

Monday 17 August 2009

Parallel session 1: Growth and metabolism

PS1.01 Muscle growth 73.00

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Abstract—Muscle growth can be divided into prenatal and postnatal events. Prenatal muscle development occurs in various steps including specification of mesodermal cells to myoblasts, myoblast proliferation, alignment of myoblast and their fusion to primitive myofibres. At birth the muscle fibre number (MFN) is constant. Besides muscle fibre number and fibre type distribution, postnatal muscle growth is related to protein accretion of the fibres as a function of the rates of protein synthesis and protein degradations (protein turnover). Satellite cell proliferation support protein turnover. This means that selection for performance of meat animals may cause correlated changes in various steps in myogenesis and/or in postnatal muscle growth. However, changes in some steps may deteriorate meat quality traits while others do not or even improve meat quality. Thus, increasing muscle fibre number may increase lightness and lower redness because increased muscle fibre number results in lower cross-sectional area of muscle. Also several studies suggest that the rate of muscle protein degradation in vivo is related to tenderization probably because μ M dependent Calpain is limiting the rate of protein degradation in vivo as well as during tenderization. This finding suggests that during selection periodical measurements of the Calpain system are needed but this finding may also be used to develop new concepts for high quality meat. In conclusion some steps in muscle development and postnatal growth is related to meat quality traits which should be taking into consideration following selection for increased performance but may also be used to develop new concepts for meat products with high quality.

Index Terms—myogenesis, postnatal growth, meat quality.

I. INTRODUCTION

Several studies have shown that some events in muscle development and postnatal growth are related to meat quality traits. Because the rate of muscle growth is highly correlated with performance traits (daily gain, feed conversion rate and meat content of the carcass) selection for increased performance traits may influence some meat quality traits. However, the relationship between events determining muscle growth and meat quality may also give rise to developing new concepts for production of meat with high meat quality. In this presentation we will, firstly, give a short introduction to basic principles of muscle development and muscle growth. Secondly, we will give examples of relations among the various events in muscle development, growth and meat quality traits. Finally, we will give an example of future perspective in the borderline between muscle growth and meat quality. An earlier review was given by Koohmaraie et al [5] and Andersen et al [1].

II. RESULTS AND DISCUSSION

Muscle fibre formation (myogenesis) takes place during foetal development. Highly specialised muscle fibres develop from mesodermal cells which are specified to become myoblasts. These myoblasts proliferate several times before they align and fuse to become premature myofibres. By innervation these myotubes differentiate to mature muscle fibres. Two populations of fibres develop at different times. The first population, termed Primary fibres, develops from late first trimester, while the second population, termed secondary fibres develop from mid second trimester to mid third trimester and at birth the number of muscle fibres is fixed in most livestock animals. The muscle fibre number (MFN) is directly related with daily gain and inversely related to the feed conversion ratio [16].

Besides the MFN, postnatal muscle growth is due to two events; i.e., protein accretion and satellite cell proliferation. Although the myonuclei are mitotic inactive the amount of DNA or number of myonuclei in the muscles increases along with muscle growth. This is due to a population of mononucleated cells

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residing between the basement-membrane and the sarcolemma, called satellite cells. These cells proliferate when stimulated and one or both daughter cells fuse with the muscle fibre and add additional DNA to the fibre. This is important because the DNA provide the machinery for protein synthesis [16]. The second event, protein accretion, is the difference between two dynamic processes the rates of protein synthesis and protein degradation. Protein accretion results in increased cross-sectional area and length of the muscle fibres. Disassembly of myofibrillar proteins by the calpain system, $\mu\text{M Ca}^{++}$ dependent calpain and its inhibitor, calpastatin, initiate protein degradation and the constituent proteins is further degraded in the sarcoplasm by the proteasome and in the lysosomes by the cathepsins [2].

