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Review Article

Nutritional regulation of skeletal muscle energy metabolism, lipid accumulation and meat quality in pigs

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A B S T R A C T

The quality of pork determines consumers' purchase intention, which directly affects the economic value of pork. Minimizing the proportion of inferior pork and producing high quality pork are the ultimate goals of the pig industry. Muscle energy metabolism, serving as a regulative hub in organism energy expenditure and storage as a fat deposit, is compatible with myofiber type composition, affecting meat color, intramuscular fat content, tenderness, pH values and drip loss. Increasing data illustrate that dietary nutrients and bioactive ingredients affect muscle energy metabolism, white adipose browning and fat distribution, and myofiber type composition in humans, and rodents. Recently, some studies have shown that modulating muscle energy metabolism and lipid accumulation through nutritional approaches could effectively improve meat quality. This article reviews the progress and development in this field, and specifically discusses the impacts of dietary supply of amino acids, lipids, and gut microbiota as well as maternal nutrition on skeletal muscle energy metabolism, lipid accumulation and meat quality of pigs, so as to provide comprehensive overview with respect to effective avenues for improving meat quality.

1. Introduction

Pork is the most consumed meat in most areas of the World. China is the largest meat producer, accounting for about 25% of the world's meat output and giving rise to more than 40% of the world's pork yield for most of the time since 1995 (Fig. 1). Along with the increasing public concern about environmental pollution and the shortage of feed resource, more emphasis is placed on developing efficient and environmentally friendly pig industry strategies and technologies. Considering the considerable proportion of inferior quality pork available, such as pale, soft, exudative (PSE) meat and acid meat, minimizing inferior quality pork and improving pork quality will increase pork economic value and lead to a sustainable pig industry with more efficient production and better environment outcomes.

Skeletal muscle, accounting to about 40% of the total body mass in adult mammals, not only performs normal body mechanical movements, but also plays an important role in regulating protein synthesis, energy metabolism, and glucose and lipid metabolic homeostasis via the interaction of myokines and the insulin signaling pathway, and the mechanism in turn underpins meat quality in farm animals (Rai and Demontis, 2016; Yang et al., 2019). In particular, some special nutrients and their supply status exert a critical role in regulation of skeletal muscle insulin sensitivity, energy metabolism and lipid accumulation, which has been well reviewed previously (Zhang et al., 2021a,b). In pig production, intramuscular fat content is a key factor influencing pork eating quality, such as taste and juiciness, while excess subcutaneous and visceral fat deposition will undermine the lean percentage and feed efficiency of finishing pigs. Therefore, it is desirable to increase intramuscular fat accumulation without increasing fat deposition in subcutaneous and visceral adipose tissues in pigs (Huang et al., 2022; Zhou et al., 2007).

