GENETIC IMPROVEMENT IN MEAT QUALITY : POTENTIALS AND LIMITATIONS

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INTRODUCTION

Being a commodity-driven activity, meat production will at all times be an endeavour to fulfil requirements from markets and consumer organisations in whatever form these may take. During the recent decades the focus of consumers has gradually changed towards more emphasis on quality and animal welfare, which has implied a widening of the concept of meat quality. Definitely the welfare issue will have a growing and important influence on the concept of meat quality and should somehow be incorporated in future production strategies. To avoid regulations of the production based on mistrust, which have been imposed in some countries, more openness is required. This is particularly important if more sophisticated genetic tools are being implemented to improve characteristics regardless of whether they are related to production or to meat quality, as consumer organisations or other interest groups would probably find the implementation of genetically modified animals even more offensive than the implementation of genetically modified plants. We may also see a reduction in the sales of fresh meat and an increase in processed meat of various kinds in retail. Such a change will result in demands for meat with specific processability characteristics. The wider concept of meat quality and the increasing demand for meat with specific properties will definitely imply a larger diversity in selection schemes in the future.

In the present paper we will look at the consequences in muscle morphology and physiology of selecting for increased productivity and the possible implications for meat quality and animal welfare. As it is impossible to encompass all aspects of meat quality, we will focus on those meat quality characteristics that are influenced by the pH development *post mortem*, as this development will be a decisive factor for a number of very important quality traits. A number of traits associated to selection for productivity will be highlighted, as these may represent the bottlenecks or the limitations to further improvement in productivity. It is worth emphasizing that the problem to solve is not whether we will be able to produce meat of a higher quality, it is whether we can make the production of high quality meat economically feasible.

CAUSE OF VARIATION IN GROWTH CHARACTERISTICS

Almost all muscles are composed of 3 different fibre types, which display differences in size, energy metabolism, capillary supply and substantially many other features could be mentioned. The number of fibres in a muscle as well as the distribution of the major fibre types I and II are determined in the foetal stage. After birth, growth is almost exclusively caused by increase in circumference and lengths of these fibres. Consequently the variation is caused by differences in fibre number, in proportion of type IIB fibres and sizes of the individual fibres. Selection for productivity and carcass traits may thus hypothetically infer changes in all the traits. Measures taken after birth of the animals to improve productivity, and probably selection based on feed conversion rate, mainly consist of an alteration of the net muscle protein accretion rate. Such measures will primarily result in larger fibres and an increase in the proportion of type IIB fibres at the expense of type IIA fibres, in several ways similar to the changes observed by application of growth promoters. All such changes would to a varying extent have an impact on meat quality.

CAUSE OF VARIATION IN MEAT QUALITY

The cause of variation in meat quality is much more complex and depends on some genetically determined physiological prerequisites and how these prerequisites respond to a wide variety of environmental factors acting on the animal during transport and preslaughter handling.

The conversion of muscle to meat requires energy, which is reflected in the production of lactic acid and the concomitant decrease in pH in the carcass. Both the course and the extent of the pH decrease will influence quality characteristics like drip loss, colour development, tenderness, final pH, shelf life, processability as well as eating quality and is determined by the energy stores available at the time of slaughter. These stores comprise the amount of glycogen, creatine phosphate (CP) and ATP, and all are easily affected by stress applied to the animals. Due to differences in the content of energy stores in the different fibre types (25-50%), different muscles display different content of energy stores. Any change in fibre type composition or fibre areas will thus influence meat quality because of an altered sensitivity to stress. The influence of fibre type distribution on meat quality has been reviewed by Karlsson *et al.* (1999) and Klont *et al.* (2001). The main task for a muscle is to maintain the level of ATP, and the muscle performs this task even after slaughter. Initially the ATP is produced from the conversion of CP and ADP. When the level of CP is reduced to approx. 25% of the resting value, a decrease in glycogen and a concomitant increase in lactate formation, decrease in pH and a decrease in ATP are observed (Bendall, 1973). Consequently a reduction in CP levels will imply a shorter "delay phase" and a lower pH at 45 minutes; a measure often used to indicate "rate" of pH decrease. The amount of glycogen will determine the extent of the pH decrease, but only if the glycogen concentration has reached the critical value of 53 mmol/kg wet weight (Henckel *et al.,* 2002). If this is not the case, pH_{24} will probably not be affected. So far a critical value of glycogen has only been calculated for pigs, but other reports on pigs and other animals (Howard, 1963 ; Bendall, 1973 ; Fernandez and Gueblez, 1992 ; Wittmann *et al.*, 1994) indicate the existence of a similar value for these species as well. In summary, reduction in glycogen levels may result in enhanced ultimate pH, and reduced CP levels will imply a "faster rate" of pH decrease; both with well recognised and described implications for meat quality. Also the stunning method is of importance. By CO_2-stunning the animals pass a phase of excitation during which involuntary contraction of muscles is observed. The energy for these contractions is provided by degradation of both CP and glycogen. The excitation phase is followed by a calm period during which the animals may restore CP values to resting levels, whereas the amount of glycogen is not restored (Henckel *et al.,* 2002). The situation for electrical stunning is somewhat different. Application of the electrodes immediately implies a contraction of all muscles in the animal, and the energy for this type of contraction is mainly derived from CP degradation. As a tetanic contraction of a muscle is elicited at a specified level of voltage, it is the duration of the stunning procedure, and the time from stunning to sticking, which will determine the amount of CP being degraded and thereby its influence on meat quality. The complexity of the problem and the concomitant difficulty for researchers in meat quality to provide the proper tools to breeding organisations probably explain why so few attempts have been made in the past to improve meat quality directly by selection. Going through the literature, it seems that the main improvements in meat quality have been achieved by the efforts put into making transport and preslaughter handling less stressfull to the animals.

