Managing poultry meat quality by nutrition

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Poultry products are mainly consumed as cut and processed products. Therefore, it is no longer enough for broilers to have high slaughter yields and desirable carcass conformation. Good aesthetic and functional characteristics of the meat must be taken into consideration to satisfy the demands of both processor and consumer. Meat quality is under a complex control including genetics, rearing and slaughter factors. These factors influence the chemical composition of the meat but also the post-mortem muscle metabolism which determine a large number of technological and sensory qualities. This review focuses on the recent advances showing that nutrition can be an effective tool to control muscle development and meat quality in poultry. In particular, the intake of protein, which largely determines muscle growth and yield, may also affect several molecular pathways with significant consequences on muscle post mortem metabolism and meat quality. Indeed, the amino acid supply during the finishing period or just before slaughter can shape the energy reserves of the muscle with a significant impact on meat quality, including colour, processing yield and susceptibility to oxidation. Beyond the control of muscle metabolism, protein intake will also be crucial in controlling the molecular pathways that influence muscle fibre growth and integrity. Thus, recent studies show that in modern heavy strains, improving meat yields by nutrition can also lead to poor meat quality, which results in a lower protein/fat ratio and in the most severe cases in the onset of degenerative defects. Therefore, it is essential to rethink poultry nutrition by taking into account new standards, such as functional, nutritional and storage ability of the meat, but also by developing studies to better understand which molecular pathways can be efficiently modulated by nutrition during animal growth to improve final meat quality.

Keywords: meat quality; pH; muscle growth; nutrition

Introduction

The poultry meat consumption is growing worldwide. In developed countries, meat production is mainly dedicated to cuts and further processed products, which requires specific quality traits related to meat aspect and texture but also storage and processing ability. Most of these characters are under genetic control (Le Bihan-Duval *et al.*, 2008) and are tightly related to muscle energy metabolism. In particular, the ability of the animal to store glycogen in muscle will determine the glycolysis extent post-mortem and the ultimate pH (pHu) value of the meat. In chicken, the pHu is the main determinant of functional and sensorial properties of breast meat, as it influences colour before cooking, drip loss during storage, cooking loss, shear force of cooked meat, and yield after curing-cooking (Alnahhas *et al.*, 2014). Broiler breast meat with high pHu has also been recently associated with myodegenerative defects (white striping, wooden breast) in which the muscle integrity is affected (Petracci *et al.*, 2013; Mudalal *et al.*, 2015). Therefore, controlling breast meat pHu appears as a main goal to achieve in order to decrease the high variability of breast meat quality that is often observed in slaughter plants (Petracci *et al.*, 2009). In addition to genetics, there are many rearing and slaughter conditions that can affect meat pH and quality. Some of them are likely to alter animal energy status with consequences on muscle post-mortem metabolism. This is the case for stress and bird activity before slaughter that alter post-mortem rate of glycolysis (Chabault *et al.*, 2012) or nutrition during the final phase of rearing that can modify bird intermediate metabolism and the energy amount stored in muscle cells (Berri *et al.*, 2014). The purpose of this review is to make an inventory of knowledge's on the impact of nutrition on poultry meat properties and to propose new feeding strategies allowing a joint optimization of performances and product quality.

Changing finishing protein and amino acid intake can modulate energy storage in muscle and meat quality in broiler

Growing animal are using nutrients for growth (protein accretion) and energy storage as lipid or carbohydrate. The balance between protein accretion and energy storage depends on animal needs and nutritional value of their diet. The effect of diet has been mainly studied in relation with body fatness and with muscle yield and lipid composition. Only few studies evaluated the impact of diet on muscle glycogen content. Nevertheless, the muscle glycogen content at slaughter is determinant for meat quality through its effect on the meat pHu. The more glycogen level will be high in the muscle at slaughter, the more meat produced will be acid and exhibit poor sensorial and processing quality.

Feeding strategies to modulate meat quality have been first studied in pigs (Apple, 2007 for review). There is little evidence that pork quality (in particular water holding capacity, WHC) is altered by the lysine or protein level (and source), cereal grain, or fat source used in growing-finishing diets. However, feeding low-starch, high-fibre, high-fat, glycogen-reducing diets effectively improves the WHC of pork. Moreover, supplementing alpha-tocopherol or magnesium improved pork WHC.