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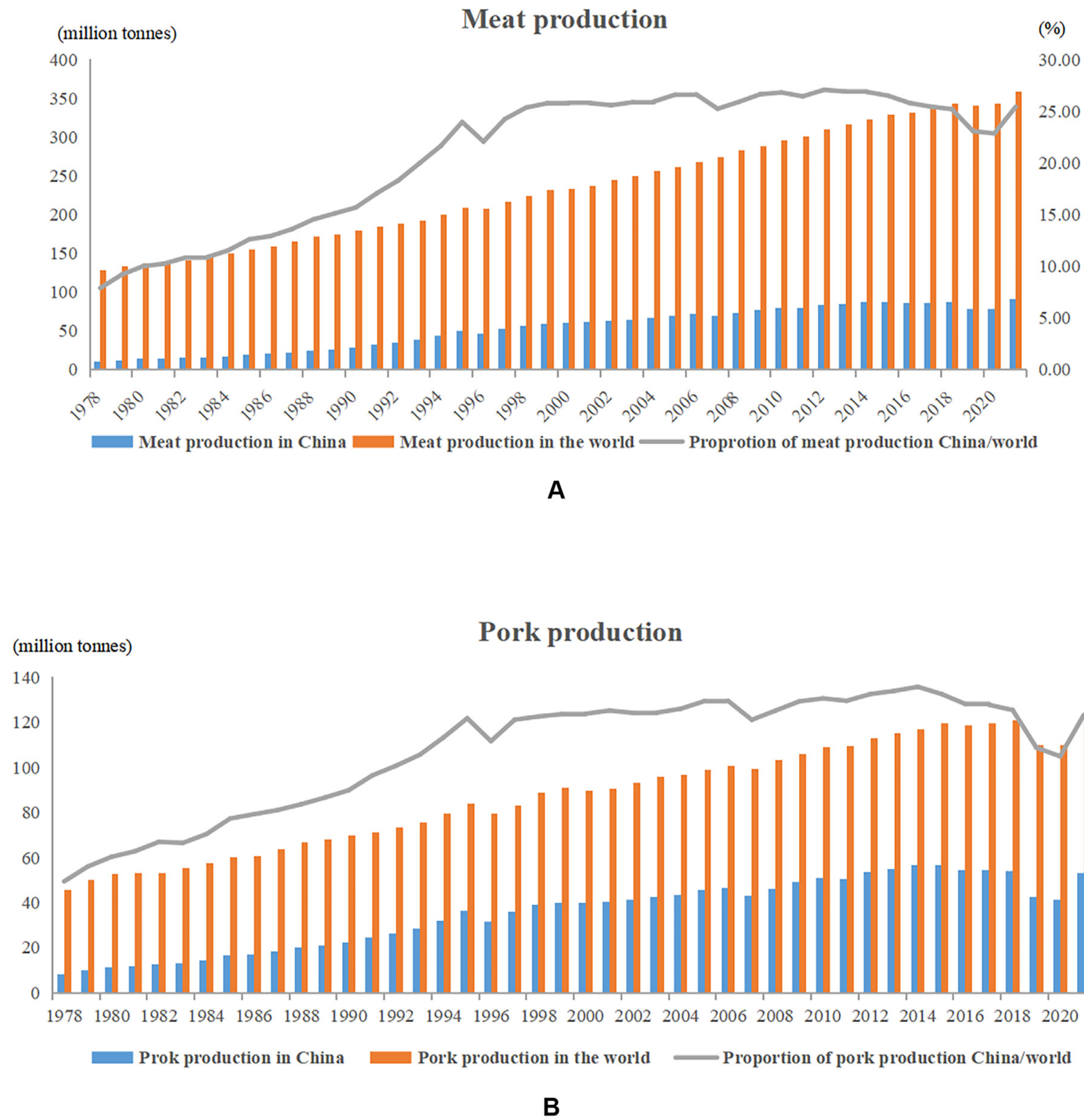

Fig. 1. Production of meat and pork in the 1978–2021 in the world and in China. (A) Meat production in the world and in China, and proportion of the world's meat produced in China. (B) Pork production in the world and in China, and proportion of the world's pork produced in China. Source: https://ourworldindata.org/.

Dietary levels of crude protein and available amino acids, the ratio of available energy to lysine, dietary fatty acid composition, gut microbiota and maternal nutrition regulate lipid accumulation, body composition and meat quality of finishing pigs. Numerous studies showed that nutritional regulation significantly affects body lipid accumulation, carcass and meat quality characteristics (Heng et al., 2020; Li et al., 2016; Wang et al., 2022). Pork eating quality and processing attributes, including meat color, flavor, tenderness, juiciness and water holding capacity, are mainly determined by two interactive biological features during muscle growth, namely muscle fiber type composition and intramuscular fat accumulation, affected by muscle energy metabolism and storage. Muscle energy metabolism mainly refers to the ATP production process by which muscle mitochondria use energy substrates, such as glucose/glycogen, lactate, fatty acids, and branched amino acids. According to oxidation types of glycogens, muscle fibers are classified into oxidative myofibers (I, IIa), glycolytic myofibers (IIb) and the intermediate (IIx). The muscle dominant with oxidative myofibers is generally superior in both color and intramuscular fat content than that dominant with glycolytic myofibers (Yan et al., 2022; Zhou et al., 2021). Therefore, in this review, we focus on advances in nutritional improvement of meat quality from the view of muscle energy metabolism in pigs over the recent ten years.