ACHIEVEMENTS AND CONSEQUENCES OF SELECTION

From a producer's point of view, the selection for productivity and carcass traits has been very successful, but whether it has been equally successful from a meat quality point of view is questionable. It might be argued that the removal of the halothane gene and the RN^- gene and the reduction of back fat and intra muscular fat content represent important achievements in the improvement of the overall meat quality. As far as the genotypes are concerned, being a product of the selection, their removal may be considered only as damage repair. As far as fat reduction is concerned, this might have slightly enhanced the nutritional value of meat, due to a positive change in the ratio of saturated to unsaturated fatty acids. However, whether the reduction of back fat and IMF in the animals has had any impact on the reduction in fat consumption of the populations, which has been an important argument for its use, remains to be verified. On the other hand low IMF content is negatively correlated to eating quality (Cameron, 1993 ; Mourot and Kouba, 1995). Several other reports (Cameron, 1990 ; Lonergan *et al.*, 2001) have demonstrated a negative relationship between production traits and meat quality characteristics as well as eating quality. Negative correlations between productivity and welfare aspects exist particularly in poultry, but to some extent also in pigs. Nearly all results seem to indicate that the huge improvements of the production traits have been at the cost of deterioration in meat quality and have had a negative influence on the welfare of the animals.

According to Cameron *et al.* (1998), the heritability of fibre types (with the exception of type I fibres) and fibre areas is generally low as are their genetic correlations to carcass traits, meat and eating quality. This implicates that selection objectives to change carcass composition traits are unlikely to change fibre type frequencies and fibre areas. Larzul (1997) on the other hand calculated somewhat higher heritability estimates for fibre types as well as for fibre areas and also reported higher genetic correlations of these to carcass and meat quality traits indicating that selection may infer changes both in fibre type distribution and in fibre size. Consequently selection for productivity traits will imply an increased fibre number, an increase in circumference of the fibres, an increased frequency of type IIB fibres and a concomitant decrease in type I fibres of which the increased fibre number most likely constitutes by far the largest contribution to the general improvement. Comparison of muscle fibre characteristics of highly selected breeds to less selected ones (Oksbjerg *et al.*, 2000 ; Pedersen *et al.*, 2001) or wild type animals (Essén-Gustavsson and Lindholm, 1984 ; Rede *et al.*, 1986) is generally in compliance with this concept. Apart from the difference in response to criteria of selection, timing may also be crucial factor. The growth curves of the individual fibre types differ (Rehfeldt *et al.*, 1987). Selection on criteria calculated over the entire growing period would favour both fibre number, size and frequency of type B fibres, whereas selection on criteria calculated over a limited growth period may favour fibre number only as demonstrated by Lax and Pisansarakit (1980) in mice. In order to apply such knowledge in practise, more research is needed on the correlated responses on fibre traits of the individual productivity traits.

Manipulating fibre formation in the foetal state of the animals at the time of differentiation of primary and secondary fibres may thus be an objective of interest, but to what extent basic fibre type distribution can be altered and particularly in what direction remains to be answered. If changes tend toward more oxidative fibres, a reduced sensitivity to stress as well as an improvement in most meat quality characteristics might be expected. If the changes tend toward more glycolytic and larger fibres, this will imply an enhanced sensitivity to stress and a concomitant deterioration of meat quality. An enhanced sensitivity to stress may be considered to be negative in terms of animal welfare, but at what level such changes compromise the normal functioning of muscles is not known and can at present only be speculated upon.

