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Correlations of genes expression in PPAR signalling pathway with porcine meat quality traits

W. Wang[1], W. Xue[2], X. Xu[3], B. Jin[4], X. Zhang[5]

[1]School of Psychology, Nanjing University of Chinese Medicine, Nanjing, P.R. China
[2]School of Basic Biomedical Science, Nanjing University of Chinese Medicine, Nanjing, P.R. China
[3]College of Life Sciences, Nanjing Normal University, Nanjing, P.R. China
[4]Department of Food Science and Nutrition, Nanjing Normal University, Nanjing, P.R. China
[5]Institute of Husbandry and Poultry Research, Nanjing, P.R. China

ABSTRACT: The correlation of expression pattern of candidate genes in PPAR signalling pathway with meat quality traits in *Longissimus dorsi* muscle of pigs was investigated. Meat quality traits were measured and correlated with the candidate genes mRNA expression, which included peroxisome proliferator-activated receptor alpha gene (*PPARα*), peroxisome proliferator-activated receptor gamma gene (*PPARγ*), stearoyl-CoA desaturase gene (*SCD*), lipoprotein lipase gene (*LPL*), and phosphoenolpyruvate carboxykinase 2 gene (*PCK2*). Results showed that expressions of *SCD* and *PCK2* were correlated with intramuscular fat content ($P < 0.05$). *PPARα* and *PPARγ* showed negative correlations with water loss and colour score ($P < 0.05$). *SCD* was positively correlated with marbling score and negatively correlated with shear force ($P < 0.05$). *LPL* was correlated with b^* value, shear force, and moisture content ($P < 0.05$). *PCK2* had a positive correlation ($P < 0.05$) with colour score. The revealed correlations indicate that these genes in PPAR signalling pathway are important for meat quality traits in pigs, and the further evaluation and investigation of these genes would help us better understand and utilize the regulation mechanisms of porcine meat quality.

Keywords: genetic markers; Real-time PCR; IMF; *Longissimus dorsi* muscle; pig

INTRODUCTION

Pig meat quality is defined by the characteristics of sensory experience, as assessed by colour, pH, shear force, intramuscular fat (IMF) content, protein content, moisture content, and sensory analysis (Reardon et al. 2010). The estimation of porcine genetic parameters for meat quality traits is essential for the demand of porcine economic value (Suzuki et al. 2005), and provides an important resource for the further improvements of this livestock species (Groenen et al. 2012).

Progress has been made in promoting desirable changes of porcine meat quality through genetics, and many candidate genes have been identified. It is considered that the candidate genes on the pathway level could provide a deeper insight into the genetic features of complex traits. Among the candidate pathways, the peroxisome proliferator-activated receptor (PPAR) signalling pathway is important for meat quality in mammals (He et al. 2013). A map of PPAR signalling pathway (KEGG PATHWAY database, map03320) is shown in Supplementary Figure S1 (for supplementary material see the electronic version).

PPARs, nuclear hormone receptors, are activated by fatty acids and their derivatives, and mainly associated with lipid metabolism, adipocyte dif-

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ferentiation, gluconeogenesis, and thermogenesis by modulating a lot of target genes. PPAR has three subtypes (PPARalpha, beta/delta, and gamma) with different expression patterns. *PPAR*α encodes peroxisome proliferator-activated receptor alpha, maps to chromosome 5 in the region near a QTL for performance and carcass traits such as backfat thickness and feed intake (Pita et al. 2003). *PPAR*α is an important regulator for transcription of genes that are involved in lipid metabolism (Srivastava 2009). *PPAR*γ encodes peroxisome proliferator-activated receptor gamma, maps to chromosome 13, and is located near a QTL for body weight (Grindflek et al. 2000). *PPAR*γ promotes adipocyte differentiation and fat deposition, and regulates lipid metabolism and glucose homeostasis (Kersten et al. 2000; Michalik et al. 2006). *SCD* encodes stearoyl-CoA desaturase, maps to chromosome 14, and catalyzes synthesis of monounsaturated fatty acids (Reardon et al. 2010). *LPL* encodes lipoprotein lipase, maps to chromosome 14 (Gu et al. 1992), and participates in fatty acids transfer and deposition (Luo et al. 2009). *PCK2* encodes phosphoenolpyruvate carboxykinase 2, maps to chromosome 7, and is involved in metabolic pathway of gluconeogenesis (Franckhauser et al. 2002; Peng et al. 2005). All the three genes (*SCD*, *LPL*, and *PCK2*) are also involved in PPAR signalling pathway and related to lipid transfer and metabolism.

Gene expression information is important for identifying genes responsible for differences in porcine meat quality traits. Therefore, in the present study, we correlate the expression pattern of candidate genes in PPAR signalling pathway with the porcine meat quality traits.

