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Advances in research on the prenatal development of skeletal muscle in animals in relation to the quality of muscle-based food. II – Genetic factors related to animal performance and advances in methodology

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Selective breeding is an effective tool to improve livestock. Several selection experiments have been conducted to study direct selection responses as well as correlated responses in traits of skeletal muscle growth and function. Moreover, comparisons of domestic with wild-type species and of extreme breeds provide information on the genetic background of the skeletal muscle phenotype. Structural muscular components that differed with increasing distance in lean growth or meat quality in mammals were found to be myofibre number, myofibre size, proportions of fibre types as well as the numbers and proportions of secondary and primary fibres. Furthermore, markers of satellite cell proliferation, metabolic enzyme activities, glycogen and fat contents, the expression of myosin heavy chain isoforms, of activated AMPKα and other proteins in skeletal muscle tissue and circulating IGF1 and IGF-binding proteins have been identified to be involved in selection responses observed in pigs, cattle and/or chicken. The use of molecular methods for selective breeding of fish has only recently been adopted in aquaculture and studies of the genetic basis of growth and flesh quality traits are scarce. Some of the molecular markers of muscle structure/metabolism in livestock have also been identified in fish, but so far no studies have linked them with selection response. Genome scans have been applied to identify genomic regions exhibiting quantitative trait loci that control traits of interest, for example, muscle structure and meat quality in pigs and growth rate in chicken. As another approach, polymorphisms in candidate genes reveal the relationship between genetic variation and target traits. Thus, in large-scale studies with pigs' associations of polymorphisms in the HMGA2, CA3, EPOR, NME1 *and* TTN *genes with traits of carcass and meat quality were detected. Other studies revealed the significance of mutations in the* IGF2 *and* RYR1 *genes for carcass lean and muscle fibre traits in pigs. Mutations in the* myostatin *(*MSTN*) gene in fish were also examined. Advances in research of the genetic and environmental control of traits related to meat quality and growth have been made by the application of holistic 'omics' techniques that studied the whole muscle-specific genome, transcriptome and proteome in relation to muscle and meat traits, the development of new methods for muscle fibre typing and the adaptation of biophysical measures to develop parameters of muscle fibre traits as well as the application of* in vitro *studies. Finally, future research priorities in the field are defined.*

Keywords: farm animal, fish, skeletal muscle, animal performance, genetic effects

Implications

Skeletal muscle development in different animal species has been an important topic of scientific research for many years.

*Authoring on behalf of all members of the COST action 925: http://www.agrsci.dk/costaction925/index.html
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The main aim of this review is to present recent knowledge on the genetic components of skeletal muscle growth in a variety of species, such as pig, sheep, cattle, rabbit, poultry and fish, and to show the consequences for growth performance, carcass quality and meat/flesh quality, which are of great economic importance in animal production.

Introduction

There is increasing evidence that influences on prenatal and early postnatal development of skeletal muscle can result in long-term effects on postnatal growth and physiological function both in animals and in human beings. In farm animals, these long-term effects of developmental origin have an impact on economically important traits such as vitality, growth performance, body composition and meat quality. However, the ways in which genotype, genome and physiology contribute to this interaction remains uncertain. Prenatal growth is determined by the genotype of the conceptus, but also depends on the maternal uterine or *in ovo* milieu of hormones, nutrients and growth factors. Understanding the mechanisms that control prenatal development and growth are critical to define strategies to reduce the incidence of developmental disorders and their long-term consequences.

In order to intensify research in this field and to stimulate scientific discussion on the developmental origin of farm animal performance, a European network, COST action 925 'The importance of prenatal events for postnatal muscle growth in relation to the quality of muscle based foods' was established. This EU-supported COST action (2004 to 2008) brought together scientists from 20 European countries and promoted the mutual exchange of scientific knowledge and resulted in a series of collaborative research projects. Moreover, training of young scientists in this research area was a priority and training grants were available for research visits to participating institutions of the member states.

This review summarizes the main outcomes of research based on the scientific results obtained from experiments with mammals, poultry and fish over 4 years (2004 to 2008) by participants of the COST 925 action and refers to previously published data that were inspirational and stimulating for pursuing research. These include prenatal regulatory mechanisms of skeletal muscle development, genetic and environmental impact on muscle development and its consequences for animal performance and meat quality as well as advances and standardization of research methodologies in this area. Moreover, this review will identify the main gaps and open questions in this field of research. Before the start of COST 925, research mainly focussed on human and laboratory animals representing mammals. The four myogenic regulatory factors (MRF), transcription factors regulating muscle-specific expression patterns, both during the prenatal stages of muscle tissue development and during postnatal muscle tissue functioning, were identified and each individual function was investigated using knockout gene technology (for a review see Te Pas and Soumillion, 2001). In livestock species, especially pigs, the associations between genetic variation at the DNA and mRNA expression levels of the MRF genes and growth and meat/muscle traits were determined (Te Pas *et al.*, 1999a, 1999b and 2000). Furthermore, in livestock the relationship between prenatal myogenesis/myofibre number on one side and growth and meat-related traits on the other side became known, as well as the evidence that myofibre number can be manipulated (for reviews see Stickland *et al.*, 2004; Rehfeldt *et al.*, 2004a). The state-of-the-art of genetics in aquaculture, with the exception of Atlantic salmon and tilapia (Circa *et al.*, 1995) was rudimentary and complicated by the diversity of species that are produced. Expressed sequence tags (ESTs) and genetic markers (e.g. randomly amplified polymorphic DNAs and amplified fragment-length polymorphisms) had been developed for a number of species of commercial interest but association of genes with phenotype was largely lacking (for review see Liu and Cordes, 2004; Canario *et al.*, 2008). Some of the factors reported in livestock to modulate postnatal growth rate and control muscle growth were also identified in some fish (for review see De-Santis and Jerry, 2007). With this knowledge, ongoing and new research during COST 925 aimed at the extension of knowledge with regard to animal muscle tissue development and function in relation to livestock performance.