POSSIBLE LIMITATIONS AND BOTTLENECKS TO IMPROVEMENT IN PRODUCTIVITY AND MEAT QUALITY

Fibre number and fibre size. Are there upper limits to fibre size and total fibre number ? Based on low correlated responses of fibre number and fibre size to selection for leanness, Rehfeldt *et al.* (2000) suggested so for the most highly selected pig lines, the Piétrain and the Large White breed. The same breeds also display very little or no response to growth promoter treatments, which supports the concept of an upper limit to fibre size. There is no direct evidence to support the concept of a limitation to increased muscle fibre number and that this will have a negative effect on meat quality and welfare aspects. However, when examining animals with extremely high fibre numbers, the double-muscled cattle, it has been shown that they have a higher frequency of type IIB fibres, smaller type I and IIA fibres, but similar size of type IIB fibres, and they have paler meat and a faster rate of pH decrease post mortem compared with normal breeds (Fiems *et al*., 1995). Overall these phenomena will result in meat of lower quality. As double-muscling is caused by a deletion mutation in the myostatin gene (Grobet *et al.,* 1997 ; Kambadur *et al.,* 1997 ; McPherron and Lee, 1997), the situation may not be comparable to the situation where increased fibre number is achieved by selection.

Poultry situation. In poultry further limitations to productivity and meat quality may be in sight. As for pigs, the selection has focussed on productive traits, mainly growth rate, and feed conversion rate. Concomitantly with an improved feed conversion rate and an enhanced growth rate, an increased frequency of ascites, of long bone problems and of various forms of myopathies, including deep pectoral myopathy, is observed. The animals have now been selected to a point where proper environmental conditions, optimal feeding strategies and handling of the animals are crucial to a positive economic outcome of the production, and no slips in any of these factors are permitted throughout the production (Decuypere *et al.*, 2000).

Post mortem pH decreases similar to those observed in pigs have been reported earlier, but our own recent investigations in broilers fail to observe this. This indicates that the animals are metabolically exhausted already at sticking which results in high ultimate pH. This apparent high sensitivity to stress is probably a major factor for the loss of glycogen as a pH decrease almost similar to that of pigs still can be produced under proper conditions. Both chicken and turkey muscles are characterised by a very high number of glycolytic fibres. Estimated from fibre type distribution, enzyme activity and capillary supply, even wild type animals like the jungle fowl display a higher sensitivity to stress in comparison to other meat-producing animals, probably because of the normal behavioural pattern of these birds (Henckel, 1996). Both chicken and turkey are non-migratory birds, which base their survival in natural life on short bursts of activity. This natural, higher sensitivity to stress may also explain why problems associated to increased productivity appear in these animals first.

Ascites. This syndrome is characterised by free fluid in the abdominal cavity or other parts of the body of the animals, eventually leading to death. The fast growth and the resulting high metabolism imply an increased need for oxygen. The animal responds to this increased need by increasing cardiac output and increasing the synthesis of erythropoietin. In the former case, this will initially lead to an increased lung arterial pressure, and the latter will imply an increased haematocrit value and an increased viscosity of the blood. The increased blood pressure will induce right ventricular hypertrophy. An increasing hypertrophy of the ventricle will at a certain stage affect the closure of the valve between the ventricle and the atrium, allowing the re-entering of blood from the atrium. The accompanying gradual reduction in cardiac output increases the venous pressure in the portal and hepatic vein, eventually leading to oedema in the abdominal cavity (Decuypere *et al.*, 2000). This disease was first recognised in chickens reared at high altitudes, but it is now also observed in chickens reared at sea level. The incidence of this disease coincides with increased improvement of growth rate and feed conversion rate.
A cause of this relationship has been suggested to be an inappropriate development of the heart in relation to the increased muscle mass. The allometry of the heart changes over time. At early ages (hatch and 14 days) the relationship between body weight and heart weight has a steeper slope than at 42 days of age. In only 3 generations, the allometric slope of the heart has decreased, primarily due to the relatively small heart weight to body weight ratio (Barbato, 1995). The results also indicated the existence of line differences in response to the selection. When comparing broiler lines of different susceptibility to ascites, Buys *et al.* (1999) observed no difference between the lines in the ratio of body weight to heart weight. These results do, however, not exclude that changes in allometric growth of the heart can be a consequence of selection, but it may signify that there are other important factors for the development of the syndrome. These factors concern the problems of hyperplasia versus hypertrophy in muscles, and whether the selection for growth causes an increased frequency of the glycolytic type IIB fibre types, making the highly selected lines more susceptible to the syndrome and to stress in general, as shown by Soike and Bergman (1998) and Remignon, *et al.* (1996). Increased incidence of PSE and DFD meat in poultry has been reported (Barbut *et al.,* 1997a ; 1997b) alongside higher frequencies of metabolic diseases like ascites and the sudden death syndrome in broilers and cardiomyopathy in turkeys. Changes in fibre type distribution and in muscle fibre area by the selection may thus be important additional factors for the development of ascites.

