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Quantitative trait loci for meat quality traits in pigs considering imprinting and epistatic effects

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ABSTRACT

The aim of the research was to gain a better understanding of the genomic regulation of meat quality by investigating individual and epistatic QTL in a three-generation full-sib population (Pietrain × crossbred dam line). In total, 386 animals were genotyped for 96 markers. Analysed traits included pH, reflectance value, conductivity, and meat colour. Thirteen significant individual QTL were identified. The most significant QTL were detected on SSC1 and SSC9 for pH, on SSC4 for meat colour, and on SSC8 for conductivity, accounting for 3.4% to 4.7% of the phenotypic variance. Nine significant epistatic QTL pairs were detected accounting for between 5.7% and 10.9% of the phenotypic variance. Epistatic QTL pairs showing the largest effects were for reflectance value between two locations of SSC4, and for pH between SSC10 and SSC13, explaining 9.5% and 10.9% of the phenotypic variance, respectively. This study indicates that meat quality traits are influenced by numerous QTL as well as a complex network of interactions.

1. Introduction

In the past 50 years, selection strategies in pigs have been mainly focussed on the genetic improvement of production traits such as growth rate, lean content, backfat thickness, and feed efficiency (Kanis, De Greef, Hiemstra & van Arendonk, 2005; Roehe, Plastow & Knap, 2003; van Wijk, Arts, Matthews, Webster, Ducro & Knol, 2005). There has been considerable progress in the genetic improvement of pigs through artificial selection of superior animals without knowledge of the underlying genomic regulation of these traits (Andersson, 2001; Dekkers & Hospital, 2002; Georges, 2001; Weller, 2001). Intensive artificial selection has resulted in a substantial increase in loin muscle area and reduction in backfat thickness, an indication that these body composition traits are highly genetically determined (Andersson, 2001; Roehe et al., 2003). This selection for increased leanness has, however, partly been unfavourably associated with meat-eating quality characteristics (Schwab, Baas, Stalder & Mabry, 2006). Understanding the genetic regulation of meat quality is therefore becoming more important (Aaslyng et al., 2007; De Vries, van der Wal, Long, Eikelenboom & Merks, 1994; Kanis et al., 2005; Karlsson, Enfalt, Essengustavsson, Lundstrom, Rydhmer & Stern, 1993; Knapp, Willam & Solkner, 1997; Oksbjerg et al., 2000).

Meat quality is a complex trait with several criteria involved from technological to subjective meat-eating quality characteristics. Technological aspects of meat quality refer to properties such as water holding capacity (e.g., drip loss during storage), intensity and homogeneity of colour, firmness, shelf-life, cooking loss, and various processing yields (Otto, Roehe, Looft, Thoelking & Kalm, 2004; Sellier, 1998). Consumer satisfaction with the product is influenced by traits associated with appearance, such as colour, leanness, amount of fat tissue, and water holding capacity (Otto et al., 2006). Commonly used indicators of meat quality are pH at 45–60 min post-mortem and pH at 24 h after slaughter (Sellier, 1998). A further indicator of meat-eating quality is the quantity of intramuscular fat content in the meat, which has a favourable influence on meat tenderness and juiciness. Too high levels of intramuscular fat can, however, have negative impacts on consumer satisfaction.

The market price of the final product should include both carcass composition and meat quality (Otto, Knap, Roehe, Looft, Cavero & Kalm, 2007). As a result, breeding goals should include meat quality as well as production traits (van Wijk et al., 2005). A large number of genomic studies have been devoted to growth and body composition traits (e.g., Andersson et al., 1994; Bidanel et al., 2001; de Koning, Rattink, Harlizius, Groenen, Brascamp & van Arendonk, 2001; Milan et al., 2002; Rohrer & Keele, 1998a, b); however, much less attention has been paid to meat quality traits. Recently, however, the interest in quantitative trait loci (QTL) associated with meat quality has increased (de Koning, Harlizius, Rattink, Groenen, Brascamp & van Arendonk, 2001; Grindflek, Szyda, Liu & Lien, 2001; Nii et al., 2005; Ovilo et al., 2002; Paszek et al., 2001; Vidal et al., 2005).

