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Consequences of divergent selection for residual feed intake in pigs on muscle energy metabolism and meat quality

J. Faure [a,b,*], L. Lefaucheur [a,b], N. Bonhomme [a,b], P. Ecolan [a,b], K. Meteau [c], S. Metayer Coustard [d], M. Kouba [a,b], H. Gilbert [e,f], B. Lebret [a,b]

[a] INRA, UMR1348 Physiologie, Environnement et Génétique pour l'Animal et les Systèmes d'Elevage, F-35590 Saint-Gilles, France
[b] Agrocampus Ouest, UMR1348 Physiologie, Environnement et Génétique pour l'Animal et les Systèmes d'Elevage, F-35000 Rennes, France
[c] INRA, UE1206 Élevage Alternatif et Santé des Monogastriques, Domaine du Magneraud, F-17700 Saint-Pierre-d'Amilly, France
[d] INRA, UR83 Recherches Avicoles, F-37380 Nouzilly, France
[e] INRA, UMR0444 Laboratoire de Génétique Cellulaire, F-31326 Castanet-Tolosan, France
[f] INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78352 Jouy-en-Josas, France

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ABSTRACT

Selection to decrease Residual Feed Intake (RFI) is a relevant way to improve feed efficiency in growing pigs. However, RFI criterion is correlated with body composition and muscle characteristics. Present study evaluated adaptive responses to divergent selection on RFI on muscle metabolism and homeostasis through AMP-activated protein kinase pathway. Consequences on technological and sensory meat quality were also analyzed in two lines of Large White pigs after six generations of divergent selection on RFI.
RFI$^-$ pigs (n = 60) exhibited similar growth rate but lower feed intake and conversion ratio, and were leaner than RFI$^+$ pigs (n = 57). Despite higher glycogen content, metabolic enzyme capacities involved in glycolytic, fatty acid oxidation pathway and energy balance were reduced in the *Longissimus* muscle of the RFI$^-$ pigs. Reduced muscle homeostasis in the RFI$^-$ line influenced post-mortem metabolism and impaired technological quality traits of loin and ham but had only slight effects on meat eating quality.

1. Introduction

In the context of intensive European pig production, producing meat as efficiently as possible strives for a sustainable production system (Olesen, Groen, & Gjerde, 2000). Thus, improving efficiency of pig production requires maintaining productivity, improving utilization of feed by animals, reducing environmental impact, and improving social acceptance of products in particular by insuring meat quality.

Different breeding objectives and selection criteria have been developed to meet these challenges of pig meat production. Regarding feed efficiency, selection for low Residual Feed Intake (RFI) is seen as a relevant way to improve sustainability of pig production (Dekkers & Gilbert, 2010). RFI represents the part of individual total feed intake unexplained by maintenance and production(Kennedy, van der Werf, & Meuwissen, 1993). This criteria is thus assumed to be independent from lean and fat tissue deposition and body composition (Herd & Arthur, 2009) when computed at the phenotypic level. However, different studies on lines selected for RFI have shown correlated responses on body leanness (Cai, Casey, & Dekkers, 2008; Gilbert et al., 2007; Hoque et al., 2009) and on muscle characteristics (Lefaucheur et al., 2011). In this last analysis, high muscle glycogen store and low intramuscular fat content in white muscle of the low RFI line were found and suspected to impair meat quality. However, a better understanding of the underlying physiological mechanisms involved in muscle adaptive responses to divergent selection for RFI is still needed to better understand the relationships between growth efficiency, muscle metabolism and meat quality traits, to avoid undesired effects of selection on meat quality.

As part of the regulating network maintaining cell homeostasis, the AMP-activated protein kinase (AMPK) enzyme has been shown to play a key role in the regulation of muscle glycogen level and post-mortem (p.m.) metabolism (Kahn, Alquier, Carling, & Hardie, 2005; Scheffler & Gerrard, 2007). In response to a cellular stress and to an increase in the AMP: ATP ratio, AMPK is activated allosterically and by phosphorylation on Thr172 of the AMPKα subunit (Scheffler, Park, & Gerrard, 2011). Overall, AMPK activation inhibits anabolic pathways and stimulates catabolic pathways to restore cellular energy level (Scheffler & Gerrard, 2007). Thus, AMPK is a cellular and whole body energy sensor potentially involved in the energy metabolism efficiency which modulates muscle metabolism and meat quality.