2. Dietary supply of amino acids influences lipid deposition in skeletal muscle

2.1. Lysine level and available energy of diets

Low levels of dietary crude protein/amino acids enhance lipid deposition in subcutaneous fat, visceral fat and intramuscular fat, and resultantly decrease the lean percentage, which due mainly to lysine limitation and unbalanced essential amino acids in diets (Madeira et al., 2013a; Qin et al., 2015; Xu et al., 2020). Two very different dietary protein sources, soybean meal and cotton seed meal, and two crude protein levels (12% vs. 14%) did not adversely affect growth, carcass traits and meat quality characteristics in finishing pigs when the essential amino acid levels were met (Qin et al., 2015). As shown in Table 1, a low-protein and lysine-deficient diet (13.0% crude protein, 0.35% lysine) promoted intramuscular fat accumulation in finishing pigs accompanied by shifting metabolic properties of muscle fibers from glycolysis to oxidation (Pires et al., 2016). Interestingly, it provides an insight that links muscle fiber type and intramuscular fat deposition through muscular energy metabolism. A deficient dietary lysine level will decrease the lean percentage of pigs but increase intramuscular fat content (Zhang et al., 2008). Indeed, dietary lysine deficiency increased intramuscular fat content without affecting fat deposition in the adipose tissue in finishing pigs (Suárez-Belloch et al., 2015). Relative to the control (0.51% lysine and 16% crude protein), the ingestion of the lysine-deficient diet (0.35% lysine and 13.0% crude protein) increased intramuscular fat content by 25% and pork juiciness by 12% (Madeira et al., 2015, Table 1). Moreover, increased intramuscular fat content in pigs by lysine deficiency may also be related to the type of pigs. It was showed that the ingestion of a lysine-deficient diet (0.40% lysine, 13% crude protein) increased intramuscular fat deposition in lean pigs but not in obese pigs (Madeira et al., 2013b, Table 1). It might be due to different requirements for lysine in different types of pigs. Therefore, compared with obese-type pigs, the protein synthesis in a lean genotype was more readily restrained in response to lysine deficiency, which in turn promoted fat accumulation. In response to reduced dietary protein to carbohydrate ratio, intramuscular fat content was increased with increasing levels of stearoyl-CoA desaturase (*SCD*) and peroxisome proliferator-activated receptor γ (*PPAR*γ) mRNA in lean-type pigs (Guo et al., 2011).

Dietary available energy to lysine ratios greatly impact growth, carcass traits and meat quality characteristics, as well as the rate of protein synthesis and lipid deposition in finishing pigs. The consumption of diets with high ratios of digestible energy (DE) to protein (amino acids) resulted in an increase in intramuscular fat levels in pigs. Szabó et al. (2001) showed that reduced dietary apparent ileal digestible lysine to DE ratio from 0.50:0.42 to 0.36:0.30 g lysine/MJ DE decreased body weight gain and the contents of protein and muscle in the body from 30 to 60 kg and from 60 to 105 kg BW, while increased crude fat and fatty tissue content. Reducing lysine:DE did not modify meat quality traits but the high lysine:DE ratio was associated with a high lean meat percentage.

2.2. Branched chain amino acids (BCAA)

Skeletal muscle is the major site for BCAA transamination in bodies. As essential amino acids of mammals, BCAA including leucine, isoleucine and valine, play critical roles in energy homeostasis and lipid metabolism in addition to the role of building blocks in protein synthesis. It has been accepted that leucine supplementation enhanced protein synthesis in skeletal muscle in a mammalian target of rapamycin complex 1 (mTORC1)-dependent mechanism in both animals and humans. We also demonstrated that increasing levels of dietary isoleucine led to elevated intramuscular fat content accompanied by heightened activity of SCD and mRNA expression levels of adipose-specific genes including adipocyte determination and differentiation factor 1 (*ADD1*), fatty acid synthase (*FAS*), and *SCD* in pigs (Luo et al., 2018). Dietary supplementation of isoleucine increased lipid accumulation and decreased the drip loss and shear force in the skeletal muscle of pigs (Luo et al., 2018, Table 1). Valine supplementation did not change lipid deposition in subcutaneous backfat and intramuscular fat tissues, however, valine metabolite 3-hydroxyisobutyrate (3-HIB) promoted fatty acid uptake and lipid accumulation in skeletal muscle by activating endothelial fatty acid transport (Zhang et al., 2021b). A high level of isoleucine supplementation (0.53% standardized ileal digestibility [SID] Ile) increased $pH_{24\ h}$ value and tended to decreased drip loss in longissimus dorsi muscle (Xu et al., 2020, Table 1).