This review (part II) focuses on genetic tools to improve animal growth performance and product quality. It describes important effects of breeding and selection and presents candidate genes, quantitative trait loci (QTL) and gene polymorphisms that are important for lean growth and meat quality. In addition, the review highlights advances in methodologies and defines future perspectives of research in the field (for part I see Rehfeldt *et al.*, 2011).

Genetic factors related to skeletal muscle growth and animal performance

Breeding and selection

Selecting animals from a base population for a certain trait improves the phenotype for that trait compared with the original population. Divergently selecting animals increases the difference for that trait, but removes the basis population. The selection response shows that a trait has an underlying genetic regulatory mechanism.

For many livestock species, selection is hampered by a relatively long generation time. Therefore, model species like mice have been used. Rehfeldt *et al.* (2004b) selected mice for 70 generations using body weight (BW) at day 42 of age. In the lines of mice generated in addition to increased growth rate and BW, modifications included changes in myoblast characteristics such that apoptosis of isolated cells was decreased *in vitro*. However, apoptosis caused by withdrawal of growth factors by serum deprivation was enhanced, and the response was largely independent of the stage of myogenic development.

The lines of mice produced were also used to study gene expression, and the effect of introducing specific mutant genes. The *myostatin* gene functions to reduce the number of myofibres formed. However, when the compact mutant

myostatin allele was introduced into a mouse line selected for high growth (HG) it had substantially increased muscle and leg weight and dressing percentage, an indicator for overall muscularity. At the same time these animals showed lighter BW. Hypermuscularity caused by mutations in the *myostatin* gene on this genetic background resulted from increased muscle fibre number rather than hypertrophy and from balanced increases in myonuclear proliferation and protein accretion. However, capillary supply was adversely affected and muscle metabolism shifted towards glycolysis, which could have negative consequences for physical fitness (Bünger *et al*., 2004; Rehfeldt *et al*., 2005). Molecular profiling of muscle in *myostatin* null mice showed a differential expression of genes and proteins related to muscle energy metabolism and cell survival/anti-apoptotic pathway and revealed the PI3K and apoptotic pathways as myostatin targets (Chelh *et al*., 2009).

Domestication of livestock species can be regarded as a long-term selection experiment improving production traits along with traits such as handling of the animals. Ruusunen and Puolanne (2004) and Rehfeldt *et al*. (2008) compared growth and muscular properties of wild and domestic pigs (DP). Despite higher weight, muscles of DP exhibited lower numbers of myofibres and were less mature at birth, which was associated with a lower proliferation rate of derived myoblasts. During postnatal growth, the higher gain in muscle mass of DP resulted mainly from accelerated myofibre hypertrophy and increased protein accretion. DP muscles exhibited higher proportions of fast-twitch (type IIb) white glycolytic fibres associated with lower capillary density than wild pigs, particularly in light muscles.

Similarly, the genetic background of traits can be studied by comparing (extreme) breeds that differ for a trait as the breeds are themselves the result of long-term selection. Lefaucheur *et al*. (2004 and 2005) compared the Meishan (MS) and local Basque breeds known to exhibit lower growth rate, poorer feed efficiency and lower lean meat content, but superior sensory meat quality compared with Large White (LW) pigs. The total fibre number in *Musculus semitendinosus* of MS and local Basque breeds were significantly lower compared with LW ($\sim$20%). Furthermore, LW muscle contained more white type muscle fibres, whereas Basque showed a higher portion of red muscle fibres. This was also supported by expression levels of myosin heavy chain (*MyHC*; *MYH*) genes. The underlying mechanisms seemed to differ between muscle portions. The reduced total number of fibres in MS pigs resulted from a lower number of primary myotubes in the portion destined to be white, and from a decreased secondary/primary ratio in the future red portion (Lefaucheur *et al*., 2004; Lefaucheur and Ecolan, 2005). Gil *et al*. (2008) compared five porcine lines based on LW, Landrace, Duroc, Piétrain and MS genetic backgrounds for meat quality traits. Meat lightness (L*) and drip loss were associated with the muscle glycolytic capacity (glycolytic ratio and fast glycolytic (FG) fibres) and inversely correlated with slow oxidative (SO) fibres and MyHCI. Conversely, muscle redness correlated positively with pigment content, SO fibres and MyHCI but correlated negatively with the glycolytic ratio. The main differences in the *Musculus longissimus* were found between the MS and Piétrain lines with regard to muscle fibre size and the percentage of FG fibres. The Duroc line was characterized by a greater proportion of SO fibres and muscle redness, and the Landrace line exhibited greater proportion of FG fibres and lighter muscles. LW tended to lie among the other breeds for many of the traits.

In the growing pig, increasing feed efficiency is a way to reduce the production cost. Lefaucheur *et al*. (2005 and 2008) selected four generations of LW pigs for residual feed intake (RFI), which is defined as the difference between the observed and the theoretical daily feed intake, estimated from maintenance and production requirements. The pigs that used feed more efficiently (RFI−) exhibited leaner carcasses with higher muscle content, lower backfat thickness and lower intramuscular fat content in *M. longissimus*. The higher muscle content of the RFI− pigs was associated with increased myofibre hypertrophy, a dramatic increase in glycogen content of fast-twitch glycolytic (FTG) fibres, a slight increase in the proportion of glycolytic fibres and a decrease in the activity of enzymes involved in fatty acid β-oxidation, associated with a higher glycolytic potential, higher drip loss and L* and a lower ultimate pH in *M. longissimus*, suggesting impaired meat quality in efficient RFI− *v.* luxurious RFI+ pigs. Using the model of simulated selection in a number of 2024 related pigs, Fiedler *et al*. (2004) were able to show that muscle fibre characteristics could be used as selection criteria for simultaneous improvement of carcass composition and meat quality by including indices developed from performance and fibre traits.