MATERIAL AND METHODS

Animals and sample collection. Samples were collected from 122 barrows (Shanzhu × Duroc commercial crossbreds) in this study. Pigs were reared on the same farm (Nanjing Husbandry and Poultry Research Institute, China), fed *ad libitum*, and kept under the same feeding and housing conditions. At a body weight of about 90 kg, pigs were slaughtered after electrical stunning in the same collaborating slaughterhouse. After slaughter, the *Longissimus dorsi* muscle samples were removed from the 13th rib of the left sides of the carcasses from each pig. Samples analyzed for meat quality traits were identified and kept frozen at –20°C. Small pieces of *Longissimus dorsi* muscle were put into 2-ml freezing tubes and kept frozen at –70°C until analysis.

Meat quality measurements. During the dissection, several carcass composition and meat quality traits (backfat thickness, body weight, carcass weight, and rib eye area) were measured. The pH was measured in *Longissimus dorsi* muscle using a microcomputer pH meter HI 9025 (Hanna Instruments, Lisbon, Portugal). The colour parameters of lightness (L^*), redness (a^*), and yellowness (b^*) were measured using SC-1 colorimeter (Beijing Chinainvent Instrument Tech Co., Ltd., Beijing, China) on day 2 postmortem at room temperature. The shear force was determined 24 h after dissection and water loss was assessed, too. The IMF content was determined on *Longissimus dorsi* muscle homogenates by Soxhlet extraction method. The mean and standard deviation (SD) of analyzed meat quality traits are presented in Table 1.

Real-time PCR reactions. Total RNA was isolated from each sample using TRIzol Reagent (Invitrogen, Carlsbad, USA), kept at –70°C, and then reverse-transcribed using SYBR® PrimeScript RT-PCR Kit (TaKaRa, Dalian, China). The cDNA samples were kept at –20°C until the real-time PCR assays were performed. Candidate genes, *PPAR*α, *PPAR*γ, *SCD*, *LPL*, and *PCK2*, were selected ac-

Table 1. Mean and standard deviation (SD) of the analyzed meat quality traits in *Longissimus dorsi* muscle of pigs (n = 122)

Trait	Mean	SD
Backfat thickness (mm)	23.37	4.31
Body weight (kg)	91.78	8.42
Carcass weight (kg)	63.39	6.28
Rib eye area (cm^2)	37.29	6.37
pH_1	6.54	0.29
pH_{24}	5.92	0.21
Water loss (%)	30.94	6.04
Marbling score	2.92	0.51
Colour score	3.21	0.56
L^* (meat lightness)	38.97	3.42
a^* (meat redness)	5.71	1.41
b^* (meat yellowness)	3.23	0.56
Shear force (N)	2.63	0.61
Intramuscular fat (%)	2.52	0.49
Protein (%)	23.07	0.43
Moisture (%)	71.42	3.58

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Table 2. Primers designed from Ensembl sequences

Gene	Ensembl ID	Primer sequences (5'→3')	Amplicon (bp)
PPARα	ENSSSCT00000000007	F: GAGTTCGCCAAGTCCATCCC R: CCGTAAGCCACCAGCATCC	140
PPARγ	ENSSSCT00000012671	F: GCAGGAGCAGAGCAAAGAGG R: AGGAGAGTTACTTGGTCATTCAGG	144
SCD	ENSSSCT00000011546	F: CTACACAACCACCACTACCATCAC R: GCAAACGCCCAGAGCAAGG	279
LPL	ENSSSCT00000010522	F: TTAACGAACCCGACTAGCATCC R: CACCACAGCCACAGCAACTC	139
PCK2	ENSSSCT00000002248	F: CACCTCTGCCACCACCAATCC R: GCCGCCATCGCTCGTCTC	88
β-actin	ENSSSCT00000008324	F: GTCCACTCCGCCAGCACAG R: CATCGTCGCCCGCAAAGC	152

cording to their involvement in PPAR signalling pathway. Six primer sets were designed using Beacon Designer 7 software, five for target genes and one for housekeeping gene (*β-actin*) (Table 2).

The real-time quantitative PCR were performed using Fast SYBR® Green Master Mix (Roche, Mannheim, Germany) on Applied Biosystems® StepOnePlus™ Real-Time PCR Systems (Applied Biosystems Inc., Foster City, USA). The reactions comprised 12.5 µl of Fast SYBR® Green Master Mix, 0.5 µl of each primer (forward and reverse, 10 pmol/µl), 2.5 µl of cDNA (50 ng/µl), and nuclease-free water to 25 µl. The real-time quantitative PCR amplification program consisted of denaturation at 95°C for 10 min, and 40 cycles of amplification at 95°C for 15 s and at 62°C for 30 s. Reactions were performed as three replicates. Data from the relative quantification were transformed using the $2^{-\Delta\Delta Ct}$ method according to Livak and Schmittgen (2001).