Myogenesis and meat quality. Selection for higher performance causes correlated changes in muscle growth. In the nineties we [13] examined the effect of selection for better performance by comparing a slow-growing purebred Landrace genotype of pigs with a modern fast-growing Landrace genotype. The pigs were slaughtered at the same weight and we found by histochemical procedures that the fast-growing pigs had smaller muscle fibres than the slow-growing pigs. As the weight of the longissimus dorsi did not differ between the two genotypes we suggested that the MFN formed during foetal development was higher in the fast-growing pigs and this may have supported the increased daily gain of 300 g/day in the fast-growing pigs. At the same time the content of myoglobin and the a^* value were lowered, while the L^* increased, giving rise to more light and less red meat. This change in colour may be due to smaller CSA of muscle fibres, which is directly related with the concentration of myoglobin. Similarly, we found lower concentration of pigment in the smaller littermates having smaller muscle fibre CSA than in larger littermates with larger muscle fibre CSA [11]. In addition, results [17] showed that MFN was genetically unrelated with technological meat quality traits but positively related with daily gain ($r_g=0.46$) and lean meat percentage ($r_g=0.38$), while muscle fibre CSA was related to drip loss ($r_g=0.65$), reflectance ($r_g=0.32$), and pH ($r_g=-0.37$).

Protein degradation in vivo and meat quality. Several pieces of evidences suggest a relationship between the rate of protein degradation and tenderness (Table 1, Shear Force):

1. Increased muscle growth by β -adrenergic agonists in ruminants and pigs is due to a reduction in muscle protein degradation and leads to increased shear force.
2. Treatment with porcine growth hormone increases muscle growth rate by increasing both the rates of muscle protein synthesis and

muscle protein degradation without altering shear force [12, 18].

3. Callipyge lamb exhibits larger muscle growth rate than controls due to reductions in both muscle protein synthesis and degradation leading to increased shear force [4].
4. The larger muscle growth rate by bulls compared to steers is due to a lower muscle protein degradation rate [8, 9].
5. Short-term feeding in lambs at maintenance level prevented growth of muscle by decreasing the rate of synthesis while the rate of protein degradation was increased. This resulted in a lower shear force [7].
6. Long-term feed restriction in pigs decreases muscle growth by decreasing both the rate of synthesis but also the rate of degradation which results in an increased shear force.[21]
7. Finally, a direct relationship between muscle protein degradation and the shear force was found in cattle [16, 19].

In most of these studies the changes in muscle protein degradation were associated with changes in μ -calpain activity or inhibitor activity of calpastatin. These studies indicate a direct relationship between the rate of muscle protein degradation and shear force of the resultant meat and that the μ -Calpain/calpastatin is responsible for this relationship because this proteolytic system is also a major determinant of tenderization [2]. Thus, if it is possible to increase the rate of protein degradation just before slaughter this may result in meat with superior tenderness. A feeding strategy involving compensatory growth could meet this requirement.

Compensatory growth response. For decades it has been recognised that compensatory growth (or catch-up growth) following re-alimentation may occur after a period of feed restriction in most farm animals, and the phenomenon has continuously been reported to take place in pigs in conventional production systems [14] and in organic pig production [15]. The degree of compensatory growth or the index is calculated as: $\text{Index}=(A-B)/A$, where A is the difference in weight between fed-restricted animals and ad libitum fed animals following the restriction period and B is the difference between ad libitum fed animals and compensatory animals at the slaughter (Figure 1). According to findings in cattle [3] both the rate of protein synthesis and degradation is elevated. Consequently, compensatory growth response may be a mean to increase tenderness of meat.

Table 1. Factors affecting protein degradation and tenderness

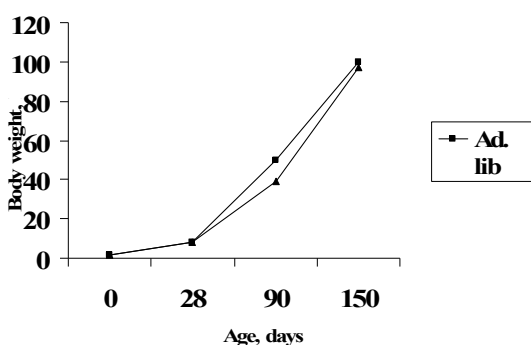
Table 1.