In cattle breeds, the segregation of the *myostatin* gene mutation causing the double-muscled phenotype is the most differentiating genetic factor for muscle/meat mass determination. The mutation causes an increase of myofibre numbers, as well as fibre hypertrophy. Deveaux *et al*. (2003) showed that myostatin was maximally expressed during fusion at early differentiation after the proliferation phase has ceased indicating a regulatory role in cattle myogenesis. Differential proteomic analysis of *M. semitendinosus* from double- and normal-muscled Belgium Blue cattle showed that 13 proteins were significantly altered in response to the *myostatin* deletion (Bouley *et al*., 2005). The differential mRNA splicing of fast troponin T was altered by the loss of myostatin function. The observed changes in protein expression are consistent with an increased fast muscle phenotype, suggesting that myostatin negatively controls mainly FTG muscle fibre number. Transcriptomic analysis also confirmed an elevated expression of genes involved in FG properties in double-muscled cattle and revealed other new markers of muscle hypertrophy (Cassar-Malek *et al*., 2007).

Analysis of muscle hypertrophy in Charolais bulls selected for a high muscle growth showed a higher total number of fibres. From the last trimester of gestation onwards, this was associated with a higher proportion of IIx fibres (FG) as in double-muscled foetuses. However, the delayed physiological

maturity of these bulls induced a delay in the plasticity of muscle fibres after birth. Consequently, the effects of selection on growth rate on muscle properties are not evident at each stage (Picard *et al.*, 2005).

In rabbits, Gondret *et al.* (2005) and Larzul *et al.* (2005) investigated the responses of a divergent growth selection (on 63 day BW) when the animals were slaughtered at the same BW or at a similar age. At same slaughter age, the differences in weight between low, control and high lines were associated with a proportional decrease in the weight and cross-sectional area, as well as myofibre area of *semitendinosus* muscle. Lipid deposition was reduced in the low line compared with the two other lines. However, none of these differences were seen when the animals were slaughtered at similar weight. In conclusion, divergent selection for growth rate had asymmetrical effects on myofibre size in rabbits slaughtered at the same age, but did not influence myofibre traits at a same weight.

In chicken, growth rate variations of genetic origin alter the cellular processes of muscle growth and differentiation and their regulation. Comparison of chickens with different growth rates, between or within lines, has shown that increased growth rate is usually associated with bigger muscle fibres and decreased glycogen stores, leading to less-acid meat and therefore a higher processing yield (Berri *et al.*, 2005 and 2007; Duclos *et al.*, 2007). Le Bihan-Duval *et al.* (2008) showed that genetic variability related to growth rate and muscle/meat quality characteristics using a heavy commercial broiler line. On average the heritability of meat quality traits in chicken such as pH, colour, water binding and shear force was approximately 0.3. The results suggested relevant selection criteria such as ultimate pH, which is strongly related to colour, water-holding capacity and texture of the meat in this heavy chicken line. Using experimentally selected chickens these authors showed that chicken with low abdominal fat had reduced glycogen stores and therefore higher pH and meat with better technological characteristics compared with fat chickens. The study outlines the potential involvement of enzymes controlling glycogen metabolism, notably AMPKα, which was phosphorylated at a higher level in lean than in fat chickens (Sibut *et al.*, 2008). It was shown that satellite cell activity was delayed in the low growth (LG) line compared with the HG line (Duclos *et al.*, 2005 and 2006; Berri *et al.*, 2006), using PAX7 and PCNA expression as measures of satellite cell number and proliferation, respectively.

For most species of fish used for aquaculture, breeding programmes have rarely been used, and only between 1% and 2% of production is based on genetically improved stocks. Notable exceptions are the Norwegian Atlantic salmon (Gjoen and Bentsen, 1997) and tilapia (Circa *et al.*, 1995), although generally uptake of genetics by the industry is poor. A large part of aquaculture production still relies on wild spawn or broodstock. Fish species such as carp, catfish, seabass, seabream and several other marine species are periodically 'refreshed' by introducing wild spawners (Gjedrem, 2000; Knibb, 2000). The diversity of fish species exploited for aquaculture, the molecular resources available and other logistical problems related to controlled breeding, the dimension and structure of the industry and the long investment period before dividend, means that genetic selection of fish for economically important traits is still in its infancy.

The increased availability of genomic tools and the reduction in the cost of their use has recently encouraged selective breeding using molecular genetics (reviewed by Canario *et al.*, 2008). QTL mapping has recently been successfully applied to traits such as BW and condition factor in full-sib families of salmonids (Reid *et al.*, 2005; Moghadam *et al.*, 2007). However, to fully reap the benefit of selective breeding a better understanding of the biology underlying complex traits such as flesh quality is required.

Expression of specific genes related to muscle content and meat quality

In rabbits, selection for growth rate for 14 generations resulted in lower MyHCI content and increased glycolytic metabolism of *M. longissimus* (higher aldolase activity) associated with lower water-holding capacity and poorer instrumental texture properties (Ramirez *et al.*, 2004). These results indicate an inverse relationship between growth rate and meat quality in rabbits, similar to other mammals.