Statistical analysis. All statistical procedures were performed using the SPSS statistical software package (Version 19.0, 2010). Pearson's correlation coefficients between meat quality parameters and the expression of each gene were estimated. In this study significance was detected at the 5% level for all statistical analyses.

Table 3. Correlation analysis of five candidate genes expression in the PPAR signalling pathway with meat quality traits

Trait	*PPARα*	*PPARγ*	*SCD*	*LPL*	*PCK2*
Backfat thickness (mm)	–0.179	0.106	0.341	0.158	0.078
Body weight (kg)	–0.094	0.155	0.316	0.109	0.127
Carcass weight (kg)	0.136	0.209	0.311	0.207	0.098
Rib eye area (cm^2)	–0.149	0.216	–0.136	–0.032	0.296
pH_1	0.182	0.092	0.148	0.271	0.197
pH_{24}	0.056	0.105	–0.318	–0.285	0.091
Water loss (%)	–0.604*	–0.576*	–0.205	0.117	0.238
Marbling score	0.233	0.432	0.572*	0.128	0.139
Colour score	–0.527*	–0.582*	0.258	–0.291	0.626*
*L** (meat lightness)	0.319	0.049	0.193	–0.171	0.273
*a** (meat redness)	0.247	0.312	–0.106	0.095	0.046
*b** (meat yellowness)	0.112	0.103	0.057	0.531*	–0.314
Shear force (N)	–0.017	0.161	–0.557*	0.516*	–0.356
Intramuscular fat (%)	–0.203	0.294	0.519*	0.121	0.616*
Protein (%)	0.231	0.134	0.158	0.082	0.181
Moisture (%)	0.087	0.103	–0.054	0.583*	–0.211

*$P < 0.05$

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RESULTS

The expression levels of five candidate genes in PPAR signalling pathway were correlated with carcass and meat quality traits of the *Longissimus dorsi* muscle in all crossbred pigs. Pearson's correlation coefficients between meat quality parameters and the expression of each gene are shown in Table 3. Overall, expression levels of *SCD* and *PCK2* had significant correlations with IMF content ($P < 0.05$), while *PPAR*α, *PPAR*γ, and *LPL* expression showed non significant ($P > 0.05$) correlation with IMF content. *PPAR*α and *PPAR*γ were negatively correlated with water loss and colour score ($P < 0.05$). *SCD* had a positive correlation with marbling score and a negative correlation with shear force ($P < 0.05$). *LPL* showed significant correlation with b^* value, shear force, as well as moisture content ($P < 0.05$). A positive correlation ($P < 0.05$) between *PCK2* expression and colour score was found.

DISCUSSION

The IMF content has a positive influence on porcine meat quality characteristics such as colour, juiciness, flavour, and tenderness (Fortin et al. 2005), and IMF content is higher in Chinese local pigs than in other commercial ones (Zhao et al. 2009). The Shanzhu pig is an indigenous breed in Jiangsu Province of China with high level of IMF but relatively poor growth characteristics (Xue et al. 2015), likely because of a higher potential for the lipid synthesis in rustic pig breeds (Serao et al. 2011). The Duroc pig is an international breed mainly focused on lean growth and has been selected for improvement of carcass leanness since the mid-1980s (Schwab et al. 2007). Shanzhu × Duroc crossbreds were developed to obtain pigs with good meat and fat quality such as high IMF content, carcass leanness, and growth efficiency. PPAR signalling pathway is considered to be important for meat quality (He et al. 2013), and it is necessary to estimate the correlation of expression pattern of genes in PPAR signalling pathway with meat quality traits in these crossbred pigs.

*PPAR*α gene plays an important role in fatty acid catabolism by transcriptional regulation of genes involved in fatty acid oxidation and can be considered as a candidate gene for porcine meat quality traits. De Rosa et al. (2013) showed that down-regulation of PPARα protein level is presumably associated with a tendency to fat accumulation in pigs. Genes encoding proteins in PPAR signalling pathway were studied by He et al. (2013), who tested 77 potentially functional single nucleotide polymorphisms (SNPs) within 20 genes in pig. However, *PPAR*α was not included in their study. Stachowiak et al. (2014) found that the 3' UTR region of *PPAR*α is highly polymorphic in commercial breeds, and the c.*636A>G SNP in *PPAR*α can be considered as a useful genetic marker for adipose tissue accumulation in Polish Landrace breed. In the present study, the observed significant correlations of *PPAR*α expression with water loss and colour score ($P < 0.05$) may indicate that there could be some links with the anaerobic metabolic pathways which contribute to pH decline and protein denaturation as well as postmortem glycolysis (Thompson et al. 2006).

