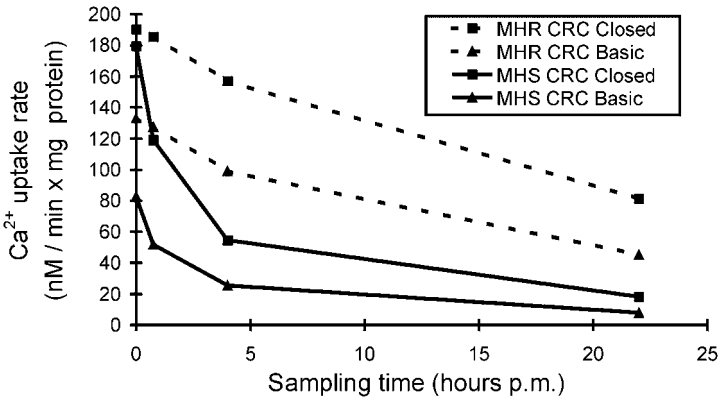

Fig. 3: Rate of Ca^{2+} uptake of *longissimus* homogenates of malignant hyperthermia susceptible (MHS) (——) and malignant hyperthermia resistant (MHR) (– – –) pigs and different states of the calcium release channel (CRC): (■), closed CRC; (▲), basic CRC (Rate der Ca^{2+} Aufnahme durch das Homogenat vom *m. longissimus dorsi* von (MHS) (——) und (MHR) (– – –) Schweinen bei verschiedenen Zuständen des CRC: (■), geschlossener CRC; (▲), unbeeinflusster CRC)

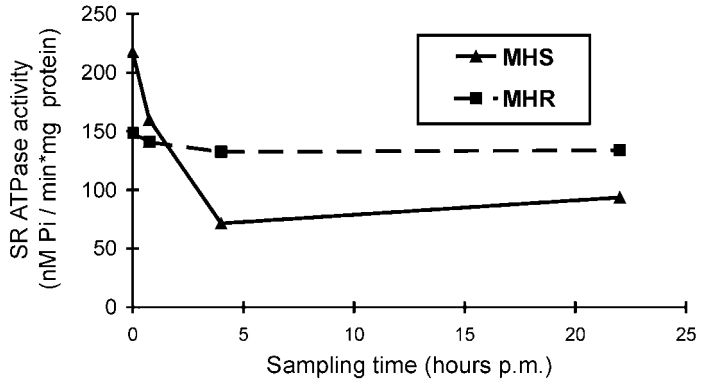

Fig. 4: SR Ca^{2+} ATPase activity of *longissimus* homogenates of MHS and MHR pigs, determined with inclusion of Ca^{2+} ionophore A23187 (Aktivität der SR Ca^{2+} ATPase des Homogenates vom *m. longissimus dorsi* von MHS und MHR Schweinen, bestimmt unter Einschluss des Ionophor A23187)

Besides an inactivation of the ATPase, there seems to be a change in the permeability to Ca^{2+} in the membrane of the SR with a greater permeability in MHS samples (KÜCHENMEISTER et al., 1999b). Investigations with heterozygous pigs indicate that the meat quality as well as the Ca^{2+} transport are intermediate to those of homozygous negative and homozygous positive pigs (O'BRIEN and LI, 1997; SHOMER et al., 1995; CHEAH et al., 1995).

Effect of stress on SR Ca^{2+} transport and on meat quality

Stressors of different kinds before slaughter have been investigated as factors for the meat quality of pigs (GRANDIN, 1980). Although the results of several investigations are not unequivocal (KÜCHENMEISTER et al., 2002a), it is generally assumed that stress is of negative influence on the meat quality.
The impact of stress on the SR Ca^{2+} transport and meat quality in stress resistant pigs has been investigated (KÜCHENMEISTER et al., 2002a). At about 80 kg live weight, pigs were stressed either by running for 4 min or by a 5 min application of a nose snare. Immediately before and after the application of this stressor, as well as 4 h after the treatment, biopsy samples of the longissimus muscle were taken and the Ca^{2+} uptake of the homogenised samples was determined. The nose snare stress as well as the running reduced the rate of Ca^{2+} uptake. Uptake rates in samples taken 4 h after the treatment of pigs were at initial levels again (Fig. 5).