The aim of this study was to gain further insight into the genomic regulation of meat quality. For this reason, QTL analysis of meat

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quality traits was carried out across several autosomes as well as chromosome X in a F_2 pig population. The mode of inheritance was investigated as additive and/or dominance, and the epigenetic effects of imprinting were tested. Furthermore, a QTL scan for epistatic QTL pairs was carried out to examine the role of epistasis in the genomic regulation of meat quality.

2. Materials and methods

2.1. Design and data

The present study was based on data of a resource family of a three-generation full-sib design. In the F_0 generation, seven unrelated Pietrain sires, which were all heterozygous at the *ryanodine receptor 1* (*RYR1*), were mated to 16 sows of a crossbred dam line (Leicoma × (Landrace × Large White)). Eight boars and 40 sows of the F_1 generation were mated, whilst avoiding inbreeding, to produce the F_2 generation, which comprised 49 families of 315 pigs across two litters. Animals of the F_2 generation were either housed individually or in groups of up to 15 pigs of mixed sex in straw-bedded pens. Individual-housed animals comprised of 48 gilts and 46 barrows. These animals were fed manually with feed consumption recorded on a weekly basis. Group-housed animals comprised 117 gilts and 104 barrows. These animals were supplied food by an electronic feeding station (ACEMA 48), which recorded feed consumption at each visit. Pigs were provided with one of three pelleted diets containing 13.8 MJ ME/kg and 1.2% lysine, 13.8 MJ ME/kg and 1.1% lysine, or 13.4 MJ ME/kg and 1.0% lysine for weight ranges 30–60, 60–90, and 90–140 kg body weight, respectively. Pigs were provided with *ad libitum* access to diets, formulated slightly above requirement, so they were able to reach maximal protein deposition. For more details about the management of this project, see the studies of Landgraf et al. (2006a), (b); Mohrmann, Roehe, Knap, Looft, Plastow and Kalm (2006); and Mohrmann, Roehe, Susenbeth, et al. (2006).

2.2. Meat quality measurements

Means and standard deviations of traits analysed in the present study are presented in Table 1. Following slaughter at 140 kg body weight, reflectance was measured 45 min post-mortem ($reflectance_{45}$) simultaneously with the carcass grading information using the Fat-O-Meter device (FOM, SKF Technology, Herlev, Denmark) perpendicular to the *longissimus* muscle between the last 3rd and 4th rib. The pH was measured 45 min post-mortem (pH_{45} loin) on the intact carcass using a pH-STAR electrode (Matthäus, Nobitz-Klausa, Germany). The pH probe was inserted 4 cm deep into the m*usculus longissimus dorsi* between the 13th and 14th thoracic vertebrae. Prior to the measurement, temperature was measured at the point the pH probe was placed and the pH was adjusted according to temperature. At 24 h post-mortem, the carcass was cut between 13th and 14th thoracic vertebrae, and pH values (pH_{24} loin) were measured at the surface of *musculus longissimus dorsi*. After cleaning the cranial surface of the *musculus longissimus dorsi*, the colour of the muscle was measured by OPTO-STAR equipment at the same location (Matthäus, Nobitz-Klausa, Germany). The OPTO-STAR equipment measures the brightness of the meat sample whereby lower and higher values indicate paler and darker meat, respectively. At 24 h post-mortem, the pH in the ham (pH_{24} ham) was measured 4 to 6 cm above the Symphisis pelvis in the *musculus semimembranosus* inserting the pH probe to a depth of 2 cm. Conductivity was taken 24 h post-mortem ($conductivity_{24}$) using LF-STAR (Matthäus, Nobitz-Klausa, Germany) inserted between the 14th and 15th thoracic vertebrae to a depth of 6 cm.