*PPAR*γ gene plays a crucial role in the control of glucose homeostasis and lipid metabolism (Ding et al. 2000), and PPARγ activator reduces the circulating glucose by storing it as a fat depot in adipocytes (Yu et al. 2003). Madeira et al. (2013) found that the increase in IMF content under the reduced protein diets was accompanied by increased *PPAR*γ mRNA levels. Wang et al. (2013a) identified two SNPs (c.-1633C>T and c.-1572G>A) in *PPAR*γ upstream the transcriptional regulatory region and showed that the *T-A* haplotype of *PPAR*γ might contribute to the relatively higher IMF content in Erhualian pigs. However, here, *PPAR*γ showed no significant correlation with IMF content ($P > 0.05$). A recent study by Madeira et al. (2016) showed that arginine-supplemented diet decreased *PPAR*γ mRNA expression level in muscle and subcutaneous adipose tissue of cross-bred pigs, but it did not influence fat content or fatty acid composition. Moreover, Li et al. (2012) found that *PPAR*γ showed differential expression between Wujin and Landrace porcine adipocytes during the early stage of differentiation. Taken together, these results indicate that the mechanisms regulating fat deposition by the key lipogenic genes such as *PPAR*γ in pigs are genotype and tissue specific.

SCD gene participates in the desaturation of saturated fatty acid (SFA) into monounsaturated fatty acid (MUFA), and helps regulate fatty acid composition of lipids (Reardon et al. 2010). Madeira et al. (2013) showed that the increase of IMF content was accompanied by increased *SCD* expression level. In our study, *SCD* expression

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showed positive correlation with IMF content ($P < 0.05$). Taniguchi et al. (2004) found that both gene expression and allelic variation in *SCD* gene correlated with the fatty acid composition in Japanese Black cattle. Moreover, herein the *SCD* expression was correlated with marbling score and shear force ($P < 0.05$). Similarly, Iida et al. (2015) also showed that an increase in crude fat content increased tenderness and juiciness in Japanese Black steers.

LPL gene is responsible for hydrolyzing triacylglycerol from triacylglycerol-rich lipoprotein particles and transferring free fatty acids to different tissues for energy utilization and storage (Luo et al. 2009). Liu et al. (2011) revealed that increased expression and activity of *LPL* played a vital role in suppressing lipid accumulation. Guo et al. (2008) reported that *LPL* expression level in adipose tissue was higher in fatty pig breed than muscular pig breed. Bakhtiarizadeh et al. (2013) found that there was no significant difference for *LPL* expression in adipose tissues of two sheep breeds with different fat deposition contents. They suggested that post-translational modification might be a mechanism of regulating *LPL* activity in the investigated adipose tissues. In the present study, we found that *LPL* expression showed no significant correlation with IMF content ($P > 0.05$). This indicated that *LPL* might control lipid deposition on protein levels, but not on mRNA levels. Moreover, this study showed that *LPL* expression correlated with b^* value and shear force as well as moisture content ($P < 0.05$). Our results indicated that *LPL* influenced tenderness in porcine muscle, and contributed to bright (higher b^* value) pork, suggesting a potential link between tenderness and colour.

PCK2 gene plays a key role in the process of gluconeogenesis which is an essential metabolic pathway. Franckhauser et al. (2002) demonstrated that *PCK2* overexpression increased gluconeogenesis and free fatty acid (FFA) re-esterification. Their results suggested that there was direct involvement of *PCK2* in glycerol 3-phosphate synthesis and showed an important role of gluconeogenesis in FFA re-esterification and subsequent fat accumulation. Here, we found that *PCK2* expression showed positive and significant correlation with IMF content ($P < 0.05$), indicating that *PCK2* expression might increase lipid deposition. Furthermore, our study showed that *PCK2* expression was correlated with colour score ($P < 0.05$), suggesting a relationship to meat quality aspects such as meat colour. This result is consistent with the findings of previous study (Wang et al. 2013b), wherein *PCK2* expression was significantly correlated with polyunsaturated fatty acid (PUFA) content which influenced the susceptibility of meat to oxidation.

In conclusion, this study demonstrates that the expression patterns of five candidate genes involved in PPAR signalling pathway have significant correlation with meat quality traits in porcine *Longissimus dorsi* muscle. The highly positive correlation between expressions of *SCD* and *PCK2* and IMF content may indicate that these two genes are important for lipid deposition. Our study suggests that these five candidate genes are useful for investigating regulation mechanisms of porcine meat quality and for improving porcine meat quality traits.

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Corresponding Authors

Wei Wang, Ph.D., Nanjing University of Chinese Medicine, School of Psychology, Nanjing 210023, P.R. China
Phone: +862 585 811 283, e-mail: wangw@njucm.edu.cn
Xiaofeng Xu, Nanjing Normal University, College of Life Sciences, Nanjing 210046, P.R. China
Phone: + 862 585 891 513, e-mail: awnuyydp1@163.com

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