Quantification of MyHC isoforms can also be used to indicate muscle and meat mass. Furthermore, muscle fibre type distributions may be quantified as indicators of differences in meat quality. Real-time PCR quantification of MyHC isoforms I, IIa, IIx and IIb showed that the relative expression of MyHC IIb was higher in animals with large *M. longissimus* area. Type IIb fibres are the most prominent in pigs having large muscle area, which implies that IIb is the determining fibre contributing to the differentiation of large and small loin eye muscle area in the pig. Frequencies of fibres, determined by ATPase muscle fibre staining, and relative abundance of MyHC isoforms, determined by quantitative reverse transcriptase (RT-PCR), of corresponding pairs of type I, IIa and IIx/IIb were significantly correlated (Ponsuksili *et al.*, 2008; Wimmers *et al.*, 2008). Bee and Deruy (2008) showed that the greater MyHC isoform gene expression corroborated with the larger myofibres in pigs of low birth weight. In chicken, it was shown that the mRNA expression of fast MyHC isoforms allows the development of the chicken *Musculus pectoralis major*, a pure FG muscle, to be followed. Higher growth rate of genetic or nutritional origin leads to faster isoform transcription, that is faster differentiation (Duclos *et al.*, 2005 and 2006; Berri *et al.*, 2006).

In a model of broiler strains divergently selected for HG or LG potential (Scanes *et al.*, 1989), circulating IGF1 levels were significantly higher in the HG line compared with the LG line at 7 weeks of age. This difference was no longer significant when measured in much older chickens (46 or 150 weeks of age). In turkeys, the comparison of a medium weight and a heavy weight line was carried out between 1 and 28 weeks of age (Goddard *et al.*, 1988). A positive phenotypic correlation was observed between plasma IGF1

levels and growth rate until 7 weeks of age and higher circulating concentrations were indeed observed in the selected line. In addition, this relationship was not conserved in older birds. Mechanisms of action of IGF have been explored in two divergently selected lines of broilers with HG or LG rate. Larger muscle fibres and a higher number of myonuclei were observed in the HG line. Higher circulating levels of total IGF were observed in HG compared with LG chickens between 1 and 12 weeks old (Beccavin *et al*., 2001). Breast muscle IGF1 mRNA also tended to be higher (Guernec *et al*., 2003). Among the three major IGF-binding proteins (IGFBPs) described earlier (28, 34 and 40 to 42 kDa), only IGFBP-(34 kDa) was higher in HG than LG chickens at 6 weeks of age (Beccavin *et al*., 2001) Therefore, higher circulating concentrations of IGF1 and IGF2 in HG compared with LG chickens, together with comparable levels of IGF receptors in the target tissues are consistent with the difference in growth rate between the two genotypes. *In vitro* experiments, using satellite cells isolated from 1- to 7-day-old chickens have also shown that stimulation of DNA synthesis by serum or IGF1 was of significantly higher amplitude in HG than in LG cells (Duclos *et al*., 1996). Chickens selected for high breast meat yields (Le Bihan-Duval *et al*., 1996) exhibited slightly higher circulating IGF1 concentrations compared with unselected controls, but similar IGF2 concentrations (Tesseraud *et al*., 2003). In the *M. pectoralis major*, IGF1 mRNA levels were significantly higher in the selected chickens at 4 and 6 weeks of age, when breast meat yields were most different (Guernec *et al*., 2003).

In cattle, the double-muscle phenotype of extreme muscle hypertrophy caused by a mutated *myostatin* (*MSTN*) gene affected growth, muscle mass and meat quality. The presence of the mutant *myostatin* gene in homozygous or heterozygous states was studied on the *M. longissimus* from yearling bulls of the Asturiana de los Valles breed. Homozygous animals presented higher glycolytic characteristics (higher lactate dehydrogenase activity, lower isocitrate dehydrogenase activity and lower pigment content), lower intramuscular fat and lower collagen content than heterozygous animals. Meat quality was also influenced by the genotype so that the *M. longissimus* from homozygous bulls showed lighter colour, lower water-holding capacity and lower background (collagen) toughness than the muscle from heterozygous bulls. Collagen solubility and shear force of cooked meat were not significantly different between the genotypes (Oliván *et al*., 2004).

In fish, molecular markers have been used until now mainly in the characterization of developmental processes and in response to nutritional factors, which is described in a companion review (part I see Rehfeldt *et al*., 2011).

QTL and polymorphisms in candidate genes – associations with muscularity and meat quality traits

The most general approach for identifying the genomic position of genes regulating specific traits is positional mapping. The inheritance of a trait is compared with the segregation of large numbers of marker genes. Microstructural properties of pig muscle and meat quality are governed by genetic variation at many *loci* distributed throughout the genome. In the pig, regions with significant QTL for either muscle fibre traits or meat quality and muscularity (or both) were detected on chromosomes SSC1, 2, 3, 4, 5, 13, 14, 15 and 16. Moreover, QTL for microstructural properties explained a larger proportion of variance than did QTL for meat quality and body composition. It is thought that genomic regions affecting complex traits of muscularity and meat quality as well as microstructural properties might point to QTL that in the first instance affect muscle fibre traits and then meat quality. Disentangling complex traits in their constituent phenotypes might facilitate the identification of QTL and the elucidation of the pleiotropic nature of QTL effects (Wimmers *et al*., 2005, 2006a and 2006b; Liu *et al*., 2007). Finally, QTL could be affected by a specific type of inheritance called epigenetic inheritance. Muráni *et al*. (2007a) describe how epigenetics underlying stage- and breed-specific differences in the transcription of *SPP 1* gene can affect porcine myogenesis. Demars *et al*. (2007) investigated metabolic and histochemical characteristics of fat and muscle tissues in homozygous and heterozygous pigs for the body composition QTL located on chromosome 7. They found that heterozygous LW_{QTL7}/MS_{QTL7} pigs at the SSC7 QTL had smaller adipocytes ($P = 0.01$) in backfat, together with a lower basal rate of glucose incorporation into lipids and lower activities of selected lipogenic enzymes in backfat isolated cells ($P < 0.05$), compared with homozygous LW_{QTL7}/LW_{QTL7} pigs. A higher number of adipocytes was also calculated in backfat of LW_{QTL7}/MS_{QTL7} pigs compared with LW_{QTL7}/LW_{QTL7} pigs. The SSC7 QTL did not influence oxidative and glycolytic metabolism of *longissimus* and *trapezius* muscles, as estimated by the activities of specific energy metabolism enzymes or myofibre type properties. Altogether, this study provides new evidence for an altered adipocyte cellularity in backfat of pigs carrying at least one MS allele for the SSC7 QTL.