Table 1
Means and standard deviations (SD) of meat quality traits measured on pigs of the F_2 generation.

Trait	Mean	SD	Number of records
pH_{45} loin	6.242	0.399	309
pH_{24} ham	5.553	0.188	313
pH_{24} loin	5.448	0.132	314
$Reflectance_{45}$ [a]	24.781	4.602	311
$Conductivity_{24}$	4.813	2.212	313
OPTO-STAR value	69.252	7.531	310

[a] Measured by the Fat-o-metre device.

2.3. Genotypic data

Blood samples were collected from all animals of the F_0, F_1, and F_2 generations from the *vena jugularis*, and their DNA was isolated. Chromosomes chosen for genotyping were SSC1, SSC2, SSC4, SSC6, SSC7, SSC8, SSC9, SSC10, SSC13, SSC14, and SSCX because of their likely associations with carcass characteristics and growth. All animals were genotyped for 96 informative microsatellite markers. Of these markers 10, 9, 9, 9, 10, 8, 9, 9, 8, 7, and 8 genomic markers were located on SSC1, SSC2, SSC4, SSC6, SSC7, SSC8, SSC9, SSC10, SSC13, SSC14, and SSCX, respectively. Markers and their distances were selected from the published USDA linkage map (http://www.marc.usda.gov; Rohrer, Alexander, Hu, Smith, Keele, & Beattie, 1996), which provided all information relating to their positions and alleles (Table 2). Average distance between markers is 16.0, 16.5, 16.3, 21.0, 17.0, 18.4, 17.3, 16.0, 18.0, 17.4, and 18.3 cM and largest gaps between markers is 28.0, 25.2, 26.5, 29.0, 26.0, 23.1, 21.7, 20.8, 24.0, 23.6, and 22.4 cM on SSC1, SSC2, SSC4, SSC6, SSC7, SSC8, SSC9, SSC10, SSC13, SSC14, and SSCX, respectively.

2.4. Statistical analysis

All QTL analyses for individual QTL and epistatic QTL were performed with QxPak version 3.0 (Perez-Enciso & Misztal, 2004). This program used the maximum likelihood method for estimation of the position and effect of the QTL. The individual QTL genome scan was applied across all autosomes and the sex chromosome X, whereas the epistasis QTL genome scan was applied only to autosomes.

2.4.1. Individual QTL analysis

In the individual QTL analysis, only additive and dominance effects were estimated. In cases where the dominance effect was not significant, an additive only model was adopted. The individual QTL analysis of all traits was performed with the following model:

$$y_i = \mathrm{sex}_i + \mathrm{MHS}_i + \mathrm{batch}_i + \mathrm{ht}_i + \mathrm{sldat}_i + \beta \mathrm{slwt}_i + C_a a + C_d d + e_i, \quad [1]$$

where y_i is the ith individual phenotype. Sex, *RYR1* genotype (*MHS*), batch, housing type (ht: individual or group housed) and slaughter date (sldat) were fitted as fixed effects in the model. Slaughter weight (slwt) was considered as a covariable β. The additive (a) and dominance (d) effects were estimated by consideration of the coefficients of C_a and C_d, respectively. The coefficient C_a was calculated for each individual and position as the probability of the individual being homozygous for alleles of the grandpaternal sire line (QQ) minus the probability of pigs being homozygous for alleles from the grandmaternal dam line (qq). The coefficient C_d is the probability of the individual being at the chromosomal position heterozygous (Qq). Moreover, traits were tested for QTL expressing paternal or maternal imprinting.

The QTL scans were performed every cM. QxPak provides the log likelihood ratios under the models tested and the associated nominal *P*-values, which were obtained by removing the QTL effect in model [1]. A previous study by Perez-Enciso et al. (2000) showed that Chi-squared (2 degrees of freedom) values, which correspond to the 5%