With respect to the ratio among BCAA, Leu:Ile:Val ratio of 1:0.75:0.75 in a low (17% crude protein) protein-diet increased intramuscular fat content of the biceps femoris muscle in growing pigs compared with the control (the normal protein diet, crude protein 20%). Meanwhile, the ratio of n-6:n-3 polyunsaturated fatty acids (PUFA) in the longissimus dorsi muscle, biceps femoris muscle and psoas major muscle was decreased, accompanied by increased mRNA expression levels of acetyl-CoA carboxylase, lipoprotein lipase, fatty acid transporter and fatty acid binding protein 4, compared with the control (Duan et al., 2016). Various leucine:isoleucine:valine ratios of 2:1:1 or 2:1:2 in a low protein diet (12% crude protein) accelerated the secretion of adipokines and fatty acid oxidation in adipose tissue (Zhang et al., 2021a, Table 1). It

Table 1
Effects of dietary protein and amino acids on meat quality.

Dietary levels of protein and amino acids	Feeding stage, kg BW	Meat quality	References
Lys			
13% CP; 0.35% Lys[1]	60–93	IMF ↑, meat juiciness ↑	Madeira et al. (2015)
13% CP; 0.40% Lys[2]	60–93	IMF (lean-type pig) ↑	Madeira et al. (2013b)
13% CP; 0.35% Lys[3]	61–94	IMF ↑, oxidative muscle fiber proportion ↑	Pires et al. (2016)
BCAA			
12% CP; 0.53% SID Ile[4]	77–105	IMF ↑, drip loss↓, shear force↓	Luo et al. (2018)
11% CP; 0.53% SID Ile[5]	74–105	$pH_{24\ h}$ value↑, drip loss↓	Xu et al. (2020)
12% CP; Leu:Ile:Val ratio of 2:1:1 or 2:1:2[6]	59–95	fat in adipose tissue ↓	Zhang et al. (2021a)
Met, Gly and Ser			
18% CP; 0.25% Met[7]	6–14	IMF ↑	Wu et al. (2019)
12% CP; Ser:Gly ratio of 1:2[8]	60–100	IMF ↑, oxidative muscle fiber proportion ↑	Zhou et al. (2021)

CP = crude protein; Lys = lysine; IMF = intramuscular fat; BCAA = branched chain amino acids; SID = standardized ileal digestibility; Met = methionine; Gly = glycine; Ser = serine; ↑ = increased; ↓ = decreased.
[1] Control diet: 16% CP; 0.51% Lys.
[2] Control diet: 17% CP; 0.7% Lys.
[3] Control diet: 16% CP; 0.51% Lys.
[4] Control diet: 12% CP; 0.39% SID Ile.
[5] Control diet: 11% CP; 0.25% SID Ile.
[6] Control diet: 16% CP; Leu:Ile:Val ratio of 2:1:1.
[7] Control diet: 18% CP; 0.49% Met.
[8] Control diet: 16% CP; Ser:Gly ratio of 1.18:1.

was supposed to be related to the regulation of branched-chain amino acids on the adipokines–adenosine monophosphate-activated protein kinase (AMPK)–sirtuin 1 (SIRT1)–PPARγ axis.

2.3. Methionine, glycine and serine

Dietary methionine restriction is shown to decrease contents of liver triglyceride and total cholesterol, inhibit hepatic steatosis, and induce adiposity resistance (Ables et al., 2016). It has been shown that S-adenosylmethionine, serving as an active form of methionine in vivo and a major methyl donor, might initiate adipogenesis of adipose precursor cells derived from both adipose and muscle tissues through suppressing Wnt/β-catenin and Hedgehog pathways (Liu et al., 2013). Methionine limitation can alter skeletal muscle composition in piglets. For example, reducing dietary methionine level by 48% improved the mitochondrial function, the formation of slow-twitch muscle fibers, and then enhanced the energy metabolism of skeletal muscle in piglets (Wu et al., 2019, Table 1). Meanwhile, methionine limitation promoted lipid deposition in skeletal muscle and increased intramuscular fat content during the fattening period. It is hypothesized that effect of dietary methionine limitation on skeletal muscle composition and function might be via enhancing AMPK–PPARγ coactivator 1α (PGC1α) signaling.