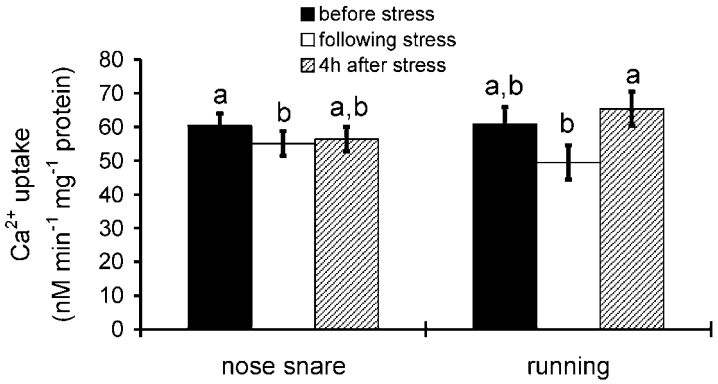

Fig. 5: Rate of Ca^{2+} uptake in the homogenate from *longissimus* muscle taken by biopsy before application of stress (nose sling for 5 min or running for about 4 min), immediately following stress, and after a recovery (4 hours) of the pigs. Different letters indicate significant differences within the kind of stress (Rate der Ca^{2+} Aufnahme durch das Homogenat vom *m. longissimus dorsi*, gewonnen durch Biopsie vor Stressanwendung, direkt nach dem Stress (5 min Oberkiefernschlinge oder Lauf für ca. 4 min) und nach einer Erholung der Tiere von 4 Stunden)

At slaughter one half of these animals were stressed by the use of a nose snare for 5 min. Although this kind of stress reduced the Ca^{2+} uptake significantly (Fig. 6), the differences in meat quality failed to attain statistical significance (KÜCHENMEISTER et al., 2002a). The changes of Ca^{2+} transport by the applied stress (Fig. 6) are clearly smaller than the changes derived by the different genotypes (Fig. 3). These results indicate that the changes in Ca^{2+} transport have to reach a certain level to affect the meat quality significantly.

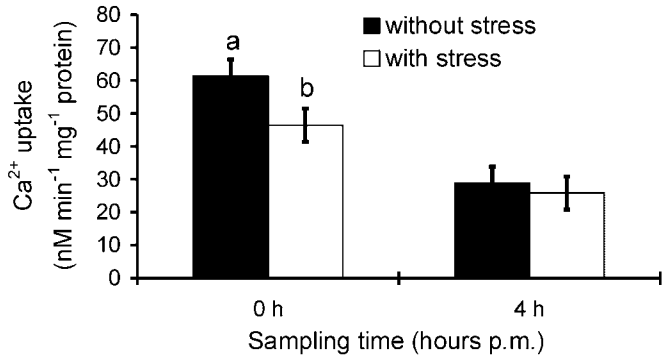

Fig. 6: Rate of Ca^{2+} uptake in the homogenate from *longissimus* muscle at slaughter sampled immediately after exsanguination and 4 hours post mortem (p.m.). One half of the pigs (n=10) were stressed just before slaughter for 5 min by using a nose snare. Different letters indicate significant differences between pigs with or without stress (Rate der Ca^{2+} Aufnahme durch das Homogenat vom *m. longissimus dorsi*, gewonnen direkt nach der Entblutung. Eine Hälfte der Schweine wurde zur Belastung für 5 min mit einer Oberkiefernschlinge fixiert)