	Muscle growth	FSR ^a	FDR ^b	Calpastatin activity	Shear force
□-agonist	↑	↔, ↑	↓	↑	↑
pGH ^c	↑	↑	↑		↔
Bull vs steer	↑	↔	↓	↑	↑
Fasting (short time)	↓	↓	↑	↓	↓
Fasting (long time)	↓	↓	↓	↑	↑
Callipyge gene	↑	↔	↓	↑	↑

^aFractional Synthesis Rate, ^bFractional Degradation Rate; ^cporcine Growth Hormone

The protein turnover, however, develops dynamically through compensatory growth, and rises from a low value initially after onset of ad libitum feeding to a high value. However, the rate of protein synthesis increases at a faster rate than the rate of degradation, but is at a level higher than control animals 42-45 days after the beginning of the re-alimentation period. This was verified by measuring total muscle RNA and eucaryotic elongation factor 2 (eEF-2) as an indicator for protein synthesis and μ M-calpain, mM-calpain and their inhibitor calpastatin as indicators of muscle protein degradation [20]. These findings were taken into consideration in our further work on compensatory growth, muscle protein turnover and tenderness. The major finding of these studies [6, 20, 21] were that both castrated male pigs and female pigs exhibit compensatory growth, while tenderness was only improved in female pigs. This result may be related to the effect of compensatory growth on intra-muscular fat which was unaltered in meat from female pigs but reduced in meat from castrated male pigs. Intra-muscular fat (IMF) is positively related to tenderness and the beneficial effect of compensatory growth on tenderness may then be abolished by a reduction in IMF in castrated male pigs.

Figure 1. Compensatory growth in pigs.
Index % (A-B)/A*100



Recently it was found that compensatory growth may abolish the negative effect of ractopamine (a β -adrenergic agonist) [10]. Consequently, compensatory growth may prevent the negative effect of gender (bulls), callipyge and β -agonist treatment on shear force. However, this needs further research.

Future perspective: trans-differentiation of myoblast to adipocytes.

It is generally accepted that intra-muscular fat (IMF) has a positive effect on the sensory quality of fresh meat and up to 3% IMF may be beneficial for the tenderness. Under Danish condition using a three way cross of Duroc x (Landrace x Large White) the IMF varies around 1.6% in Longissimus dorsi. Consequently, a higher IMF content is desirable. Existing means to increase IMF are costly and no shortcut is available at the moment. However, studies have shown that it is possible to trans-differentiate satellite cells to adipocytes in culture. PPAR- γ agonists like thiazolidinediones (TZD) were required for this process. Plants contain naturally occurring PPAR- γ agonists, which may be acceptable for consumers compared to synthetic TZD. However, future research is required in this area in order to be able to increase the IMF.

III. CONCLUSION

In conclusion, some events in muscle development and postnatal growth is related to meat quality traits which should be taking into consideration following selection for increased performance but may also be used to develop new concepts for meat products with high quality like the compensatory growth response. Furthermore, more research is needed to clarify whether Compensatory growth can be combined with factors in the production which causes deterioration in tenderness.

ACKNOWLEDGEMENT

The authors would like to thanks The Ministry of Food, Agriculture and Fishery for financial support and colleges at University of Copenhagen, Lars Kristensen, Per Ertbjerg, and René Lameatch and colleges at DMRI, Susanne Støier, Margit Aaslyng and Camilla Bejerholm. Also we want to express our gratitude to Lab Technicians. Inge Lise Sørensen and AnneGrethe Dyrvig.

REFERENCES

- [1] Andersen, H.J., Oksbjerg, N., Young, J.F., Therkildsen, M. 2005. Feeding and meat quality – a future approach. Meat Sci. 70: 543-554.