In chicken, the genetic basis of meat quality traits has been studied in a F2 cross between experimental chicken lines showing HG or LG rates (Nadaf *et al*., 2007). Notably, a strong QTL controlling meat colour was detected on chicken chromosome 11. Some QTL controlling meat pH15 and drip loss have also been found on chromosome 11 and another controlling ultimate pH (pHu) on chromosome 4.

No QTL studies on fish and rabbits were conducted in the COST community, and there are only a few available for rabbit as the rabbit genome has not been thoroughly studied until recently, and high-resolution maps necessary for identification of genes and QTL are not yet available (Chantry-Darmon *et al*., 2005).

Another approach to elucidate genetic regulation of traits uses candidate genes to evaluate the relationship between genetic variation and traits. Genes may be derived from physiological or genomic information. One such example is shown by Maak *et al*. (2006) who performed a comparative sequence analysis of the myogenic factors (*MYF*) *5* or *6* locus in swine, cattle, dog, chicken and zebrafish on the basis of

structural and functional information from human and mouse. As the *MYF5* and *MYF6* are integral to the initiation and development of skeletal muscle and to the maintenance of its phenotype, these genes may be important candidate genes. Four more conserved elements and 21 single nucleotide polymorphisms were found in the promoter area of the genes. The conserved organization of the *locus* in vertebrates indicates a common basic mechanism of muscle development. However, the existence of numerous regulatory elements at large distances to *MYF5* and *MYF6* points to a very complex pattern of gene regulation with significant differences between species.

Another example detected differential gene expression between Piétrain and Duroc pig breeds differing for muscle traits. Prenatal muscle samples were taken at seven time points covering proliferation and differentiation processes of both primary and secondary waves of muscle development (Te Pas *et al*., 2005a, 2005b and 2006; Cagnazzo *et al*., 2006; Muráni *et al*., 2007b). A total of 10 genes ([1]*ANK1*, *bR10D1*, *CA3*, *EPOR*, *HMGA2*, *MYPN*, *NME1*, *PDGFRA*, *RAB6IP2* and *TTN*) were examined for association between polymorphisms and meat quality and carcass traits in 1700 performance-tested fattening pigs of commercial purebred and crossbred herds of Duroc, Piétrain, Piétrain × (Landrace × LW), Duroc × (Landrace × LW) as well as an experimental F2-population based on a reciprocal cross of Duroc and Piétrain. Nine of these genes showed associations at a nominal *P*-value $\leqslant 0.05$, except for *PDGFRA*. In particular, *HMGA2*, *CA3*, *EPOR*, *NME1* and *TTN* were associated with meat colour, pH and conductivity of loin 24 h *post mortem*; *CA3* and *MYPN* exhibited association with ham weight and lean content (fibre-optic measurement; FOM), respectively, at *P*-values <0.003 that correspond to false discovery rates <0.05. However, none of the genes showed significant associations for a particular trait across all populations (Wimmers *et al*., 2007). Muráni *et al*. (2008) reported similar investigations with the porcine *SMAD7*[1] gene using these same samples.

The *IGF2* mutation is a specific example of candidate gene research. The *IGF2* intron 3 mutation increased carcass lean meat percentage with approximately 4.5% as a result of decreased backfat thickness and to a lesser extent of muscle accretion but without any noticeable effect on meat quality or on the properties of cured cooked loin production. The mutation is located in the regulatory sequence of the paternal expressed *IGF2* gene. An elevated IGF2 mRNA expression in the muscle is responsible for the increased lean meat content. The effects were studied at four different ages (4, 8, 16 and 26 weeks of age) and by identifying the changes due to the *IGF2* mutation in biochemical and histochemical muscle fibre characteristics in pigs at slaughter weight. The effect of the *IGF2* mutation was studied in relation to the mutation in the *RYR1*[1] gene because they both increase lean meat content in pigs but with different effects on meat quality. However, there were no interaction effects of the two mutations on meat quality. At the cellular level, fibre type composition and metabolic enzyme activities were not significantly affected by the *IGF2* and *RYR1* mutations. A prenatal effect of the *IGF2* mutation on muscle fibre hyperplasia could not be completely ruled out and did not seem to be the main factor involved in the higher lean meat percentage of these animals. In contrast, the increased muscle hypertrophy due to the *IGF2* and *RYR1* mutations was clearly related to an increased mean cross-sectional area of the muscle fibres and a higher proliferative capacity of satellite cells. In addition, the differences in proteolytic potential of m-calpain (ratio of m-calpain : calpastatin) can be linked to satellite cell activity. Differences in calpastatin activity and proteolytic potential of m-calpain suggested that the higher percentage muscle mass in animals bearing the *IGF2* mutation may be associated with decreased protein degradation or increased protein accretion. In addition, the presence of two-way interactions between the *IGF2* and *RYR1* genotype for muscle fibre characteristics suggested that the mechanisms involved in increased leanness due to the impaired RYR1 receptor influenced the effects of the *IGF2* mutation and *vice versa* (Stinckens *et al*., 2007; Van den Maagdenberg *et al*., 2007a, 2007b and 2008; Gardan *et al*., 2008).