Dietary supply of non-essential amino acids may be one of the limiting factors for growth performance of pigs fed low-protein diets. While pigs are feeding on low-protein diets, glycine and serine in vivo may be decreased, and resultantly, the endogenous metabolic processes would slow down in the absence of sufficient metabolic precursors, which in turn could affect the energy metabolism of pigs (Powell et al., 2011). A recent study showed that a serine:glycine ratio at 1:2 in low protein-diets (12% crude protein) not only increased the proportion of oxidized muscle fibers through AMPK–PGC1α and calcineurin–myocyte enhancer factor 2 (MEF2)/nuclear factor of activated T cells (NFAT) pathways, but also increased intramuscular fat content of growing finishing pigs (Zhou et al., 2021, Table 1).

3. Impact of dietary fatty acids on energy metabolism, lipid accumulation in skeletal muscle

3.1. Ratios of n-6 to n-3 PUFA

Dietary fatty acids are incorporated in lipogenesis and energy metabolism in skeletal muscle and adipose tissue of pigs. Dietary supplementation of PUFA increased the expression of key genes involved in mitochondrial energy metabolism (SIRT1, PGC-1α and protein kinase AMP-activated catalytic subunit α1 [Prkaa1]), enhanced energy metabolism in myocytes, and exerted an important role in regulating skeletal muscle development (Du et al., 2020; Risha et al., 2021). Moreover, dietary supplemental PUFA increased intramuscular fat content of finishing pigs, thereby improving meat quality (Wang et al., 2022). Appropriate fatty acid composition increased intramuscular fat content while reduced fat accumulation in adipose tissues (Dannenberger et al., 2012; Sobotka et al., 2012). Thus, it is proposed that appropriate ratio of unsaturated fatty acids (UFA) to saturated fatty acids (SFA) might improve meat quality. While finishing pigs were offered with diets with UFA:SFA ratio of 1:1, 2:1 and 3:1, respectively, the proportion of C18:2n-6, C20:4n-6 and PUFA in the *M. longissimus* thoracis was increased linearly with the ratio of dietary UFA to SFA. Drip loss and cooking loss also increased linearly, but backfat thickness was decreased linearly (Chen et al., 2021).

Essential fatty acids n-6 and n-3 PUFA cannot be mutually converted in vivo. The ratio of n-6:n-3 PUFA is critical for regulating muscle energy metabolism, lipid accumulation and improving meat quality. Diets rich in n-3 PUFA can promote hypertrophy in the *M. longissimus* thoracis, quadriceps femoris muscle and semitendinosus muscle of pigs, indicating that n-3 PUFA have a positive effect on muscle proteins anabolism (Huang et al., 2008). It is shown that dietary flaxseed oil increases pork n-3 fatty acid content and decreases n-6:n-3 PUFA ratio, which is beneficial to human health (Dannenberger et al., 2012). PUFA enhanced the proliferation and differentiation of skeletal muscle cells by activating extracellular signal-regulated kinase 1/2 (ERK1/2) mediated signaling pathway, which may enhance muscle energy metabolism (Lee et al., 2009). It has been shown that optimum dietary n-6:n-3 PUFA ratio is 1:1 for increasing muscle mass and decreasing adipose tissue mass in pigs relative to ratios of 2.5:1, 5:1 and 10:1, indicating that appropriate n-6:n-3 PUFA ratio could reduce body fat deposition and improve the lean percentage of pigs (Duan et al., 2014).

3.2. Conjugated linoleic acids (CLA)

Conjugated linoleic acid supplementation significantly reduces body fat deposition across humans, rodents and pigs (House et al., 2005). Interestingly, CLA supplementation increases intramuscular fat deposition in pigs. It has also been shown that skeletal muscle contains a high proportion of preadipocytes that can be induced by CLA to differentiate and mature, ultimately leading to an increase in intramuscular fat content (Meadus et al., 2002). Zhou et al. (2007) demonstrated that CLA differently regulates adipogenesis in stromal vascular cells from porcine subcutaneous adipose and the skeletal muscle. In particular, t10,c12-CLA specifically promotes the adipogenesis of fat precursor cells in the skeletal muscle while restrains adipogenesis in the subcutaneous adipose tissue. In addition, t10,c12-CLA could enter fetal tissue through umbilical cord blood (Peng et al., 2010). These results suggest that maternal t10,c12-CLA may specifically mediating the distribution of fat and improve carcass traits and intramuscular fat deposition in pigs. Accordingly, in growing-finishing pigs (56 to 133.5 kg body weight) fed diets containing 1% and 2% CLA, the fat content in the M. Logissimus thoracis was increased (Cordero et al., 2010). In addition, dietary CLA (25 g CLA/kg diet) significantly affected the abundance of proteins related to energy metabolism, fatty acid oxidation and synthesis, and amino acid metabolism whilst increasing the content of intramuscular fat in finishing pigs (Zhong et al., 2011).