- [2] Goll, D.E., Thomson, V.F., Taylor, R.G., and Christiansen, J.A. 1992. Role of Calpain system in muscle growth. *Biochimie*. 74:225-237.
- [3] Jones, S.J., Starky, D.L., Calkins, C.R., and Crouse, J.D. 1990. Myofibrillar protein turnover in feed-restricted and realimented beef cattle. *J. Anim. Sci.* 68:2707-2715.
- [4] Lorenzen, C.L., Koohmaraie, M., Shackelford, S.D., Jahoor, F., Freetly, H.C., Wheeler, T.L., Savell, J.W., and Fiorotto, M.L. 2000. Protein kinetics in callipyge lambs. *J. Anim. Sci.* 78:78-87.
- [5] Koohmaraie, M., Kent, M.P., Shackelford, S.D., Veiseth, E., and Wheeler, T.L. 2002. Meat tenderness and muscle growth: is there any relationship? *Meat Sci.* 62:345-352.
- [6] Kristensen, L., Therkildsen, M., Aaslyng, M.D., Oksbjerg, N., and Ertbjerg, P. 2004. Compensatory growth improves meat tenderness in gilts but not in barrows. *J. Anim. Sci.* 82:3617-3624.
- [7] McDonagh, M.B. Fernandez, C., and Oddy, M.V.H. 1999. Hind-limb protein metabolism and calpain system activity influence post-mortem change in meat quality in lamb. *Meat Science*. 52:9-18.
- [8] Morgan, J.B., Wheeler, T.L., Koohmaraie, M., Savell, J.W., and Crouse, J.D. 1993. Meat tenderness and the calpain proteolytic system in longissimus muscle of young bulls and steers. *J. Anim. Sci.* 71:1471-1476.
- [9] Morgan, J.B., Wheeler, T.L., Koohmaraie, M., Crouse, J.D., and Savell, J.W. 1993. Effect of castration on myofibrillar protein turnover, endogenous proteinase activities, and muscle growth in bovine skeletal muscle. *J. Anim. Sci.* 71:408-414.
- [10] Mitchell, A.D. 2009. Effect of ractopamine on growth and body composition of pigs during compensatory growth. *Animal*. 3: 173-180
- [11] Nissen, P.M., Jorgensen, P.F., and Oksbjerg, N. 2004. Within-litter variation in muscle fiber characteristics, pig performance, and meat quality. *J. Anim. Sci.* 82:414-421.
- [12] Oksbjerg, N., Petersen, J.S., Sørensen, M.T., Henckel, P., Agergaard, N., Bejerholm, C., and Erlandsen, E. 1995. The influence of porcine growth hormone on muscle fibre characteristics, metabolic potential and meat quality. *Meat Sci.* 39:375-385.
- [13] Oksbjerg, N., Petersen, J.S., Sørensen, I.L., Henckel, P., Vestergaard, M., Ertbjerg, P., Møller, A.J., Bejerholm, C., and Støier, S. 2000. Long term changes in performance and meat quality of Danish Landrace pigs: a study on a current compared to an unimproved genotype. *Animal Science*. 71:81-92.
- [14] Oksbjerg, N., Sørensen, M.T., and Vestergaard, M. 2002. Compensatory growth and its effect on muscularity and technologic meat quality. *Acta Agric. Scand., Sect. A, Animal Sci.* 52:85-90.
- [15] Oksbjerg, N., Strudsholm, K., Lindahl, G., Hermansen, J.E. 2005. Meat quality of fully or partly outdoor reared pigs in organic production. *Acta Agric. Scand. Sect. A, Animal Sci.* 55:106-112.
- [16] Oksbjerg, N., Gondret, F., and Vestergaard, M. 2004. Basic principles of muscle development and growth in meat-producing mammals as affected by the insulin-like growth factor (IGF) system. *Dom. Anim. Endocrinol.* 27:219-240.
- [17] Rehfeldt, C., Fiedler, I., Dietl, G., and Ender, K. 2000. Myogenesis and postnatal skeletal muscle cell growth as influenced by selection. *Livest. Prod. Sci.* 66:177-188.
- [18] Séve, B., Ballèvre, O., Ganier, P., Noblet, J., Prugnaud, J., and Obled, C. Recombinant porcine somatotropin and dietary protein enhance protein synthesis in growing pigs. *J. Nutr.* 123:529-540.
- [19] Shackelford, S.D., Koohmaraie, M., Cundiff, L.V., Gregory, K.E., Rohrer, G.A., and Savell, J.W. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield and growth rate. *J. Anim. Sci.* 72:857-863.
- [20] Therkildsen, M., Riis, B., Karlsson, A., Kristensen, L., Ertbjerg, P., Purslow, P.P., Aaslyng, M.D., and Oksbjerg, N. 2002. Compensatory growth response in pigs, muscle protein turnover and meat texture: effects of restriction/realimentation period. *Anim. Sci.* 75:367-377.
- [21] Therkildsen, M., Vestergaard, M., Busk, H., Jensen, M.T., Riis, B., Karlsson, A., Kristensen, L., Ertbjerg, P., and Oksbjerg, N. 2004. Compensatory growth in slaughter pigs – In vitro muscle protein turnover at slaughter, circulating IGF-I, performance and carcass quality. *Livest. Prod. Sci.* 88:63-74.