In chickens, recent research indicates that modifying protein or amino acid intake can influence muscle pHu and related quality traits (colour, WHC, etc.). Indeed, increasing the level of lysine in the diet of broilers (beyond the needs for growth) improved breast meat yield and reduced drip loss during storage by increasing its pHu (Berri *et al.*, 2008). This result was consistent with the general hypothesis that breast muscle hypertrophy in broilers is accompanied by a decrease in glycogen storage (Berri *et al.*, 2007). Breast muscle glycogen content was also decreased and meat pHu was increased when levels of protein and energy intake were simultaneously increased (Zhao *et al.*, 2012). On the other hand, increasing the finishing protein intake (17 to 23%) without modifying the energy level of the diet resulted in increased muscle glycogen storage, decreased pHu, and impaired colour and WHC (Jlali *et al.*, 2012). However the impact of protein intake on breast meat characteristics may depend on the genetic type, broilers that are more prone to fattening being less sensitive to dietary variations than leaner broilers (Jlali *et al.*, 2012). In general, the impact of protein intake on meat pH and quality is variable and probably dependent on many factors related either to animal or diet characteristics (Yalcin *et al.*, 2010; Lilly et al, 2011; Zhao *et al.*, 2012).

In addition to the amount of protein, the amino acid profile of the diet can affect the pHu of the meat and certain associated traits (colour, WHC). This was shown in a study initially designed to estimate the response of broilers to amino acids during the finishing period by varying levels of digestible lysine (0.7, 0.85, 1.0, and 1.15%) and essential amino acids (90, 100 and 110% of ideal protein described by Mack *et al.*, 1999) at constant energy levels (Lessire *et al.*, 2013). The results showed that deficiency of amino acid provision (-10%) combined with a reduced lysine content (0.7%) favoured the production of meat with high pHu (> 6.0), while the most acid meat (< 5.85) was produced with excess provision of amino acids (+10%) combined with a low lysine intake (0.7%). The pH variations between diets had significant effects on colour and drip loss during storage.

All the studies presented above have considered long-term feeding strategies which also significantly affect broiler growth performance and body composition. However, one study on intermittent feeding suggested that a daily-switch in dietary protein to energy ratio may affect the breast muscle glycogen content from day to day (Mameri *et al.*, 2010), probably with a limited impact on bird growth. We evaluated the possibility of improving the quality of breast meat without impairing broiler growth performance and body composition by distributing diets varying in amino acid content but not energy intake over a very short period (3 days) before slaughter (Guardia *et al.*, 2014). The experimental diets consisted of a control diet with sufficient amounts of amino acids including lysine (1.0%), three lysine-deficient (0.8%) and three lysine-rich (1.2%) diets each with a sufficient, a low (-10%) or a high (+10%) amount of other essential amino acids calculated in proportion to lysine. As in the long-term study (Lessire *et al.*, 2013), lower pHu values were recorded in broilers fed lysine-deficient diets containing high (+10%) amounts of other AA than in broilers fed diets containing low (-10%) or sufficient amounts of other amino acids. Compared to the long-term study cited above, changes in pHu caused by variations in dietary amino acid profiles were fairly moderate. However they significantly affected breast meat lightness that is itself strongly correlated with WHC of meat and therefore processing yield (Qiao *et al.*, 2002; Petracci *et al.*, 2004; Zhuang and Savage, 2010).

Given the extremely close relationship between meat pHu and muscle glycogen at death, it is likely that the changes in pH induced by variations in the intake of amino acids occur through modulation of muscle energy reserves. The hypothesis is that a chicken subjected to amino acid provision in excess of its needs for protein synthesis and muscle growth uses part of its nutrient intake for energy storage, such as glycogen in muscle, thus explaining the decrease in pHu observed. On the other hand, reducing the intake of amino acids may limit the ability to store glycogen in muscle and explain the high pH levels observed in these conditions.

Limiting oxidation by nutrition can improve the storage and processing ability of meat

Improving poultry meat quality can be achieved by increasing oxidative stability during storage and further processing. Oxidative stress, which occurs when the formation of oxidants exceeds the ability of antioxidant systems to remove the reactive oxygen species (ROS), can provoke modifications of lipids and proteins that can change their physical and chemical properties. These modifications can be involved in the regulation of fresh meat quality and also influence the processing properties of meat products. It is known that oxidative stability of poultry meat can be improved by dietary strategies. These strategies, recently reviewed in Estevez (2015), involve reducing the concentration of polyunsaturated lipids in poultry tissues by modifying the lipid composition of the feeds and the supplementation with α-tocopherol and ascorbate alone or in combination with other elements with antioxidant potential, such as selenium, magnesium, and zinc. Dietary strategies based on phenolic-rich plant materials have also been found to be effective against lipid and protein oxidation in various poultry meat and processed poultry products. This includes tea catechins, grape pomace, camelina meal, tomato extract, pea seeds, ginger root, purple coneflower, rosehips, and rosemary leaves.