4. Gut microbiota and muscle fiber profiles and intramuscular lipid accumulation

The gut–muscle axis exerts an important regulatory role in the body (Chen et al., 2022), and phenotype of the animal and metabolism of the skeletal muscle are closely associated with gut microorganisms via maintaining intestinal integrity and the modulation of redox homeostasis, inflammation reaction and gut-brain peptide secretion (Chen et al., 2020; Wang et al., 2017). As shown in Fig. 2, we summarized the interaction between gut microbiota-skeletal muscle and its possible impacts on meat quality. Gut microecology balance can be disturbed by environmental factors, damaged intestinal integrity, presence of pathogenic microorganisms and antibiotic administration. It is usually restored through fecal microbiota transplantation and dietary interventions, such as oral administration of probiotics, prebiotics, synbiotics and eubiotics as well as postbiotics (Cheng et al., 2019; Koyun et al., 2022).

It is established that fecal microbiota transplantation favors gut microbiota restoration and intestinal health, and probably improves meat quality in pigs. Transplanting sow fecal microbiota into newborn piglets sped up the establishment of gut microecology of

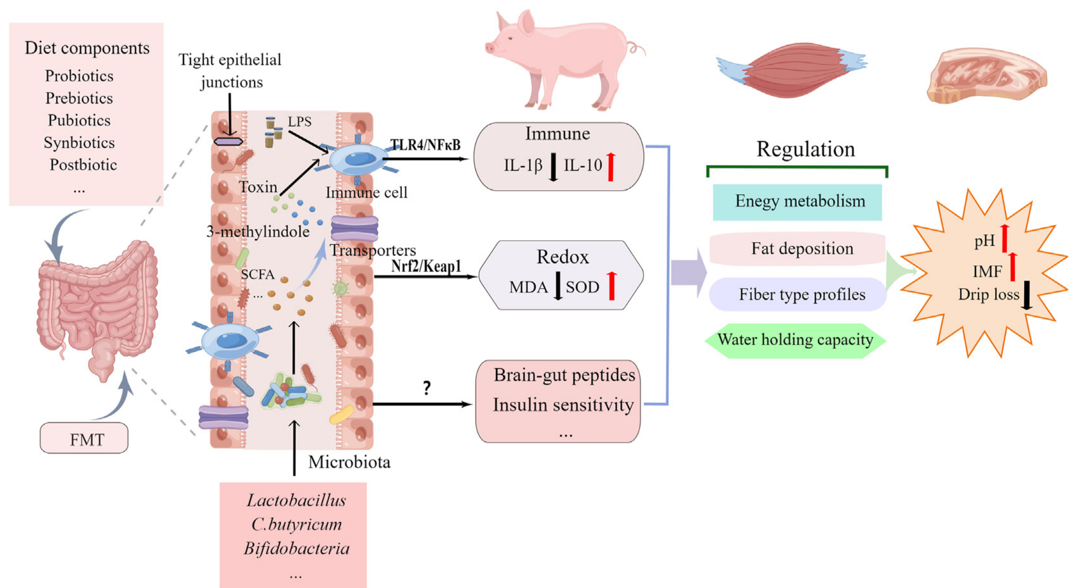

Fig. 2. A schematic diagram regarding role of gut microbiota in improving meat quality. FMT = faecal microbiota transplantation; IL-1β = interleukin-1β; IL-10 = interleukin 10; IMF = intramuscular fat; Keap1 = Kelch-like ECH-associated protein l; LPS = lipopolysaccharide; MDA = malonaldehyde; NFκB = nuclear factor kappa B; Nrf2 = nuclear factor erythroid 2-related factor 2; SCFA = short chain fatty acid; SOD = superoxide dismutase; TLR4 = toll like receptor 4.

piglets in terms of the composition and metabolism of gut microbiota, thereby influencing muscle energy metabolism and later lipid accumulation in pigs (Cheng et al., 2019). The functional prediction of microbiota showed that fatty acid synthesis of the gut microbiota was stronger in obese-type pigs relative to lean-type pigs (Xiao et al., 2018). Accordingly, gut microbiota of obese-type pigs might deposit more energy and then convert more fat distribution in skeletal muscle (Yang, 2018).