Comparing high (RFI$^+$, luxurious) and low (RFI$^-$, efficient) RFI pig lines after six generations of divergent selection, our study aimed at confirming adaptive responses of muscle metabolism to divergent

* Corresponding author at: Agrocampus Ouest- INRA, UMR 1348 Physiologie, Environnement et Génétique pour l'Animal et les Systèmes d'Elevage, 65, rue de St Brieuc, 35 042 Rennes cedex, France. Tel.: +33 223485848; fax: +33 223485080.
E-mail address: justine.faure@rennes.inra.fr (J. Faure).

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selection reported in Lefaucheur et al. (2011) after two additional generations of divergent selection in the same population on a larger number of animals and understanding how these adaptations affect energy homeostasis and technological and sensory meat quality, with a special emphasis on the AMPK pathway.

2. Materials and methods

2.1. Ethic statement

The experiment was conducted following French guidelines for animal care and use edited by the French Ministries of High Education and Research, and of Agriculture and Fisheries (http://ethique.ipbs.fr/sdv/charteexpeanimale.pdf).

2.2. Animals and selection

Divergent selection on RFI was conducted within the Large White breed according to the experimental design previously described by Gilbert et al. (2007). Briefly, selection has been carried out on non castrated males, tested between 35 and 95 kg of body weight (BW), whereas one female was randomly replaced its dam in the following generation. After six generations of selection, the predicted residual feed intake was calculated by multiple regression as follows: RFI, g = DFI, g − 106.34 MBW, kg − 1.30 ADG, g/d − 5.03 BT, mm + 22.37 LMC, point + fixed effects, where DFI is daily feed intake, MBW is metabolic body weight, ADG is average daily gain, BT is average back-fat thickness, and LMC is lean meat content.

The present study included a total of 117 Large White females (F) and castrated males (CM) from the sixth generation of selection (60 from RFI^- and 57 RFI^+ lines). The difference of average breeding values between lines for this sub samples were similar to their sibs tested in a large sample for all traits. To avoid aberrant post-mortem (p.m.) metabolism, pigs were homozygous NN for the HAL (RYR1) gene and were free of the PRKAG3 R225Q gene mutation coding for an altered isoform of AMP-activated protein kinase (Scheffler & Gerrard, 2007).

From weaning to slaughter, all animals were raised under the same rearing conditions, animal density and controlled temperature in three successive contemporary groups in the GEPA experimental farm of INRA (Rouillé locations France). Pigs were placed within sex and RFI line in collective pens of 12 animals fed *ad libitum* with an energy and protein balanced diet (9.7 MJ net energy /kg, 16% crude protein). All pigs were tested individually during the growing-finishing period (30 ± 5 kg to 108 ± 8 kg, i.e. 70 up to 171 ± 4 d) for body weight (BW), back-fat thickness (BT) and daily feed consumption using a single-place electronic feeder (ACEMA 64, Pontivy, France) to compute average daily gain (ADG) during the test.

2.3. Handling and slaughtering

Pigs were slaughtered at the experimental slaughterhouse of INRA (PEGASE, St Gilles, France) in six slaughtering sessions, each including 5 pigs per sex and line, i.e. 2 slaughtering sessions per contemporary groups separated by an 8-d interval, and with standardization of slaughter conditions between all slaughter sessions.