Valente *et al*. (2006) investigated the association between rainbow trout growth rate and polymorphisms in the *myostatin* genes by comparing fast and slow growing strains. The authors reported several silent mutations in the two *myostatin* genes studied, but no missense mutation. Other allelic polymorphisms, probably related to the existence of heterozygosis within strains, were also detected in *myostatin 1*. No sequence variation was found in the two *myostatin* genes, which would obviously modify the functional properties of the corresponding proteins in either of the two fish strains.

Le Bihan-Duval *et al*. (2007) conducted experiments to develop tools linking QTL and functional genomic expression studies in chicken (microarrays, genetic markers and resource chicken populations segregating traits of growth rate or body composition). Ongoing studies outline that these resources are useful for the identification of genes controlling growth and meat quality traits. Therefore, in section 'Advances in methodology' we describe the reported studies using functional genomics (i.e. transcriptomic and proteomic studies) aimed at understanding the genetic regulation of muscle traits, especially meat quality related traits.

Advances in methodology

Advances in research of the genetic control and endogenous and exogenous effects modifying the expression of traits related to meat quality and growth have been made by the application of holistic 'omics' techniques, the development of new methods for muscle fibre typing and the adaptation of biophysical measures to develop parameters of muscle fibre traits as well as the application of *in vitro* studies.

[1] ANK1, Ankyrin-1; bR10D1, EST (Muráni *et al*., 2007b); CA3, carbonic anhydrase 3; EPOR, erythropoietin receptor; HMGA2, high mobility group protein A2; MYPN, myopalladin; NME1, nucleoside diphosphate kinase A2; PDGFRA, PDGF receptor alpha; RAB6IP2, Rab6-interacting protein 2; TTN, titin; SMAD7, mothers against decapentaplegic homolog 7; RYR, ryanodine receptor.

In animal science, attempts to use holistic transcriptomics and proteomics were made in order to elucidate tissue-specific differential gene expression in relation to developmental processes and/or phenotypes. The results significantly improve and specify lists of candidate genes for economically important traits including meat quality. These traits depend on prenatal events and postnatal nutrient utilization affecting growth and tissue deposition (Wu *et al*., 2008). Consequently, prenatal and postnatal expression patterns were surveyed to obtain comprehensive inventories of genes and functional networks relevant to traits related to body composition and meat quality.

Transcriptomics

Microarrays were successfully used to identify genes that are differentially expressed in muscle tissue due to developmental stage/age, breed or phenotype in the pig. Application-specific cDNA macro- and microarrays have been used to monitor the expression of several hundred to thousands of genes during myogenesis (Seo and Beever, 2001; Ernst *et al*., 2002; Bai *et al*., 2003; Zhao *et al*., 2003). Using targeted microarrays covering 509 genes known to affect myogenesis, muscle structural proteins and energy metabolism expression profiles at seven key prenatal developmental stages of muscle were studied. Genes were assigned to biological processes such as myoblast proliferation and differentiation and energy metabolism. Analyses during myogenesis revealed the highest expression of differentiation regulating genes at time points of formation of primary and secondary myofibre formation, preceded by peaked expression of genes stimulating myoblast proliferation. Genes regulating energy metabolism had lowered expression values around the time when myogenic differentiation was taking place (Te Pas *et al*., 2005a, 2005b and 2006). Comparisons of gene expression in the Duroc and Piétrain pig breeds, which differ in muscularity and meat quality, revealed delayed myogenesis in Piétrain and a higher energy metabolism but lower lipid metabolism and deposition in Piétrain compared with Duroc (Cagnazzo *et al*., 2006). The development of bioinformatics tools enabled refining the results by making use of pathway information accessible via Gene Ontology and KEGG databases (Te Pas *et al*., 2007a and 2007b). As an alternative approach to microarray analysis the mRNA differential display technique (DD-RT-PCR) was applied as an open system potentially displaying all transcripts. Comparisons between Duroc and Piétrain at seven stages of myogenesis revealed 448 fragments varying either in their intensity or presence. The most frequent functional categories represented genes encoding myofibrillar proteins, genes involved in cell adhesion, cell–cell signalling and extracellular matrix synthesis/remodelling, genes regulating gene expression and metabolism genes. On the basis of the analysis of breed differences the study revealed several genes differentially expressed during skeletal muscle development of DP that were not yet associated with myogenesis and thus provide novel insights into molecular pathways employed in mammalian myogenesis (e.g. the autophagy pathway) (Wimmers *et al*., 2005; Muráni *et al*., 2007b). Expression profiling by microarrays and DD-RT-PCR revealed a number of genes whose candidacy for meat quality and carcass traits in pigs arises from their differential expression among divergent breeds during myogenesis. Statistical–genetic evidence for association of the functional candidate genes with traits related to meat quality and muscle deposition was provided by Wimmers *et al*. (2007). In addition, application-specific microarrays were developed for cattle and chicken. Comparisons of expression profiles of *M. longissimus thoracis* from 25 Charolais bull calves of high and low meat quality using a microarray of $>$5000 muscle expressed genes revealed 215 genes that were differentially expressed according to tenderness, juiciness, and/or flavour including *DNAJA1*, which encodes a heat shock protein that became a patented marker of beef sensory quality (Bernard *et al*., 2007). In chicken, several application-specific microarrays have been established based on $>$35 000 ESTs (Cogburn *et al*., 2004 and 2007). Ongoing studies outline that these resources are useful for the identification of genes controlling growth and meat quality traits.