It was showed that microbial metabolites could transform muscle fiber types and mediate skeletal muscle energy metabolism (Qi et al., 2021). Short chain fatty acids (SCFA) are important microbial metabolites that can regulate host glucose and lipid metabolism. For example, SCFA promoted glucose uptake and glycogen synthesis in skeletal muscle (Han et al., 2022; Koh et al., 2016). The direct ingestion of SCFA also increased the proportion of type I muscle fibers and enhanced muscle aerobic metabolism in rodents (Henagan et al., 2015; Pan et al., 2015). In addition, dietary supplementation of SCFA is shown to regulate the synthesis and metabolism of fatty acids in the skeletal muscle and adipose tissue of growing-finishing pigs to improve meat quality (Jiao et al., 2021).

As the in-feed use of antibiotics are banned in the pig industry in most countries and regions, nutritional alternatives such as probiotics and synbiotics have received great attention. Several cecal microbial taxa are significantly correlated with backfat thickness and abdominal lipid deposition in pigs (He et al., 2016). The result of a 16S rRNA gene-based association analysis indicated that some microorganisms such as Coriobacteriaceae, *Bifidobacterium* and *Roseburia* contributed to intramuscular fat accumulation in finishing pigs (Fang et al., 2017). It was suggested that dietary supplemental probiotics significantly improved the function of intestinal flora, fresh meat color score, marbling score and redness value (Meng et al., 2010), as well as meat flavor of finishing pigs (Cheng et al., 2019). The mechanism underlying the beneficial effect of dietary supplemental probiotics or synbiotics on muscle energy metabolism and lipid deposition remains unclear. It might be associated with gut microbial metabolites, for example, dietary supplemental synbiotics could increase the fecal content of SCFA in pigs (Śliżewska and Chlebicz, 2019).

5. Maternal nutrition and regulation of offspring skeletal muscle fiber type profiles, intramuscular fat accumulation

5.1. Maternal nutrition influences energy metabolism and muscle fiber type of offspring skeletal muscle

Muscle phenotypes, such as the proportion of muscle fiber types and corresponding features of energy metabolism, are significantly influenced by embryonic, fetal and subsequent neonatal

Table 2
Effects of maternal nutrition on offspring muscle fiber type composition and adipose distribution.

Nutrition treatments	Muscle fiber types		Fat accumulation		References
	Slow-twitch	Fast-twitch	Adipose tissue	Skeletal muscle	
Resveratrol[1]	↑	↓	↑	↑	Meng et al. (2020)
High-energy diet[2]	No change	↓	/	/	Zou et al. (2016)
Low-protein diet[3]	/	/	↑	/	Rehfeldt et al. (2012)
Low-protein diet[4]	/	/	↓	/	Pan et al. (2018)
High-fat diet[5]	/	/	/	↑	Ci et al. (2014)

DE = digestible energy; CP = crude protein; / = the corresponding indexes were not measured; ↑ = increased; ↓ = decreased.
[1] Resveratrol is at 300 mg/kg diet.
[2] Normal-energy diet (30.96 MJ DE/day), High-energy diet (34.15 MJ DE/day).
[3] Adequate-protein diet (12.1% CP), Low-protein diet (6.5% CP).
[4] Standard-protein diet (15% and 18% CP), Low-protein diet (7.5% and 9% CP).
[5] High-fat diet (8% corn oil).

development, which are the narrow windows where mediate muscle development occurs. Known as the sole source of nutrition for offspring muscle development in pregnancy, maternal nutrition plays a key role in regulating skeletal muscle development during the window periods. Meanwhile, muscle features of the offspring are more responsive to nutritional regulation during these stages.

As shown in Table 2, maternal nutrition altered muscle fiber type composition in the offspring and resulted in long-term effects on offspring muscular energy metabolism and subsequent meat quality characteristics. For example, maternal dietary supplementation with 300 mg/kg resveratrol during pregnancy and lactation increased the proportion of type I fibers, but decreased the proportion of muscle type II fibers, thereby promoting aerobic metabolism in skeletal muscle (Meng et al., 2020).