Hypoxia. Other problems associated to hypoxia are various forms of local myopathies and deep pectoral myopathy (Oregon disease) observed in both turkeys and broilers (Siller *et al.,* 1979 ; Sosnicki and Wilson, 1991). The local myopathies are characterised by necrosis of single fibres or small groups of fibres followed by infiltration of endomysial connective tissue with mononuclear cells, and fatty tissue replacement in the necrotic area. Localised microischemia caused by lower capillary density and lower capillary to fibre ratio was suggested as a proximate cause of the development (Sosnicki and Wilson, 1991). The deep pectoral myopathy is characterised by degeneration and green discoloration of the inner part of the pectoral muscle and is found in both broilers and turkeys. Selection for large breast muscles and restriction of movement were suggested as contributory factors for the development of this disease (Swash *et al.,* 1980). Siller (1985) actually described this development as "the penalty of successful selection for muscle growth".

Hypothyroidism. The function of the thyroid constitutes an important regulatory mechanism for the overall metabolic rate of an animal. A linkage between functional hypothyroidism and susceptibility to ascites was provided by Buys *et al.* (1993). Scheele *et al.* (1991 ; 1992) suggested the functional hypothyroidism to be a reduction in capacity for T_4 production, which was confirmed by Buys *et al.* (1999). They also showed that the reduced oxygen consumption due to low T_4 production was associated to the lines with favourable feed conversion rates and fast growth.

Tibial dyschondroplasia. Tibial dyschondroplasia (TD) - a disorder in which growth plate cartilage is accumulated in the proximal region of the tibia and femur - is another major problem in poultry meat production. In 1996 it was estimated that 50% of broilers suffered from this disorder (Leach, 1996). The problems associated with TD include lameness, increased fractures of the fibula and an increased susceptibility to osteomyelitis. The etiology of this syndrom has been investigated by Orth (1999) and Rath *et al.* (1998). Osteochondrosis (OCD) is a developing cartilage disorder with similarities to TD. It is characterised by a failure of the endochondral ossification in the articular/epiphyseal and growth plate cartilage in the weight-bearing regions of the long bones. This syndrome has also been demonstrated in pigs where growth rate and hormonal imbalance have been implicated in the disease. In accordance with this the application of porcine somatotropin has been shown to increase the incidence of OCD in Yorkshire pigs (He *et al.*, 1994). The change in load on the weight-bearing regions of the joints as well as the slightly changed angles of the joints due to a change in muscle form - in general changes in the biomechanics of the animals - may be contributory factors for the development of the syndrome.

CONCLUSIONS

There are two ways in which meat quality can be improved or maintained. Either efforts can be made to adapt the environment to the physiological capacity of the animals, or their sensitivity to stress can be reduced. Apparently there are still some possibilities of improving meat quality by improving conditions under which animals are transported, treated at the slaughterhouse, stunned and killed. And such improvements should be pursued. Concerning selection the best suggestion would be to apply it to a trait with a high genetic positive correlation to muscle fibre number, with no correlated response to fibre type distribution and a negative or insignificant correlation to fibre area. Unfortunately such a trait is not available at present. Furthermore the development of organs that are fuelling the muscles, the heart and the vascular bed, or structures that have to carry the ever-increasing burdens of heavier animals, i.e. bones, connective tissue and joints, should be monitored. These diseases can of course be included in the selection as an immediate precaution, but good traits that predict the development of these symptoms would be much more efficient. Both genome knowledge and proteome analyses can become important new tools in this future task. For the quantitative geneticist, it will imply the construction and implementation of much more complex selection schemes.

There are some recent reviews on the use of gene technology for further improvement in meat quantity and meat quality (Klont *et al.,* 2001 ; de Vries *et al.,* 2000). One of the apparent "beauties" of these methods is the speed at which progress in certain traits can be made. This will probably also infer that if correlated responses which are negative to meat quality or animal welfare occur, they will be revealed equally rapidly and most likely be clearer when compared with standard selection procedures. Such knowledge could, when used properly, secure that animals at the production sites do not suffer from syndromes that can be linked to breeding in any way. In time and with proper information, this might reduce the general mistrust to meat production and could improve its image in the public eye.

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