Microarrays have also been used to study transcriptional changes during muscle recovery after fasting in the rainbow trout (Rescan *et al*., 2007). Among the genes induced were several unexpected transcriptional regulators (e.g. *AATF*) and signalling molecules (e.g. *seraf*), which might be important for the gene-specific transcriptional adaptations that underlie the burst of muscle growth induced by re-feeding.

Proteomics

The level of protein expression was surveyed during myogenesis and in relation to meat quality. Two-dimensional gel electrophoresis combined with mass spectrometry of *M. semitendinosus* from Charolais foetuses, at three specific stages of myogenesis revealed $>$170 differentially expressed proteins that were assigned to biological functions such as the control of cell cycle activity and apoptosis, the establishment of cellular metabolism and muscle contractile properties and muscle cell reorganization (Chaze *et al*., 2006 and 2008). The study of trait-dependent gene/protein expression also contributes to progress in understanding the mechanisms controlling *post mortem* muscle metabolism and meat quality. Consequently, during COST 925 a protein reference map of bovine *M. semitendinosus* muscle was established using proteomics techniques covering 129 protein spots corresponding to 75 different gene products involved in metabolism (25.5%), cell structure (17%), cell defence (16%) and contractile apparatus (14.5%; Bouley *et al*., 2004). Differential proteomic analysis revealed that 13 proteins, corresponding to 28 protein spots, were significantly altered in response to the myostatin deletion in cattle (Bouley *et al*., 2005). In the pig, during prenatal and postnatal muscle development 295 spots were identified that represent differentially expressed proteins (Lefaucheur and Ecolan, 2007). In addition, proteomic approaches were used to focus on intramuscular fat content and meat quality. Therefore, trait-dependent protein expression profiles and

profiles of *post mortem* protein degradation were studied (van de Wiel and Zhang, 2007; Bérard *et al*., 2008; Te Pas *et al*., 2008; Liu *et al*., 2009).

Muscle fibre traits

The importance of muscle fibre number, size and type for meat quality and growth has been reproducibly demonstrated. However, the relationships between muscle fibre characteristics, meat quality and carcass composition are not quite consistent across different studies. In COST 925 it was discussed that in terms of sensory meat quality and consumers perception, muscle fibre traits are optimum curve traits similar to many technological characteristics of meat quality. Therefore, correlations between these traits are not linear. There is a need for improved phenotyping in terms of muscle fibre traits in order to better describe the relationship between traits related to muscle fibres, sensory and technological meat quality (Lefaucheur, 2006). Typing and counting of muscle fibres is based on histochemical differentiation by their metabolic (oxidative, oxido-glycolytic or glycolytic) and/or contractile (fast and slow) characteristics and subsequent microscopic evaluation (Ashmore *et al*., 1972; Peter *et al*., 1972). Classification based on myofibrillar ATPase histochemistry distinguishes three types of fibres in adult pig muscle (Harrison *et al*., 1997; Henckel *et al*., 1997; Ruusunen and Puolanne, 2004; Gil *et al*., 2008) named slow-twitch type I and fast-twitch type IIa and IIb according to Brooke and Kaiser (1970). A combination of ATPase reaction and enzymatic activities of NADH-tetrazolium reductase or succinate dehydrogenase reveals slow-twitch oxidative, fast-twitch oxidative and FTG fibres. A survey towards the repeatability of measurements of muscle fibre characteristics by ATPase staining revealed that three samples were sufficient for estimation of total fibre number in porcine *M. longissimus*. However, five or more samples per muscle should be analysed in order to accurately determine other muscle fibre traits, such as mean fibre area, fibre type composition and the relative area occupied by each fibre type (Cerisuelo *et al*., 2007). In skeletal muscle, myosin represents the vast majority of the contractile apparatus (Picard *et al*., 2002). Four out of eight isoforms of *MyHC* genes known in mammals have been identified in porcine muscle (Chang and Fernandes, 1997). Immunohistochemistry (Graziotti *et al*., 2001; da Costa *et al*., 2002; Lefaucheur *et al*., 2004), *in situ* hybridization (Graziotti *et al*., 2001; da Costa *et al*., 2002; Lefaucheur *et al*., 2004) and electrophoresis (Bee *et al*., 1999) have been used to examine muscle fibre typing essentially based on the discrimination of MyHC isoforms. Newly developed real-time PCR assays have been reported to distinguish four isoforms in pig skeletal muscle (da Costa *et al*., 2002; Lefaucheur *et al*., 2004). Frequencies of fibres determined by muscle fibre staining for ATPase and relative abundance of MyHC isoforms determined by quantitative reverse transcription-PCR of corresponding pairs of type I, IIa and IIx/IIb were correlated ($r = 0.71$, 0.67 and 0.52, respectively) (Ponsuksili *et al*., 2008; Wimmers *et al*., 2008). It was concluded that the real-time PCR assay represents a new phenotype close to the effect of genes, which is probably more suitable to unravel the genetic background in variation of traits related to muscle and meat properties depending on muscle fibre distribution. In sheep, a quantitative PCR method for determining ovine skeletal muscle fibre type composition based upon the expression of different adult MyHC isoform transcripts was shown to be suitable to observe changes in muscle fibre type composition at the molecular level (Hemmings *et al*., 2008a and 2008b).

Within COST 925 there were also attempts to determine the length of muscle fibres in order to enable estimation of total number of fibres in a muscle (Räsänen and Puolanne, 2004; Puolanne and Räsänen, 2008). The authors estimated the average length of fibres in porcine *M. longissimus* to be 173 mm based on the proportion of tapered ends from the cumulative length of counted fractions.