Creatine kinase (CK) and lactate dehydrogenase (LDH) play key roles in skeletal muscle energy metabolism (Lefaucheur et al., 2003; Rehfeldt et al., 2001). Correspondingly, feeding pregnant sows with the high energy diet decreased the activities of CK and LDH enzymes in fetal skeletal muscle (Zou et al., 2016, Table 2).

The decrease in the number of fetal muscle fibers limits the potential for skeletal muscle development in life, resulting in lowered growth performance and reduced lean meat percentage and increased intramuscular fat accumulation. It was shown that excess protein supply to sows during gestation had little effect on fetal phenotypic programming in growing-finishing pigs, while maternal low protein intake impaired prenatal myogenesis and myofiber formation, and consequently reduced the potential of postnatal lean growth in the offspring (Rehfeldt et al., 2012, Table 2). It was thought to be associated with the myogenic proliferation and function of insulin growth factor 2 (IGF2).

Maternal nutrition is involved in epigenetic regulation, such as methylation of DNA and chromatin, and genomic imprinting of the metabolic process of fetal skeletal muscle. For example, deficiency or excessive intake of methyl-donor micronutrients during pregnancy impacted the normal growth and development of the fetus (Hoile et al., 2012; Shaw et al., 1995). Supplementation with an appropriate amount of methylated micronutrients, such as methionine, folate, choline, vitamin B_6 and vitamin B_{12} as well as zinc in pregnant sows increases IGF2 levels in fetuses, which may affect insulin sensitivity and energy metabolism in fetal skeletal muscle (Oster et al., 2016). Maternal supplementation of methyl-donor micronutrients during gestation promoted skeletal muscle differentiation, maturity and improve skeletal muscle mass of the piglets (He et al., 2020).

5.2. Effects of maternal nutrition on lipid accumulation and meat quality of the offspring

Maternal nutrition during pregnancy and lactation plays an important role in regulation of lipid deposition in the offspring. As shown in Table 2, the dietary supply of the diet containing 300 mg/kg resveratrol to sows during pregnancy and lactation promoted offspring fat development, and increased back fat thickness and intramuscular fat content of the offspring during the subsequent finishing-period (Meng et al., 2020). Feeding sows with a low-protein diet (reduced 6.5% crude protein level) increased fat accumulation in the perirenal and subcutaneous adipose tissues in adult offspring especially born in large litters (Rehfeldt et al., 2012). However, it was also showed that maternal ingestion of low-protein diets (7.5% and 9% protein content) during gestation and lactation decreased fat synthesis and increased lipolysis in offspring piglets (Pan et al., 2018, Table 2). The authors thought that maternal feeding low protein diets might activate the autophagy lysosomal pathway leading to autophagy in adipose tissue and a reduction of subcutaneous fat deposition.

Maternal nutrition may exert a programming role in regulation of offspring fatty acid composition. It has been reported that feeding sows with a diet containing 8% corn oil during lactation will not only alter the fatty acid composition of offspring, but also improve offspring meat quality (Ci et al., 2014, Table 2). In addition, these authors noticed that feeding lactating sows on the high-fat diet increased muscular content of PUFA and n-6 fatty acids together with the pH_{24} value of the M. Longissimus thoracis muscle in the offspring, thereby improving offspring meat quality.

6. Conclusion

Skeletal muscle energy metabolism is not only associated with muscle fiber type, but also influence intramuscular fat accumulation in finishing pigs. This review reviewed advances in nutritional approaches to improve meat quality, including the directly dietary supply of amino acids, fatty acids, and probiotics and synbiotics as well as through maternal nutrition. To the best of our knowledge, this review is the first to specifically discuss nutritional regulation of muscle energy metabolism, lipid accumulation and meat quality and the relationship among them in pigs. However, the mechanism underlying synergetic regulation of energy metabolism, fatty acid synthesis and lipid accumulation in skeletal muscle as well as all the factors determining pork quality are not yet fully understood. In particular, to date, the extent to which nutritional strategies improve meat quality remain controversial, especially under vague quantitative relationships among meat quality traits.

Author contributions

Enfa Yan: conceptualization, collecting the materials, writing - original draft preparation. **Jianxin Guo:** collecting the materials and discussing the organization. **Jingdong Yin:** conceptualization, supervision, writing - review & editing.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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