The day before slaughter, all pigs from the 4 pens were fasted at 8 h00. At 13 h00, 5 pigs per pen (i.e. per line and sex) selected in order to maximize genetic diversity (boar and litter of origin) within slaughter date were weighed, marked on their back and loaded onto a lorry. Within sex 5 pigs from both lines were placed in the same compartment of the lorry (i.e. 2 compartments of 10 pigs), thus allowing standardized mixing of animals in order to get close to commercial conditions of pre-slaughter stress, and transported for about 4 h to the slaughterhouse. Then, pigs were placed overnight in lairage in two pens (one by sex) where they had free access to water. Next morning, every 10 min, one pig from each sex and line was showered with a small water jet for 1 min, 5 min before the pig walked to the stunning area. Pigs were slaughtered by electrical stunning and exsanguination, in compliance with the current national French regulations applied in slaughterhouses.

2.4. Carcass traits and body composition

Weights of hot carcass and perirenal fat were recorded on the day of slaughter. Backfat (G2) and muscle (M2) depths were measured on one dorsal spot between the 3rd and 4th last ribs — using a CGM device as described by Daumas (2008): Lean Meat Content (LMC) CGM = 62.19 − 0.729 G2 + 0.144 M2.

After 24 h shilling at 4 °C, weights of fresh carcass and wholesale cuts (ham, loin, shoulder, belly and backfat) of the left half carcasses were recorded. Joint weights were expressed as a percentage of the weight of the half-carcass defined as Ham + Shoulder + Belly + Loin + Backfat + Feet in order to be compared without impact of carcass weights. These data were used according to Daumas (2008) to calculate LMC from carcass cuts percentages: LMC Cut (2008) = 25.08 + 0.73% ham + 0.87% loin − 1.23% belly.

Carcass drip loss (difference between hot and cold carcass weights corresponding to cooler shrink in the first 24 h p.m.) and composition (proportion of wholesale cuts to the left side) were calculated.

2.5. Muscle characteristics and meat quality traits

This study aimed at determining meat quality traits on muscles differing in function, location and metabolism (oxidative or glycolytic), with a particular focusing on the *Longissimus* muscle (LM) to evaluate a wide range of biological as well as meat quality parameters. Sample of LM (around 10 g) was taken just after exsanguination (T0) at the last rib level, immediately frozen in liquid nitrogen and stored at −80 °C to represent the "in vivo" physiological situation for the further determination of the AMPK status (cf. 2.6.). Thirty minutes after slaughter (T30), another LM sample was collected at the last rib level, frozen in liquid nitrogen and stored at −80 °C before determination of pH1 and glycolytic potential (GP), as described previously by Lebret et al. (2006). Activities of lactate deshydrogenase (LDH), citrate synthase (CS) and β-hydroxy-acyl-CoA deshydrogenase (HAD) were also determined on these samples to assess the glycolytic, oxidative and fatty acid β-oxidation capacities respectively (Lefaucheur et al., 2011), and evaluation of AMPK Thr 172 phosphorylation (cf. 2.6).

The following day, i.e. 24 h p.m., ultimate pH (pHu) was determined directly on the right carcass side for LM, *Semispinalis capitis* (SC), *Adductor femoris* (AF), *Semimembranosus* (SM) and *Gluteus superficialis (GS)* muscles with a portable pH meter (Ingold Xerolyte electrode, Knick pH-meter, Berlin, Germany).

Meat color was evaluated through lightness (L^*), redness (a^*), yellowness(b^*), saturation (C^*) and hue (h°) parameters measured fifteen minutes after ham's cut on *Gluteus medius (GM)* and GS muscles (one determination) and on fresh section of LM after blooming for 1 h at 4 °C under artificial light (average values of 3 different determinations), using a chromameter Minolta CR 300 (Osaka, Japan) with a D65 illuminant and a 1-cm diameter aperture. LM slices were then trimmed of external fat, minced and freeze-dried before determination of lipid content (Folch, Lee, & Stanley, 1957). LM muscle water content was determined from the weight of minced muscle before and after freeze-drying, and used for calculation of lipid content per gram of fresh muscle. Additionally, water holding capacity (WHC) was also determined from the time needed for a piece of filter paper to become wet when put on the freshly cut surface of GS. This last measurement allowed to calculate the global meat quality index (MQI) which is a predictor of the ratio between weight of cooked ham to weight of defatted and boneless fresh ham, and was calculated using the