In addition, some biophysical methods were also evaluated within COST 925 to investigate their potential use to characterize muscle fibre traits. Functional near infrared spectroscopy (fNIRS) is a novel, non-invasive, rapid and inexpensive method that uses light sources and detectors placed on the skin surface to probe the oxygen metabolism of the underlying tissues. Sirin *et al*. (2008) found significant positive correlations between the proportion of oxidative muscle fibres in *Musculus semimembranosus* and the decrease in oxygen consumption (μmol/s) in response to electrical stimulation. Negative correlations were observed for proportions of type I or type IIb muscle fibres and decrease in oxygen consumption. In addition, there were negative correlations between the number of muscle fibres per unit area and decrease in oxygen consumption. The preliminary results indicate that fNIRS can be used to study the oxidative status of muscle tissue in sheep and may be a new method to determine metabolic types of muscle fibres in sheep non-invasively.

Evoked surface electromyography (SEMG) giving rise to recordings of compound muscle action potentials (CMAPs) offers a safe, quick, pain-free, non-invasive and repeatable technique for the assessment of the physiological processes that cause muscles to generate force and produce movement. Consequently, SEMG was evaluated as another non-invasive *in vivo* measurement of muscle (Tygesen and Harrison, 2005; Andersen *et al*., 2008). It could be shown that the shape of SEMG signals reflects postnatal growth in lamb (Tygesen *et al*., 2007). Furthermore, the shear force of muscle *post mortem* could be approximated from the CMAP parameter area (mV/s); however, the exact relationship between these parameters and fibre type composition of porcine muscles still remains to be elucidated (Andersen *et al*., 2008).

In vitro *studies*

In vitro models of porcine myoblasts have been established during the COST 925 action and successfully used as a helpful tool in studying a series of physiological processes in proliferating and differentiating muscle cells. Studies using porcine satellite cell cultures focused on the regulation of

IGFs due to metabolic state, the role of estrogens and effects of nutrition and dietary isoflavones (Nissen *et al*., 2005; Theil *et al*., 2006; Kalbe *et al*., 2007 and 2008; Mau *et al*., 2008a and 2008b). Proliferation and differentiation of satellite cells derived from low weight pigs showed lower differentiation rates than cells from medium and heavy weight littermates (Nissen and Oksbjerg, 2009). Cultures of muscle cells from gilthead seabream and rainbow trout were used to elucidate the role of IGFs in the regulation of metabolism and growth of fish muscle. In these fish species IGF1 and IGF2 exhibit mitogenic and metabolic effects via the MAPK and PI3K/Akt signalling pathways (Castillo *et al*., 2004 and 2006; Montserrat *et al*., 2007; Codina *et al*., 2008). In L6 muscle cells linoleic acid, oleic acid and the *c*9, *t*11 isomer of conjugated linoleic acid (CLA) all stimulated muscle differentiation, whereas *t*10, *c*12 CLA inhibited differentiation (Hurley *et al*., 2006). Other *in vitro* experiments focused on the role and regulation of members of the insulin signalling pathways and myostatin during myogenesis (Kwiecinska *et al*., 2005; Orzechowski *et al*., 2005; Pawlikowska *et al*., 2007a and 2007b).

Future perspectives

The present reviews (for part I: Regulation of myogenesis and environmental impact, see Rehfeldt *et al*., 2011) highlight the contribution of the COST action 925 to understand '*The importance of prenatal events for postnatal muscle growth in relation to the quality of muscle based foods*'. In summary, study carried out by members of COST 925 has defined some of the prenatal events that are important for postnatal muscle growth and meat quality of livestock. The gathering together of scientists working on diverse livestock including fish stimulated exchange of information and technology, which is evident from the comparative considerations about muscle growth in fish, poultry and mammalian species. Furthermore, significant additional knowledge on environmental and genetic regulation of prenatal events and consequences for postnatal growth and product quality has been provided. An important target of COST 925 was to discuss alternative methodological approaches for the assessment of muscle, and progress was made in methodologies utilized in this research area (see Archives of Animal Breeding 2005, 2006, 2007 and 2008), although it was acknowledged that challenges remain (e.g. fibre number *v.* quality). Moreover, it is expected that the collaborative links established between groups working on different species will consolidate in the future the power of comparative cross-species approaches. It is our hope that these reviews will show the importance of understanding the biological basis of muscle development and growth for sustainable meat production, and that a systems biology approach that integrates molecules to the whole organism and its environment is required.

This research area is buoyant and has many more scientists in Europe and throughout the world than those who participated in the COST 925 action. These reviews highlight the contribution of members of the COST action to this area of research and it should be apparent that there are still many challenges, including basic scientific questions as well as more applied questions. Moreover, recent technological advances (e.g. image analysis, transcriptomics and proteomics, etc.) are having a major impact and allowing new hypotheses to be generated and offering solutions to questions, which have until now remained intractable. Towards the end of the COST925 action, which had two main working groups; WG1 – environmental variation in prenatal events in relation to postnatal growth and meat/fish quality (see review, part I Rehfeldt *et al*., 2011) and WG2 – genetic variation in prenatal events and its effect on postnatal growth and meat/fish quality (this review), it was possible to draw up a common list of research priorities despite the very different scientific background and research interests of the scientists involved and these are now highlighted: (i) progress was made during the COST action in identifying some prenatal events important for postnatal growth performance and meat quality but this is a very complex issue which is multi-factorial and much more study will be required to reach a basic understanding about this interaction; (ii) the impact of environmental and genetic factors (and importantly their interaction) on prenatal events needs to be established and this then has to be linked with postnatal growth performance and meat quality; (iii) the wealth of data arising from molecular genetics studies, functional genomics, transcriptomics, proteomics and metabolomics need to be integrated with muscle tissue research and then translated into the context of high-quality food for humans; and (iv) from a food technology and human health perspective characterization of meat and fish quality at the genomic and proteomic levels may provide tools for prediction and management of food quality during food production, processing and storage.

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