According the methionine source provided in the diet (DL-methionine, DLM or hydroxy analogue of methionine, DL-HMTBA), the oxidative stress and lipid peroxidation will be more or less marked (Martin-Venegas *et al.*, 2006, Swennen *et al.*, 2011, Willemsen *et al*., 2011). Indeed, fully or partly replacing DLM by its hydroxyl-analog HMTBA was efficient to reduce breast meat susceptibility to oxidation (leg and breast meat) and also increased its pHu, with positive consequences on storage and processing ability (Mercier *et al.*, 2009).

Several factors related to animal or its finishing diet play a role in the occurrence and severity of oxidation process. For instance, oxidation is favored in heavy male turkeys whose daily average gain and fattening during the finishing period are increased (Bourin *et al.*, 2015). Such conditions promote the production of meat containing high haem iron content and low pHu, two factors promoting oxidation process post-mortem. These conditions have been related to low dietary protein/energy ratio during the finishing period, highlighting the importance to rethink animal finishing diet to limit the occurrence of meat quality defects related to low pH or chemical status promoting oxidation post-mortem.

Molecular mechanisms involved in muscle metabolism and meat quality changes related to animal nutrition

As in mammals, the AMP-activated protein kinase (AMPK) complex is a key regulator of the glycogen turn-over in muscle. It also affects its post-mortem depletion in relation to the animal energy status and muscle activity. In broiler breast muscle, differences in muscle glycogen content and pHu have been shown to correspond to difference in AMPK activation (measured through its phosphorylation status), suggesting a role of this cell energy sensor in determining poultry meat quality traits (Sibut *et al.*, 2008). Later on, it was shown that the activation of AMPK complex can be modulated by the diet with consequences on muscle glycogen content. Indeed, a limited protein intake in the finishing diet (17% vs. 23%) resulted in high phosphorylation of the AMPK, reduced glycogen content and improvement of meat color and WHC (Jlali *et al.*, 2012). The use of a 48 h cycle sequential feeding varying in both protein and energy contents also induced changes in AMPK phosphorylation status concomitant to changes in breast muscle glycogen content (Mameri *et al.*, 2010). This indicates that muscle energy metabolism can be modulated on a short-term basis and reinforces our previous hypothesis that pre-slaughter nutrition can efficiently impact meat quality.

A recent study investigated the molecular regulation underlying the control of muscle growth related to protein intake of the diet (Berri *et al.*, 2015). It focused on a population of 36-day-old heavy broilers fed with two different levels of dietary proteins and that showed variable growth performance and breast meat yield. Results showed that the inherent capacity of protein synthesis, estimated by the ratio RNA/protein (also referred as ribosomal capacity), was positively related to growth capacity of animals. Similarly, there was a positive relationship between body weight and muscle expression of the growth factor IGF-1. However, increasing body weight and breast meat yield was inversely related to muscle protein content. Moreover, the breast muscle yield was negatively correlated with markers of mRNA translation into proteins and instead positively with markers of proteolysis. This suggests that in animals that had the highest growth and breast meat yield, stimulation of protein synthesis is impaired and on the contrary proteolysis is increased in the muscle, which may partly explain its lower protein contents. Altogether our observations can be related to the fact that over a certain limit, increased growth rate and live weight can lead to the occurrence of severe breast muscle abnormalities, such as white striping or wooden breast, in which muscle deposition tends to shift from protein to fat and fibrous tissue (Mudalal *et al.*, 2014).