Effect of season (temperature) on Ca^{2+} transport and meat quality

Pigs are susceptible not only for physical stress. Hot summer weather can also be of influence on meat quality. In the course of an experiment MHR as well as MHS pigs were slaughtered in summer (temperatures 25 to 30°C) or in winter (temperatures –3 to +3°C) (KÜCHENMEISTER et al., 2000). The Table shows meat quality parameters determined in this experiment. As expected the meat quality of MHS pigs was inferior to that of MHR ones. However, not really expected, the colour L* of MHR/summer carcasses was the same as in MHS/winter ones. Also, the driploss of MHR/summer pigs was increased in comparison to the MHR/winter pigs and reached the value of the MHS/winter pigs. Although the conductivity of MHR/summer pigs was significantly increased compared to MHR/winter ones these values did not reach the MHS/winter conductivity. Altogether, the results not only show inferior meat quality in summer (in MHS as well as in MHR pigs), but also document that at least in colour and drip loss the meat quality of MHR/summer pigs is affected by summer (temperature) that these values are comparable to that of pigs with a mutated CRC, slaughtered in winter.

Table
Meat quality (*longissimus muscle*) of pigs with different MH-status, slaughtered in summer or winter (LSM ± SE) (Fleischbeschaffenheit des *m. longissimus dorsi* von Schweinen mit unterschiedlichem MH-Status, geschlachtet im Sommer oder Winter (LSM ± SE))

	MHS/summer	MHS/winter	MHR/summer	MHR/winter
pH 45 min	5.46 ± 0.10 a	5.62 ± 0.10 a	6.20 ± 0.06 b	6.36 ± 0.08 b
pH 22 h	5.45 ± 0.03	5.42 ± 0.03	5.43 ± 0.02	5.49 ± 0.03
Conductivity 22 h (mS)	9.05 ± 0.60 a	7.80 ± 0.60 a	4.59 ± 0.38 b	2.47 ± 0.49 c
Colour L* (Minolta)	54.0 ± 1.2 a	47.5 ± 1.2 bc	48.5 ± 0.8 b	45.6 ± 1.0 c
Drip loss (%)	7.76 ± 0.65 a	3.77 ± 0.65 b	3.90 ± 0.41 b	1.35 ± 0.53 c
Lean meat (%)	61.4 ± 1.0 ac	63.4 ± 1.0 a	59.5 ± 0.65 bc	57.8 ± 0.84 b

a, b, c different letters indicate significant differences between experimental groups ($p<0.05$)

The results of the SR Ca^{2+} transport determinations emphasize the general relationship between Ca^{2+} transport and meat quality results. Figure 7 shows the differences in the rate of Ca^{2+} uptake of homogenates of MHR as well as MHS muscle in the time course post mortem. Immediately after slaughter the uptake rate of MHS summer muscle is lower than that of muscle sampled at winter. The differences are significant at least up

to 4 hour p.m. The uptake rates of MHS muscle (summer and winter) do not differ from that of MHR summer muscle, which is reflected in the meat quality and is an indicator of disturbed Ca^{2+} transport in MHR pigs slaughtered in summer.