In general, understanding of the molecular pathways that control the quality of the meat is essential for an integrated management of the latter. For this purpose, the study of 'nutrigenetic' models can help to unravel the mechanisms and to propose breeding and nutritional strategies that fit both to specific characteristics of the animals and to production objectives. One example is the control of the xanthophyll pigment content of the broiler meat that directly influences its coloration. In chickens, two fully-linked single nucleotide polymorphisms (SNP) located within the promoter of BCMO1 (encoding the β-carotene 15, 15′-monooxygenase that converts β-carotene into colourless retinal) were identified as the most likely causal mutations that explain the variation in yellow colour and in lutein and zeaxanthin pigments content of the breast meat (Le Bihan-Duval et al., 2011). Thanks to a fast genetic test developed for the screening of the two SNPs within a population, we showed that the mutations in BCMO1 could alter the efficacy to metabolize dietary carotenoids and impact bird growth, body composition and meat quality (Jlali et al., 2014). As illustrated by these results on a single gene, birds' response to feeding can be dependent on its genetics. Thus, understanding the genetic control of meat quality could help to adapt animal nutrition accordingly and prevent meat defects.

How could early nutrition contribute to meat quality?

After-hatch, muscle growth is mainly achieved by cell hypertrophy, i.e, increase in diameter and length of muscle fibers. Moreover, the weight and yield of muscles are closely related to the size of fibers, especially their diameter (Berri *et al.*, 2007). This last decade, progress in genetics and nutrition have dramatically increase breast meat yield and current broiler strains are characterized by very high muscle fiber diameter (Berri *et al.*, 2014). In the same time, myodegenerative defects, such as white striping and wooden breast, have appeared that are clearly related to animal growth rate and muscle yield (Kuttapan *et al.*, 2012, 2013; Sihvo *et al.*, 2014; Mudalal *et al.*, 2015). So far, no study has shown any impact of nutrition on the occurrence of these defects, although it is suspected that diet optimizing the genetic potential of animals is an additional risk factor. However, if we assume that the very high muscle fiber diameter can be the cause of muscle integrity problems, it would be appropriate to find early nutritional solutions to hasten muscle fiber proliferation and obtain muscles with smaller but more numerous fibers.

Several studies demonstrate that the timing of early post hatch feed restrictions to chicks is critical for the early and late development of the Pectoralis major muscle (Halevy *et al.*, 2000; Bigot *et al.*, 2003). It decreases satellite cell proliferation and alter the expression pattern of genes required for muscle satellite cell proliferation and differentiation (Halevy *et al.*, 2000; Velleman *et al.*, 2014). More precisely, the expression of MyoD and MRF4 (proliferation markers) was significantly increased by feed restriction during the first week post hatch, while the expression of myogenin (that is required for differentiation) was significantly decreased. In the same way, the improvement of vitamin D status by replacing the majority of D3 in the diet with 25OHD3 stimulated the early expression of MyoD and Pax7 and delayed the transition between embryonic and neonatal myosin heavy chain isoforms in the skeletal muscle of 7-day-old chicks (Berri *et al.*, 2013). Even if the consequences on muscle properties of such changes is still unknown, it is interesting to note that breast meat from birds fed 25OHD3 contained more protein and less fat and water than those fed D3 (Petracci and Sirri, not published). Myoblast proliferation can also be promoted by *in ovo* feeding with long-term consequences on muscle weight and yield (Kornasio *et al.*, 2011). Taken together, these studies highlighted the importance of considering early chick nutrition as a tool to control morphological development of the breast muscle in poultry in order to limit the occurrence of muscle abnormalities or myopathies due to intense genetic selection on growth rate and breast meat yield.

Conclusions

Even if the meat quality has become a crucial issue for the poultry meat industry, it is still poorly controlled. The reasons are many but include the rather low interest of breeders and nutritionists for years and the multitude of variation factors involved. However, serious quality defects that are currently observed in slaughterhouses have sparked a renewed interest for the quality of poultry meat. If it is known that the structural and metabolic abnormalities within muscles are a direct consequence of the intensive selection for growth and meat yield, it is also very important to know the role of diet on the emergence of these defects. Indeed, in most cases the defects observed involve metabolic dysfunction and, in the most severe cases, cell degeneration associated with muscle fiber hypertrophy. So better control the muscle growth and improve its energy metabolism and integrity may go through a change of food programs, including during the early periods of myogenesis. Such improvements, however, will require further research to understand the biological basis of meat quality and the role of nutrients in the control of muscle development, and to implement appropriate nutritional strategies to reduce the incidence of meat quality defects in poultry.

Acknowledgements

Some of the studies presented as examples in this review received financial support from INRA, French Minister of Agriculture and professionals of animal feed industry (Adisseo, Ajinomoto Eurolysine, CCPA, DSM).

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