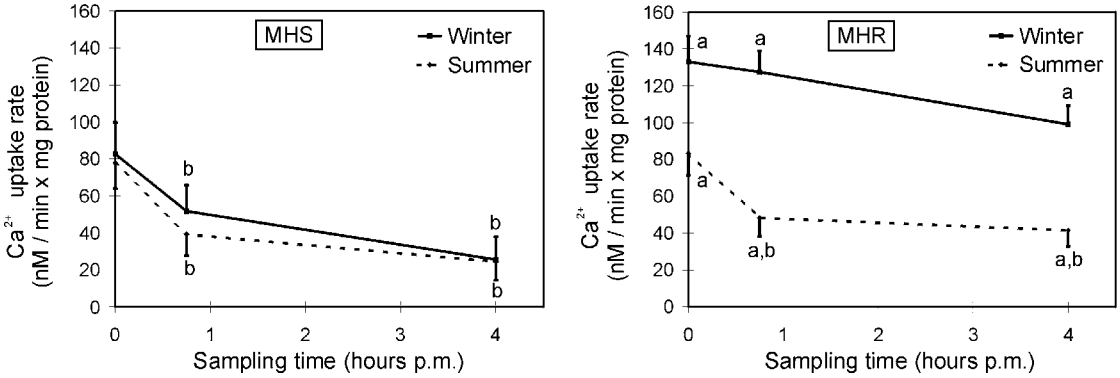

Fig. 7: Rate of Ca^{2+} uptake of *longissimus* homogenates from pigs slaughtered in summer or winter, with basic calcium release channel (without incubation with ryanodine). The muscles were sampled at different intervals post mortem from pigs with mutated CRC (MHS), and from normal ones (MHR) (Rate der Ca^{2+} Aufnahme durch das Homogenat vom *m. longissimus dorsi* von Schweinen, die im Sommer oder im Winter geschlachtet wurden (unbeeinflusster CRC, ohne Inkubation mit Ryanodin). Die Muskeln wurden zu verschiedenen Zeiten post mortem von normalen Schweinen (MHR) und Schweinen mit mutiertem CRC (MHS) gewonnen.)
a - significantly different between season ($p<0.05$)
b - significantly different from 0 h sample ($p<0.05$)

Ca^{2+} transport, meat quality and tenderness

Although tenderness is mostly taken into account in beef investigations, it is also an essential parameter for pig meat quality. Tenderness of meat develops by the proteolytic action of the calpain/calpastatin system on different interfilament proteins like titin, nebulin or different costameres (MARUYAMA, 1997; TAYLOR, 1995), loosening the myofibrillar structure. The calpain is activated by Ca^{2+}, indicating the role of the intracellular Ca^{2+} concentration on the tenderness.

The effect of Ca^{2+} on tenderisation is manifested by several investigations injecting Ca^{2+} (KERTH et al., 1995), marinating meat in Ca^{2+} containing solutions (YOUNG and LYON, 1997), or inducing Ca^{2+} release by high pressure (OKAMOTO et al., 1995). The rate of glycolysis affects the extend of the tenderisation at least in beef. A low glycolytic rate post mortem results in high shear force, whereas a high glycolytic rate leads to lower shear values (O'HALLORAN et al., 1997), probably related to lower or higher intracellular Ca^{2+} concentrations, respectively. A very fast p.m. metabolism however has been shown to produce tough meat, indicating a quadratic relationship between glycolytic rate and tenderness (MARSH et al., 1987; PIKE et al., 1993). In pork, calcium infusion tenderised the meat, but had detrimental effects on drip loss and meat colour (REES et al., 2002). Also in pork, a reduced SR Ca^{2+} uptake rate resulted in inferior meat quality, but improved the tenderness (KÜCHENMEISTER et al., 2002b). Generally, a disturbed regulation of the intracellular Ca^{2+} concentration results in inferior meat quality parameters pH, drip loss, and colour, but on the other hand an increased Ca^{2+} concentration may activate the protease calpain, tenderising the meat. Altogether, the field of Ca^{2+} transport, tenderness and meat quality in pigs has not yet received enough attention, so it should be worthwhile to do more investigative work in this field.

Conclusions

As evidenced by numerous investigations in pigs with mutated calcium release channels, a disturbed regulation of the intracellular Ca^{2+} concentration is of major influence on the quality of pork. This is one reason why such pigs should be eliminated from breeding. The causes for variation in meat quality in pigs with normal CRC are not yet fully understood. In muscle of pigs with normal CRC pre-slaughter stress can reduce Ca^{2+} transport significantly, however, the effect on meat quality was limited. The season seems of influence on meat quality as well as on Ca^{2+} transport.
It can be concluded that more basic research is needed to elucidate causes for meat quality variability in pigs to allow recommendations for the producer and meat processor.

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